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Thirteen Years of Homologous Function in Normal and Supernumerary Grafted Limbs.

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For nearly twenty years it has been known that when a supernumerary limb in urodele amphibians is grafted adjacent to a normal limb, so that it acquires innervation from a portion of the normal limb plexus, the corresponding muscles of the two limbs always contract synchronously and with the same degree of intensity. This phenomenon has been called "homologous function" by Weiss who, in order to explain the mechanism, proposed the so-called "Resonance Theory" of reflex activity.[1]

In his earlier experiments, Weiss grafted fully differentiated limbs (fore and hind) of *Salamandra maculosa* larvæ close to the normal. In making the wound for the insertion of the limb, one or more of the normal limb nerves were cut. These were found to regenerate into those muscles of the orthotopic limb which were rendered nerveless by the nerve section, as well as into the denervated muscles of the supernumerary limb. Weiss pointed out that there occurred an "at random" regeneration of the nerves, consequently homologous function could not be explained upon any structural specificity in regenerating nerve pathways.

Homologous function has been described also by the author[2] in limbs that have been grafted as embryonic rudiments. In these cases, the normal forelimb rudiment of Amblystoma embryos was excised and grafted 3 or 4 segments caudal to the normal position. The wound was left uncovered—thus providing for regeneration of a limb in the original site (Fig. 1). Under such conditions one might obtain 3 limbs, *viz.*, a regenerant and a double limb arising from the graft. When this occurred, synchronized movements of the homologous muscles ensued, regardless

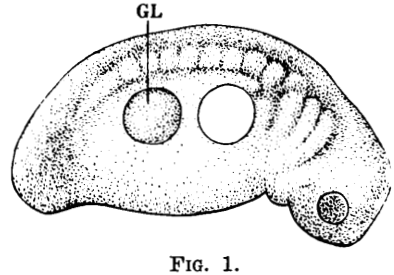

FIG. 1.
Drawing of Amblystoma embryo (stage 28) showing anterior limb rudiment (GL) grafted 4 segments caudal to the normal position. The clear disc represents the uncovered wound, from the margin of which a limb regenerated. × 10.

of the peripheral nerve pattern, provided all 3 limbs received some innervation from the brachial region of the cord (third, fourth, and fifth spinal segments). Homologous function was found not to depend upon the distribution of any single brachial nerve to 2 or more limbs. In some cases the limbs were supplied entirely by separate brachial nerves.

The case reported in this communication is of interest mainly because it was kept under observation for 13 years. In the fall of 1929, I obtained several batches of fertilized eggs from adult axolotls in the laboratory. In Harrison's stage 29 (tail bud stage), numerous limb grafts were made in the manner described above.

In many cases the grafted limb reduplicated and a limb regenerated in the normal site. The case shown in Fig. 2 illustrates the condition. This animal exhibited synchronized movements in the homologous muscles after the limbs became functional, and the muscles continued to function in

[1] Although Weiss has published many papers in various journals on the phenomenon of homologous function and the "Resonance Theory," the reader, if unfamiliar, is referred to his review paper in *Biological Reviews*, 1936, **2**, 494-531, for a general account of the facts, a discussion of the theory, and bibliographic references to his earlier work.

[2] Detwiler, S. R., *J. Exp. Zool.*, 1925, **38**, 461.

this manner without any change during the thirteen years under observation. A gross dissection of the brachial nerves showed that the third and fourth spinal nerves supplied

FIG. 2.

Ventral view of preserved axolotl (*A. mexicanum*) showing three limbs on the right side. Limbs 2 and 3 are mirror image reduplicants developed from a graft as shown in Fig. 1. Limb 1 regenerated from the wound as indicated in Fig. 1. The animal when fixed was 13 years old and measured approximately 9 inches in length.

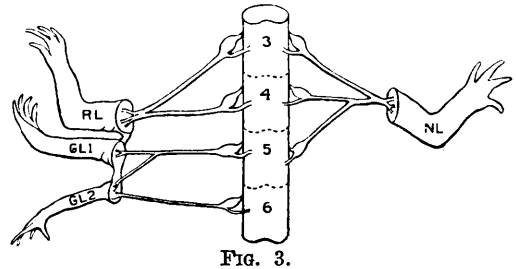

FIG. 3.

Diagrammatic representation of the nerve supply to the limbs shown in Fig. 2. The regenerated limb (RL) is supplied by the third and fourth (brachial) nerves. The two members of the grafted reduplicant (GL1 and GL2) are supplied by the fifth (brachial) nerve. The sixth (post brachial) nerve also enters the posterior member of the reduplicant. The normal (left) limb (NL) is supplied by the third, fourth and fifth (brachial) nerves.

the regenerated limb (RL). The two members of the reduplicated grafted limb (GL1 and GL2) were supplied by the fifth nerve (Fig. 3). The sixth nerve also supplied the posterior member of the reduplicant, but it is known from previous experiments[3,4] that supernumerary grafted limb muscles when supplied by spinal nerves below the brachial region fail to exhibit coördinated or homologous movements.

The case herewith described offers proof that when the nervous pattern for homologous movement is once established, it continues to function without change—a condition which would be expected. It is of interest to point out also, that homologous function in the muscles of a normal and an adjacent supernumerary limb does not depend upon the distribution of the same nerves to the two limbs, nor does it depend upon any peripheral nerve communications between the brachial nerves (Fig. 3). The origin of the nerves from the original brachial region of the cord is the essential condition regardless of their peripheral distribution to 2 or even 3 limbs.

[3] Detwiler, S. R., *J. Exp. Zool.*, 1920, **31**, 117.

[4] Detwiler, S. R., and Carpenter, R. L., *J. Comp. Neur.*, 1929, **47**, 427.