1943 ✓ (11)

Reprinted from THE JOURNAL OF EXPERIMENTAL ZOOLOGY
Vol. 92, No. 3, April, 1943

EFFECT OF 180 DEGREE ROTATION OF THE RETINAL FIELD ON VISUOMOTOR COORDINATION

R. W. SPERRY [1]
Yerkes Laboratories of Primate Biology, Orange Park, Florida

ONE FIGURE

In the past, numerous reports have appeared of rapid restoration of normal function after rearrangement of the anatomical relations between central nervous system and periphery by the crossing of nerves, transposition of muscles, or the relocation of sense organs. These results have been taken by many (Marina, '12; Bethe, '31; Anokhin, '35; Goldstein, '39 and others) to indicate an extreme dynamic plasticity of central nervous organization and to disprove the more traditional theories of neural integration which assume the existence of specific and rather stable functional relations between nerve centers and periphery and between the various nuclei of the brain and spinal cord.

More recently, however, operative interchange of muscles, motor nerves, and sensory nerves of the limbs has been found to produce in the rat clear-cut corresponding disturbances of function which are persistent. These maladaptive functional disorders not only show no spontaneous readjustment, but remain uncorrected despite long training under conditions favoring reeducation (Sperry, '40–'43). Analogous transplantation experiments in amphibians have also demonstrated a striking absence of functional plasticity in the neural mechanisms coordinating limb and trunk movements of these animals

[1] This research was done at the Harvard Biological Laboratories while the author was on appointment as a Zoology Fellow of the National Research Council.

(Weiss, '41 b). In contradiction to the earlier conclusions drawn from this type of experiment, the more recent results thus indicate strongly that the vertebrate spinal system operates through a basic organization and differentiation that is remarkably implastic and involves a distinct specificity in the anatomical relations with the periphery.

There are certain indications that similar experiments carried out on the retina and optic nerve might reveal in the visual system a plasticity of interneuronal organization quite in contrast to the basic stability of spinal mechanisms. First, the higher brain centers in which the optic nerve terminates may well possess greater capacity for adaptive readjustment than do the spinal centers. Second, the optic nerve, developmentally and histologically, is a brain tract (fasciculus opticus) rather than a true peripheral nerve, and in function also may simulate a central tract. It is possible that the elements of central nervous tracts have much greater equipotentiality and interchangeability of function than do elements of peripheral nerves (Bethe and Fischer, '31, p. 1128). Third, the retina is a distance receptor and thus retinal stimuli, more than stimuli transmitted over spinal nerves, tend to initiate and guide general bodily movements rather than localized reactions. Such over-all activity may be easier to readjust than the more locally circumscribed reflexes.

The adjustments made to inversion of the visual field produced by lens systems fitted in tubes worn over the eyes (Stratton, 1897; Ewert, '30) indicate that considerable, perhaps complete reorganization of the visual system is possible in man. Analysis of normal visual perception has supported strongly a "field" theory of vision refuting the assumption that each retinal point has specific functional relations with the brain centers (Köhler, '29). The development of a new center of acute vision, the "pseudo-fovea," in hemianopic patients has been said to involve a transformation in function of all retinal points with respect to their visual acuity, color, and space values. This functional shift is not the result of training apparently, but occurs suddenly without the patient's knowledge. Moreover the pseudo-fovea in such cases is not anatomically fixed but shows transient variations in position (Fuchs, '22). Sudden shifts in the spatial attributes of retinal points has also been reported after operations for strabismus (Helmholtz, '24). These and similar observations have led Goldstein ('39, chap. I) to the conclusion that there is no constant relationship between a particular part of the retina and a particular performance.

Restoration of normal vision has been demonstrated by Stone and Zaur ('40) and others after regeneration of the optic nerve of transplanted eyes in adult urodeles. These animals show correct visual localization in that they are able to turn toward a moving object, follow it about, and snap vigorously at it when they have approached within close range. Since the redistribution of individual fibers by nerve regeneration has repeatedly been shown to take place in a random, non-selective manner (Langley and Hashimoto, '17; Dogliotti, '35; Weiss, '41 a; Kilvington, '41), recovery of normal spatial localization in these cases suggests further the possibility that functional specificity of nerve connections between periphery and center, even in the lower vertebrates, is much less rigid in the visual system than in the spinal system.

It was partly for the purpose of following up, from a neurological standpoint, these promising data on recovery of normal vision in urodeles that the red-spotted newt, Triturus viridescens, was selected as the experimental animal on which to begin investigation of the adaptation capacity of the visual centers. The present paper concerns the functional results of rotating the eyeball 180 degrees leaving the optic nerve intact. The object was to find out if a reintegration of the normal visuomotor coordination would restore normal function, and if so, how rapid and how complete such central reorganization would be.

OPERATION AND METHOD

The eyeball was detached from the lids by gently tearing the thin conjunctiva with fine jeweler's forceps. It was loosened further by severing to a variable extent the outermost insertions of the ocular muscles. The eyeball was then grasped by the free rim of conjunctiva at opposite points across the cornea and twisted on its axis anterodorsally a little more than 180 degrees. The bulb was pressed well into the orbit and allowed to remain in place for a minute to stretch the remaining attachments. It was then rotated back slightly

Fig. 1 A control case (top) with eye in normal position is shown with two experimental cases with eyes rotated 180 degrees, 4½ months after operation. The golden ventral surface of the eyeball, after rotation, shows through the translucent upper lids making them appear lighter. Contrast between the characteristic brownish black dorsal surface of the control case and the light olive green of the cases with rotated eyes is only poorly indicated in the black and white photograph.

and left at exactly 180 degrees from the normal resting position. Any tilt of its mediolateral axis produced by twisting was corrected. In cases where the resultant torsion on the blood vessels had completely blocked circulation through the iris, the eyeball was manipulated further until the blood flow was restored.

After a few days the tension exerted by the intact ocular muscles began in some cases to tilt and pull the eyeball back toward its normal orientation. This was remedied by excising the major bulk of the rectus and retractor bulbi muscles through an incision in the roof of the mouth, in all cases about 48 hours after the primary operation. At this time the eyeball was twisted loose again and readjusted in the exact position desired. It is easy to estimate quite precisely the degree of rotation of the eyeball in these newts because they have a horizontal black line running across the iris as shown in figure 1.

All operations were done under ether anesthesia. The animals were anesthetized in a finger bowl containing about a centimeter's depth of water to which a little ether was added. Molds of either paraffin or moist towel paper were used to hold the animals in position. Small hooks made from the tips of fine insect pins and attached to lead weights with thin gold chain were employed to retract the jaws when operating through the mouth. The operations were performed under a dissecting microscope with a magnification of about twenty times. The newts were kept in a moist chamber for several days after operation before they were returned to water.

If any stable functional specificity exists in the central connections of the ganglion cells of different retinal points, rotation of the eyeball on its optic axis 180 degrees should result in a complete inversion and reversal of the appearance of the visual field with consequent disturbances of visuomotor coordination. The animals were tested immediately after operation to determine the extent of such visuomotor disturbances and then retained for later examination to see if central nervous reorganization would eventually compensate for the retinal displacement.

Tests of visual function involving spatial localization of small objects and perception of direction of movement are easily made in these newts. Their eyes are well developed and are used considerably in guiding locomotion, catching prey, avoiding predators, and in other general activities. The animals are particularly responsive to visual stimuli from small moving objects. They will commonly turn and swim from a distance of at least 25 cm. directly toward a small lure oscillating within a space of 1.5 cc. outside the glass wall of their aquarium. If, as they approach the lure, it is moved in any direction away from its starting position, the animals will turn in the correct direction and follow it persistently as it is moved about outside the glass. When they are within close range, they frequently try to snap at the lure through the glass. Because the animals often come to rest in mid-water on water plants, their visual localization can be easily and accurately tested for nearly all directions in space. Visual localizing reactions of this sort furnish, of course, an excellent index of the specific function of various retinal loci.

The newts also show pronounced compensatory movements of the head to rotation of the visual field. These photokinetic reactions are comparable to the common nystagmus movements of the eyeball in mammals. They were tested by placing the animals in a covered fingerbowl, with or without water, about which was rotated an upright cylindrical drum 25 cm. in diameter with large vertical black and white stripes on its inner wall. Such reactions indicate a functional specificity of the retinal ganglion cells with respect to their horizontal alignment.

Movements of the eyeball which are not pronounced but which may be elicited in Triturus to a slight extent by visual stimuli could not be used as test responses because the ocular muscles were excised in the operations. Phototactic responses are also shown by these animals, but they were not used as tests of vision in these experiments, because they are rather variable and are complicated by light sensitivity of the integument (Pearse, '10). Further criteria of visual function that were employed but which are indicative of inverted and reversed vision rather than of normal vision will be described in the results.

The newts were all freshly collected during the breeding season in April and the experiments were carried on through the summer to the middle of September. The experimental cases were separated into three groups. In group I (fifteen cases) both eyes were rotated as described above. As wide a range as was available in size, and presumably in age, was included. The smallest individual measured 5.5 cm., the largest a little over 10 cm. in length.

In group II (seven cases) one eye only was rotated and the other eye was excised. This group was prepared because of the possibility that it might be simpler to make adjustments for reversed vision on one side only than on both. The smallest case was 6 cm., the largest 10 cm. in length.

Because adjustment to rotation of the retinal field on one side might possibly be aided by normal visual cues from the opposite eye, group III (seven cases) was prepared in which only one eye was rotated and the other eye was left in normal position. The smallest case was 7.5 cm., the largest 10 cm. in length.

Nine control animals (three for each group) were also prepared. These control cases were operated in exactly the same manner as the experimental cases of the corresponding groups except that instead of being allowed to heal in the rotated position, the eyeball was twisted back to its normal orientation after excision of the ocular muscles. Three additional controls were also used in which both eyes were excised. All the control cases measured close to 9 cm. in length.

IMMEDIATE EFFECTS OF THE OPERATION

As soon as the effect of the anesthesia had disappeared, usually within ½ hour after rotation of the eyeball, the newts showed compensatory head movements to rotation of the visual field, indicating that the optic nerve and retina had not been damaged by the operation. Normal animals move the head slowly in the direction in which the visual field is rotated. When the head reaches a position far to the side, it may be sharply straightened and again slowly turned with the revolving drum, or the animals may start walking or swimming in the direction in which the visual field is moving. Animals with only one eye, but otherwise normal, will make the compensatory head movements in only one direction, toward the eyeless side, and these reactions occur only when the visual field moves past the remaining eye in a posteroanterior direction.

The experimental cases with both eyes rotated (group I) turned the head slowly in the direction opposite to that in which the drum revolved. The photokinetic reactions of these newts were quite like those of normal animals except that the movements were made in the reverse direction. The animals with one eye rotated and the other excised (group II) also showed the reversed head movements but only when the visual field moved past the remaining eye in an anteroposterior direction. Compensatory movements did not occur when the drum was revolved in the opposite direction. The cases with one eye rotated and the other normal (group III) showed no photokinetic reactions to rotation of the drum in either direction. Apparently movement of the visual field in the direction which tended to elicit the natural response through the normal eye tended at the same time to elicit the reversed response through the rotated eye with a resultant neutralization of both responses. Rotation of the retina through 180 degrees had thus resulted in a clear-cut reversal of the photokinetic reactions to a revolving visual field. In the control cases subjected to mock operations the photokinetic responses were similar to those of normal animals as described above.

When returned to aquaria the visuomotor disturbances in the experimental cases, particularly of the first two groups, were quite striking. Most obvious was the tendency to swim and walk continually in circles. The circles thus made varied in diameter at different times from about 25 cm. to about 4 cm., so small the newts' heads almost touched their tails. These circling movements were sometimes executed very slowly and at other times at frantic speed. In swimming up or down the animals traveled in spirals. The cases with both eyes rotated (group I) circled in either direction, depending apparently on the way the head turned in starting. They were commonly observed to circle vigorously several times in one direction, pause, then go on circling just as rapidly in the opposite direction. The animals in group II always circled with the remaining eye on the outside. Those in group III showed little tendency to make these circus movements but did so occasionally, especially when objects on the side of the rotated eye were more brightly illuminated than on the other side.

When at rest the animals of groups I and II often displayed slow swaying movements of the head rather like the compensatory response evoked by revolution of the visual field. The head was swung evenly through an arc until turned far to the side or until it collided with some obstacle. Oftentimes it was snapped back and the slow phase of the movement repeated. Group I showed these swaying movements of the head in both directions, group II only toward the side of the excised eye. The movements were rare in group III and absent in the normal and control animals. These swaying and circling reactions were both due, probably, to an apparent movement of the visual field set up whenever the head was moved. The labyrinthine and other kinesthetic impulses which act normally to stabilize the appearance of the visual field when images are moving across the retina as a result of the animals' own motion fail to counteract and perhaps even exaggerate the illusion of outside movement after 180 degree rotation of the retina. When returned to aquaria, the behavior of the control cases was quite like that of normal animals except for a mere absence of visual response correlated with excision of the eyes.

Visual localization of small moving objects was not noticeably impaired by the mock operations in the control series. In the experimental groups, however, it was obviously inverted and reversed about the optic axis by rotation of the retinal field. The lure used in testing visual localization consisted of a small piece of fresh meat impaled on the end of a thin wire. When the piece of meat was moved back and forth in the water several centimeters above and a little to one side of the animals, they tilted their heads downward on that side and began to move toward the bottom of the aquarium. Even though the newts happened to be resting on the bottom when the lure was thus waved above them, they cocked their heads down under them and began pushing about among the pebbles of the bottom with the nose and forefeet. If the lure was first placed below the animals, the head and forebody were tilted upward and the newts started toward the surface. If already near the surface, the animals usually lifted the head slightly and started swimming in circles with just the tip of the nose out of water. Occasionally they snapped at the air above. If the lure was waved in front of them and a little to one side, they turned and looked behind them on that side. Conversely if it was waved behind them when the head was turned slightly backward, the head was extended forward and they started to move ahead.

These movements away from the lure were definitely erroneous approach responses caused by false spatial localization and were not avoidance reactions. At the sight and smell of food under the above conditions the newts became extremely excited and attacked voraciously any moving object which they bumped into including each other. When, after they had failed repeatedly to locate the food, it was touched to the tip of the nose, the animals snapped at it savagely until they succeeded in catching and swallowing it. The animals of group III showed the reverse localization responses on the side with the rotated eye and the natural approaching and snapping responses on the side with the normal eye.

The reversed reactions in the animals of group I were somewhat more complicated than described above when light from the moving object was allowed to reach both eyes either simultaneously or successively. Having little if any binocular vision, the animals localized objects on the correct side of the mid-sagittal plane in spite of the rotation of the eyes. Thus if the newts turned to look behind them to the left when the lure was placed in front of them, the left eye which was originally stimulated was turned away so that the lure in the same position was seen only with the right eye. It was then localized on the correct or right side of the mid-line and the animals turned back toward the lure until they had overshot the mark and the object was again seen by the left eye. The newts often made such alternate turning movements back and forth to the right and left sides when the lure was waved steadily in front of them. More frequently, however, they turned rapidly completely about on the first or second trial and began swimming in circles.

Certain other abnormalities of visuomotor performance were also noticed. Normal animals in glass-walled aquaria will often swim persistently against the glass as if trying to get through. The control cases with mock operations and those of group III also exhibited this behavior. It was absent, however, in groups I and II. On occasions when these animals happened to approach the glass they soon veered away from it. The animals of groups I and II in the course of general locomotion bumped directly into obstacles more frequently and with greater force than did the blind control cases. The experimental cases usually had no difficulty in swimming upward when seeking air nor in swimming downward when startled at the surface. The semicircular canals are apparently more important in controlling these reactions than are the eyes. Occasionally, however, in swimming upright toward the surface, the newts of group I tilted themselves well beyond the vertical position so that the ventral surface of the body was uppermost. Normal and control animals under similar circumstances were not observed to swim with the body tilted over backward in this manner.

The reversal of compensatory movements of the head to rotation of the visual field, the false spatial localization, the circus locomotion and the swaying movements, together with the other abnormalities of reaction just mentioned, show unquestionably that rotation of the retinal field had resulted in a complete inversion and reversal of normal visual perception. The operation had produced more than a confusion and hesitancy in visuomotor activity. It had resulted in positive erroneous performances, deliberate, and diagrammatically clear in their correlation with the rotated position of the retinal field.

Chromatophoric responses. At the end of the first 2 weeks after operation it was noticed that the animals with rotated eyes had become considerably lighter in color than normal and control cases in the same tanks. Animals whose dorsal surface had been almost black before operation had become a light olive green. The control cases that had been equally dark before operation had not perceptibly lightened. Three cases that had become quite light after rotation of the eyes were put with a normal dark animal in a covered dark-walled container lighted only through a glass bottom. The experimental cases had again become almost black on the dorsal surface after 15 days, while the dark normal animal in the same container had become considerably lighter in color during the same period.

Apparently the melanophoric responses tend normally to make the color of the newts' backs match that of the bottom. After rotation of the eyeball the animals' color tends to match the overhead lighting rather than that of the bottom. Thus as in the fish, Fundulus (Butcher, '38), there is a dorsal-ventral differentiation of retinal function with respect to the control of chromatophoric reactions, and rotation of the retinal field causes a reversal of the normal color adaptations.

ABSENCE OF FUNCTIONAL REORGANIZATION

To find out if the maladaptations of visuomotor coordination would eventually be corrected by experience, the animals were retained under observation for a little over 4½ months after operation. They were kept in well water in glass-walled aquaria about 70 cm. long, 30 cm. wide, and 30 cm. deep. The bottom was covered with sand in which a few water plants were firmly rooted. Two or three large stones were placed about the bottom in permanent positions. The topography of the aquaria was thus made fairly simple and constant in order to favor the relearning of correct spatial localization. The aquaria were kept in a constant position on a table near the author's working desk were frequent daily observation was possible. In addition to this general examination, special tests of visual localization and of the compensatory movements to rotation of the visual field were made every 2 weeks.

In some of the cases the eyeball, at the end of 4 weeks, had begun to rotate out of its intended position due to the action of eye muscles incompletely excised. These cases were reoperated. The eyeball was set back at 180 degrees of rotation and the remaining ocular muscles were removed.

No correction of the maladaptive visuomotor responses was observed in the course of time. When the final tests of vision were applied 142 days after operation, photokinetic reactions and spatial localization of small objects were as strikingly reversed in groups I and II as they had been directly after operation. These cases still exhibited circus locomotion and collided just as frequently with stones, water plants and their fellow newts. The cases of group III continued to show no compensatory head movement to rotation of the visual field and the same erroneous localization of objects seen by the rotated eye. When the normal eye was removed, they behaved exactly as did the animals of group II.

That the newts had even come to rely less upon vision and more upon other senses was not apparent in any of the tests used nor from daily observation of their general activity. They appeared to be as completely misguided by visual stimuli at the end of 4½ months as they had been during the first week after rotation of the retinal field. The abnormal color change also persisted so that the cases of groups I and II could be distinguished at a glance from control cases in the same aquarium by the differences in color.

The control cases with both eyes removed were able to locate pieces of food more quickly by means of olfactory cues and vibratory movements of the water than could the animals with inverted vision. These controls swam straight instead of in circles and were able to move about the aquarium without colliding as frequently and forcibly with objects as did the experimental animals. Their dorsal surface remained normally dark. These blind animals were thus decidedly better adapted to living conditions with complete absence of vision than were the experimental cases after 4½ months of experience with disoriented retinas.

In six cases, two from each group, the eyes were restored to normal position after the other animals had been discarded. Before recovery from anesthesia, they were placed in a moist chamber in complete darkness. The moist container was filled with water on the third day after operation without permitting any light to enter the darkroom. Thirty minutes later the newts were lifted out of the dark chamber and dropped into a lighted aquarium. During the following 15 minutes the animals showed no signs of the characteristic circus locomotion. Accurate visual localizing reactions were elicited, and also correct photokinetic responses. There was no sign of any disturbances of visuomotor activity that would indicate the presence of previous central adjustments to the rotated position of the retinal field. Ten days later the four cases from groups I and II had become considerably darker on their dorsal surfaces than they had been during the 4 months preceding restoration of the eyeball to its normal orientation.

DISCUSSION

Rotation of the retinal field 180 degrees resulted in a complete inversion and reversal of visual perception. This was evident not by a mere hesitancy or confusion in the newts' responses to visual stimuli, but by deliberate, clear-cut erroneous reactions and misguided performances that were consistent and directly correlated with the retinal disorientation. Although this reversed vision was worse than useless to the newts in that it put them at a greater disadvantage than if they had been completely blind, it nevertheless persisted without any correction during the 4½ months in which the animals were studied and regularly tested.

Like stimulation of different cutaneous points, stimulation of different retinal loci results normally in differential central excitations and motor responses. The fact that these normal functional values of the various retinal points remained unaltered after surgical rearrangement had rendered them quite maladaptive and detrimental to the animals, demonstrates the rigid fixation of the central integrating mechanisms on which they depend. Their perverse intractability to correction by experience suggests that, like the spinal motor patterns (Weiss, '41 b), they are organized in the beginning by the growth process itself rather than through trial and error adjustment. The present results on the visual system fall into line with those of previous experiments involving rearrangement of relations between spinal cord and periphery (Sperry, '40–'43; Weiss, '41 b), and thus permit extension of the former conclusions regarding the spinal system to include the higher centers mediating visuomotor coordination.

The contention of Marina ('15), Bethe ('31), Goldstein ('39) and others that the paleencephalon and spinal cord of vertebrates is essentially a homogeneous conducting network permitting ready and complete reintegration of coordination patterns to suit derangements of the normal relations between center and periphery must be abandoned in view of the increasing mass of contradictory evidence. The flexibility and adaptability of normal coordination is apparently made possible not by virtue of an equipotentiality of central inter-relations but by means of precise integrative mechanisms expressly designed to effect adaptive excitation patterns under normal anatomical conditions. We may assume a definite specificity of central nervous organization in both the intra-central and peripheral relations of brain stem and spinal cord, a basic implastic organization which is established in large part by growth processes. Functional adaptation, particularly in the lower vertebrates, is predetermined and definitely limited by this basic central organization. Whether the greater adaptation capacity of higher vertebrate forms is due to less stable specificity in the spinal system, or instead to increased specificity and individuation, equally rigid but accompanied by greater differential control through adjustable cortical processes is still a problem.

Since the chromatophoric reactions reversed by rotation of the retina are mediated through the hormonal system in amphibians, the fact that they were not readjusted was to be expected.

SUMMARY

1. In fifteen newts both eyeballs were rotated on the optic axis 180 degrees leaving the optic nerves intact. In seven newts only one eyeball was rotated and the other eye was excised. In seven more cases only one eye was rotated and the other eye was left in normal position.

2. The 180 degree rotation of the retinal field resulted in a complete inversion and reversal of visual perception clearly manifest in deliberate erroneous reactions and various abnormal performances directly correlated with retinal rotation. Rotation of the retinal field also produced a dorsoventral reversal in chromatophoric adaptation mediated through the eyes.

3. With reversed vision, the animals were at a greater disadvantage than control cases totally blind. Nevertheless the maladaptive visuomotor coordinations, correlated with retinal disorientation, persisted in all cases without any sign of inhibition or correction by central nervous reintegration.

4. The results demonstrate an unadaptable rigidity of central coordination mechanisms in the visuomotor system of urodeles comparable to the implasticity of spinal organization found in amphibians and rats.

LITERATURE CITED

ANOKHIN, P. 1935 Reports on the problem of centre and periphery in the physiology of nervous activity. Gorky State Publishing House.

BETHE, A. 1931 Plastizität und Zentrenlehre. Handb. d. norm. u. path. Physiol., Bd. 15, S. 1175–1220.

BETHE, A., AND E. FISCHER 1931 Die Anpassungsfähigkeit (Plastizität) des Nervensystems. Handb. d. norm. u. path. Physiol., Bd. 15, S. 1045–1130.

BUTCHER, E. O. 1938 The regions of the retina related to the different chromatophoric responses in Fundulus heteroclitus. Bull. Mt. Des. Is. Biol. Lab., pp. 18–19.

DOGLIOTTI, A. M. 1935 Études expérimentales et première application clinique d'une nouvelle opération destinée à augmenter et à équilibrer la fonction neuro-musculaire dans la paralysie partielle des nerfs. J. de Chir., vol. 45, pp. 30–48.

EWERT, P. H. 1930 A study of the effect of inverted retinal stimulation upon spatially coordinated behavior. Genet. Psych. Monog., vol. 7, pp. 177–363.

FUCHS, W. 1922 Eine Pseudofovea bei Hemianopikern. Psych. Forsch., Bd. I, S. 157–186.

GOLDSTEIN, K. 1939 The organism. American Book Co., New York.

VON HELMHOLTZ, H. 1924 Physiological optics. Vol. III. George Banta Publ. Co., Menasha, Wis.

KILVINGTON, B. 1941 Some experiments on nerve regeneration. Aust. and New Zeal. J. Surg., vol. 10, pp. 266–272.

KÖHLER, W. 1929 Gestalt psychology. Horace Liveright, New York.

LANGLEY, J. N., AND M. HASHIMOTO 1917 On the suture of separate nerve bundles in a nerve trunk and on internal nerve plexus. J. Physiol., vol. 51, pp. 318–346.

MARINA, A. 1912 Die Theorien über den Mechanismus der assoziierten Konvergenz- und Seitwärtsbewegungen, studiert auf Grundlage experimenteller Forschungsergebnisse mittels Augenmuskeltransplantationen an Affen. Dtsch. Z. f. Nervenheilk., Bd. 44, S. 138–162.

——— 1915 Die Relationen des Paläencephalons (Edinger) sind nicht fix. Neurol. Centrblt., Bd. 34, S. 338–345.

PEARSE, A. S. 1910 Reactions of amphibians to light. Proc. Am. Acad. Arts and Sci., vol. 45, pp. 159–208.

SPERRY, R. W. 1940 The functional results of muscle transposition in the hind limb of the rat. J. Comp. Neur., vol. 73, pp. 379–404.

——— 1941 The effect of crossing nerves to antagonistic muscles in the hind limb of the rat. J. Comp. Neur., vol. 75, pp. 1–19.

——— 1942 Transplantation of motor nerves and muscles in the forelimb of the rat. J. Comp. Neur., vol. 76, pp. 283–321.

——— 1943 Functional results of crossing sensory nerves in the rat. J. Comp. Neur., vol. 78, pp. 59–90.

STONE, L. S., AND I. ZAUR 1940 Reimplantation and transplantation of adult eyes in the salamander (Triturus viridescens) with return of vision. J. Exp. Zool., vol. 85, pp. 243–269.

STRATTON, G. M. 1897 Vision without inversion of the retinal image. Psych. Rev., vol. 4, pp. 341–360, 463–481.

WEISS, PAUL 1941 a Nerve patterns: the mechanics of nerve growth. Growth, Third Growth Symposium, vol. 5, pp. 163–203.

——— 1941 b Self-differentiation of the basic patterns of coordination. Comp. Psych. Monog., vol. 17, pp. 1–96.