sociation with swarming in wasps, even though it resembles the orientation-recruitment seen in foraging behavior of some stingless bees (*10*). The swarm formation and emigration processes that occur after nest loss may not be fundamentally different from those of colony founding, but the retention of the colony's ability to initiate the process at any time in its nesting cycle, regardless of the nature of the colony population, is probably also a response to predatory pressure on the nest.

MARTIN G. NAUMANN*
Biological Sciences Group,
University of Connecticut, Storrs 06268

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4. Even though both types of swarms result in the construction of a new nest, a founding swarm may be considered as founding a new colony with population characteristics different from those of the mother colony. The absconding swarm, in retaining the same adult population, is constructing a replacement nest.
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9. M. Lindauer, *Z. Vgl. Physiol.* **37**, 315 (1955), described the *Schwirrlauf* in honey bees in which a bee runs with vibrating wings through a hive. The run and the associated sounds elicit swarm formation. The run has been termed "breaking" behavior by R. A. Morse and R. Boch, *Ann. Entomol. Soc. Am.* **64**, 1415 (1971).
10. A foraging bee, having found a food source, deposits a droplet of mandibular gland secretion every 2 to 3 m on her nestward flight. Alerted nest mates follow the trail [M. Lindauer, *Communication Among Social Bees* (Harvard Univ. Press, Cambridge, Mass., 1960), p. 78].
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* Present address: Simon's Rock, Great Barrington, Mass. 01230.

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Persistence of Foreign Innervation on Reinnervated Goldfish Extraocular Muscles

Abstract. *Behavioral observations have suggested that the function of foreign synapses on goldfish extraocular muscles can be repressed after reinnervation by the original nerve without any ultrastructural alterations. The present experiments demonstrate that even after behavioral repression foreign synapses are physiologically functional and that the original and foreign nerves can simultaneously innervate goldfish extraocular muscles.*

A number of investigators have suggested that although a foreign nerve can temporarily innervate an experimentally denervated target, these foreign synapses cease to function or are displaced when the original, appropriate nerve regenerates (*1*–*3*). These conclusions are largely inferential, since most of the experiments involve the demonstration of foreign innervation in one group of animals soon after removal of the nerve and the demonstration of less foreign innervation in another group of animals after the original nerve has regenerated. Behavioral observations and electron microscopic examination of seemingly functionless synapses led Mark and co-workers (*3*) to conclude that in fish extraocular muscles foreign synapses are rapidly shut off or "repressed" without ultrastructural alteration when the original nerve reinnervates the muscle.

The phenomenon of repression has further been implicated in the reestablishment of coordinated movement following the regeneration of severed nerves to muscles that receive polyneuronal innervation (*4*) but not to those innervated by a single nerve fiber (*5*). The appropriate motoneurons may regain control of multiply innervated fibers through a process of competition for various synaptic sites followed by repression of inappropriate synapses. Such competition apparently cannot happen on singly innervated fibers (*6*). A similar process may occur during embryonic development (*6, 7*). It has even been suggested that synaptic repression plays a role in learning and memory (*8*).

If repression occurs during normal embryonic and postnatal development, during nerve regeneration, and during memory storage, then morphologically normal but functionless synapses should be common, and many neuroanatomical studies would need to be reevaluated. The phenomenon of repression is thus of great importance, yet it has never been properly tested physiologically. The following experiments were designed to test the physiological function of foreign synapses on extraocular muscle fibers in goldfish using the same preparation that Mark used to demonstrate behavioral repression (*3*).

The inferior (IOM) and superior (SOM) oblique extraocular muscles, innervated by the oculomotor (NIII) and trochlear (NIV) nerves, respectively, mediate a reflexive ocular counterrotation that tends to keep the eye horizontal when the body is tilted. This reflex can be employed to assess innervation behaviorally (*2, 3*). When a fish is tilted to a head-up position NIV fires, the SOM contracts, and the eye rotates downward. When a fish is tilted head-down NIII fires and the IOM contracts, rotating the eye upward. The separate sources of innervation allow selective stimulation of either an entirely appropriate or entirely foreign population of motoneurons. In order to demonstrate repression physiologically Marotte and Mark's behavioral experiments (*2*), which involve observations of behavioral manifestations of cross innervation, reinnervation, and repression, were repeated. In addition, animals in which behavioral repression occurred were killed, and muscle tension in response to stimulation of the appropriate and foreign nerves was measured in vitro in order to determine whether foreign synapses were actually functionless.

Goldfish, 7 to 10 cm long, were anesthetized with MS-222 (Eastman). The IOM was removed, NIII was tied to NIV near the SOM, and NIV was cut just as it entered the orbit. As a result, NIII had a shorter distance to grow to reach the SOM than did NIV, which enhanced initial foreign innervation. Behavioral reflexes were tested about every 3 days. Thirty-four animals were killed 3 to 14 weeks after surgery. The intracranial portions of NIII and NIV were exposed and stimulated with suction electrodes. In some animals contraction of the SOM was only observed visually, while in others isometric tetanic tension (expressed as kilograms per square centimeter) in response to indirect stimulation (500-msec train of 0.01- to 0.05-msec pulses, 200 to 300 per second) was measured with a Harvard Apparatus model 363 force transducer. Animals that had not undergone surgery served as controls.

The surgery described above does not completely abolish reflex eye rotation. The residual ocular rotation is presumably mediated by the four remaining rectus extraocular muscles. The behavioral manifestation of cross innervation of the SOM by NIII is therefore usually a lessening of the residual upward rotation when the fish is tipped head-down, for NIII fires and the SOM contracts, rotating the eye down. In some cross-innervated animals downward eye rotation actually predominates. Reinnervation of the SOM by NIV is signaled by an increase in downward eye rotation in the head-up position. Behavioral repression following reinnervation is marked by resumption of the residual upward eye rotation in the head-down position.

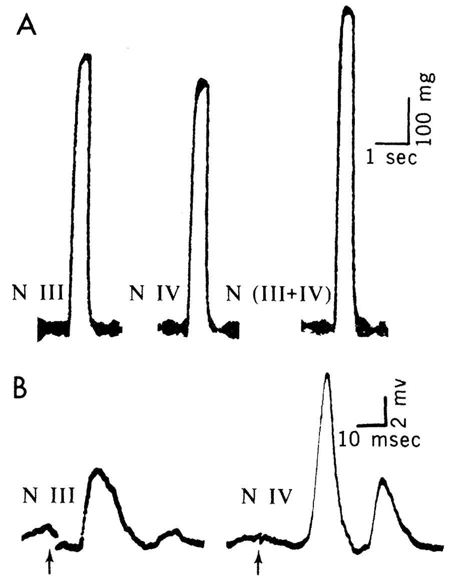

Fig. 1. Dually innervated superior oblique muscle. (A) Isometric tetanic tension in response to stimulation of NIII and NIV separately and simultaneously [N(III + IV)] (500-msec train of 0.01-msec pulses, 200 per second) was measured 48 days after surgery. Tension excess is 63.4 percent, which indicates extensive dual innervation of single fibers. Traces have been retouched. (B) Junction potentials elicited from a single fiber by stimulation of foreign NIII and regenerated NIV were recorded 63 days after surgery. Stimulation of NIV resulted in two junction potentials, a common occurrence in these multiply innervated muscle fibers. All three junction potentials were recorded intracellularly at the same site without moving the microelectrode. Arrow indicates stimulus.

In nine animals behavioral observations indicated that NIII had initially made functional connections with the SOM, but had been behaviorally repressed by regeneration of NIV. However, in all those animals (24 to 101 days after surgery) the SOM contracted in response to stimulation of both NIII and NIV, which demonstrates that synapses from NIII were still functional. Regeneration of the appropriate nerve to a cross-innervated SOM does not immediately repress foreign innervation. Fourteen experimental animals in which behavioral repression was not observed also received functional innervation from both NIII and NIV. Clearly, both foreign and appropriate nerves can simultaneously innervate the SOM.

Since fish extraocular muscle fibers are innervated by more than one axon, any individual fiber in a dually innervated experimental muscle may receive synaptic contact from both NIII and NIV. To test for dual innervation of single fibers, tetanic tension from the SOM was measured in response to stimulation of each nerve separately and both nerves together (Fig. 1A). An excess in the sum of tetanic tensions generated by stimulating NIII and NIV separately compared to the tension generated by stimulating both nerves simultaneously suggests the presence of dual innervation of single fibers. The tension excess, expressed as a percentage of the maximal tension generated by simultaneous stimulation of both nerves, ranged from 0 to 63.4 percent, with an average of 21.0 ± 16.7 percent (mean ± standard deviation) in 14 animals with double innervation. This strongly suggests that both NIII and NIV can make functional synaptic contacts on the same muscle fiber. Intracellular recordings from four dually innervated muscles confirm this, for junction potentials could be recorded in single fibers in response to stimulation of both NIII and NIV (Fig. 1B).

Tetanic tension measurements suggest not only that some synapses from NIII on the SOM remain functional after NIV regenerates, but also that NIV does not displace foreign synapses as it reinnervates the SOM. NIII innervates the SOM to about the same extent regardless of the presence or absence of NIV (see Fig. 2). In fact, NIII appears to impede reinnervation of the SOM by NIV. Stimulation of NIV in animals in which the SOM was reinnervated only by NIV caused the same amount of tension as it did in control fish. However, in animals in which NIII also cross-innervated the SOM, stimulation of NIV caused less tension than it did in control animals (Fig. 2).

If physiological repression does not occur, how then can behavioral repression be explained? In these experiments and in Mark's experiments the IOM was removed. If this muscle regenerates and is reinnervated by NIII, during head-down tilts it will oppose eye rotation caused by the cross-innervated SOM. This opposition could mask behavioral signs of cross innervation and make it appear as if synapses from NIII on the SOM are repressed. To avoid this problem animals were operated on again 14 to 28 days after the initial surgery. In most fish the IOM had regenerated and was again removed. This second surgery usually revealed that functional cross innervation was still present in behaviorally repressed animals and it occasionally unmasked behavioral signs of cross innervation that had not been previously apparent. In the final experiment any muscle or connective tissue located in the area normally occupied by the IOM was attached to the transducer as if it were muscle. In all of the behaviorally repressed fish some IOM fibers had regenerated and could produce measurable tension. Thus, contraction of the regenerated IOM fibers simultaneously with the cross-innervated SOM may be responsible for behavioral repression. Alternatively, the persistence of functional foreign synapses in behaviorally repressed animals might be explained by reorganization of synapses in the central nervous system, a hypothesis that is currently being tested.

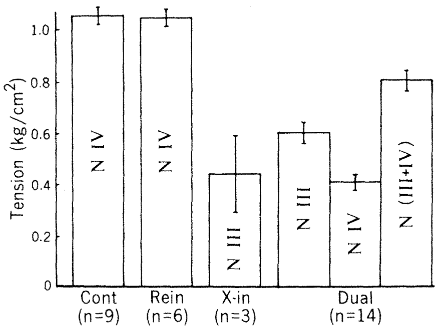

Fig. 2. Average isometric tetanic tension (± standard error of the mean) generated by the superior oblique muscle in response to stimulation of NIV in control (*Cont*) and reinnervated (*Rein*) muscles, of NIII in cross-innervated muscles (*X-in*), and of NIII and NIV separately and then simultaneously in dually innervated muscles (*Dual*).

It is clear that behavioral repression in the goldfish extraocular muscles can occur in the absence of any detectable physiological repression of foreign synapses. Likewise, other types of observed behaviors did not always correlate with the physiology. The behavior adequately revealed the existence of functional synaptic connections in only 3 of the 23 animals whose SOM was innervated by both nerves and in 10 of the 11 animals whose SOM was innervated by only one nerve. Behavioral observations alone are not sufficient evidence for drawing conclusions about the restoration of function of neuromuscular connections, at least in this system.

The behavioral repression described by Mark and co-workers (*2, 3*) is rapid, occurring within 2 days after NIV regenerates. In the present experiments, however, real synaptic repression, as tested physiologically, was not observed to occur during the first 3 months after NIV regenerated. Thus it is not surprising that all of the synapses examined by Mark and co-workers (*3*) appeared ultrastructurally normal, since they were probably all functional. It is possible that some type of repression may ultimately occur and that NIV may in time displace NIII, but if it does, the process must take many months.

A similar type of persistent functional dual innervation has been described in frog fast muscle (*9*), and in mammalian (*10–12*) and avian (*13*) muscles. In mammals the regenerating original nerve does not displace the foreign nerve (*12*), and foreign innervation impedes reinnervation by the appropriate nerve (*10*). Fish extraocular muscles seem to be similar in their ability to accept and retain functional dual innervation.

The phenomenon of repression is an intriguing one, but it does not appear to be involved in the restoration of normal behavior in cross-innervated goldfish extraocular muscles. Repression may be implicated in other systems, but it must be physiologically demonstrated before it can be accepted.

Note added in proof: Recent experiments testing the hypothesis that behavioral repression is the result of rearrangement of synapses in the central nervous system demonstrate that after behavioral repression NIII still fires in the head-down position, which indicates that no central reorganization occurs.

SHERYL A. SCOTT
Department of Biology, Yale University, New Haven, Connecticut 06520

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Anomalous Myopias and the Intermediate Dark Focus of Accommodation

Abstract. *The dark focus of accommodation for an individual observer correlates highly with the magnitude of night, empty field, and instrument myopia. These anomalous myopias are interpreted as resulting from the passive return of accommodation to an individually determined intermediate dark focus when the stimulus for accommodation is degraded or absent, or when the need for accommodation is eliminated.*

Accommodation represents one of the initial responses of the visual system, the objective of which is to maintain a clearly focused image on the retina. The accuracy of this process determines how much information is extractable from visual stimulation and is therefore essential to virtually every visual task. Under most viewing conditions, the accommodation reflex results in a rapid and accurate adjustment of the refractive power of the lens. In view of this normally adaptive closed loop feedback system, the manifestation of sustained and inappropriate myopia under certain stimulus conditions represents an anomaly.

With lowered illumination level, the refractive power of the eye typically increases for distant objects. This phenomenon, which was first reported by Lord Maskelyne in the late 18th century and is referred to as twilight or night myopia, might be considered maladaptive since it degrades the quality of the retinal image (*1*). Moreover, night myopia is only one of a series of potentially maladaptive manifestations of the refractive system which are here referred to as the anomalous myopias. Another example is the nearsightedness reported when viewing an unstructured field (*Ganzfeld*) such as a clear sky, or during a snow storm or fog. This phenomenon, known as space, sky, or empty field myopia, should be considered maladaptive since the focus of the eye corresponds to relatively close distances in spite of the fact that the objects of interest are ordinarily located at a distance (*2*). Similarly, nearsightedness is frequently observed when viewing through optical instruments, particularly microscopes, and is known as instrument myopia (*3, 4*).

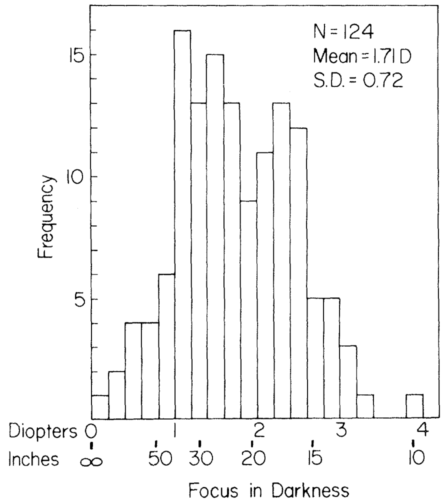

Fig. 1. Frequency distribution of the magnitude of the focus in total darkness, as measured with the laser optometer, for 124 college-age observers.

The theoretical treatment of these phenomena, in particular of night myopia, has been both extensive and varied (*5*). A critical issue in any analysis of these anomalous myopias is the state of accommodation under the conditions producing anomalous myopia. The classic assumption is that in the absence of visual stimulation or a stimulus for accommodation, the ciliary body relaxes and, assuming no refractive error, the eye is focused to correspond to optical infinity (*6*). This has been the prevailing interpretation in the literature and is implicit in ophthalmological and optometric clinical practice and the design of optical instruments such as microscopes, dissecting microscopes, and stereoscopes. However, an alternative point of view, which has appeared sporadically in the literature, is that the focus in the absence of stimulation is not to infinity but rather to some intermediate distance. This neutral focus has been estimated to be of the order of 1 diopter of accommodation, corresponding to a distance of 1 m. According to some investigators (*7, 8*), no accommodative effort is involved at this neutral focus, which has been referred to as the *Akkommodationsruhelage*, or resting state of accommodation. With adequate stimulation, the refractive power is then actively increased or decreased to correspond to the distance of the stimulus.

The intermediate focus hypothesis is particularly heuristic in relation to the anomalous myopias. In the classical context of the "resting" focus at infinity, any increase in refractive power is considered to be an active process. However, it is difficult to explain inappropriate accommodation in a system that is normally highly adaptive. On the other hand, if the resting focus is assumed to be at some intermediate value, the anomalous myopias may be simply considered as passive return of the lens to this neutral or equilibrium state.

A major methodological difficulty in the literature dealing with these problems has been the previous unavailability of a convenient technique for measuring accommodation which did not, in itself, influence the results. Although there are several precise clinical and experimental methods to assess accommodation, many do not per-