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Suppression of Reflex Postural Tonus: A Role of Peripheral Inhibition in Insects

Abstract. *Postural reflexes act through a single excitatory motoneuron of the several that innervate a flexor muscle of the cockroach leg. A peripheral inhibitory neuron whose axon accompanies this excitatory motoneuron is able to suppress muscle tensions developed from postural reflexes without affecting centrally generated muscle tensions. The inhibitory neuron could thus serve to rapidly suppress postural tensions at the initiation of escape.*

Posture and locomotion are viewed as being programmed by the central nervous system and modulated by sensory feedback (*1*). Elements of central pattern generators for walking have been identified in vertebrates and invertebrates (*2*), but little is known about how postural reflexes interact with them. In rapid running, for example, such reflexes may be incompatible with centrally programmed locomotor patterns (*3*). Are these reflexes then suppressed or overridden? We studied this problem in the American cockroach and found an effective mechanism for the rapid suppression of reflexly developed muscle tension through the action of inhibitory motoneurons at muscle cells.

The posterior flexor muscle of the trochanter (*4*) lifts the cockroach leg in upright walking (*5*) and provides postural support when the animal is climbing or standing inverted (*6*). The nerve to this muscle contains at least 12 axons, but no more than four (axons 3, 4, 5, and 6) are active in quiescent or walking cockroaches (*5*). Each of these four motoneurons can be accurately identified in extracellular recordings (*7*). Axons 4, 5, and 6 are slow excitatory motoneurons that generate graded tension by facilitating depolarizing postsynaptic potentials (*8*). Axon 3 is a branch of the common inhibitory neuron that produces hyperpolarizing potentials in muscle cells and decreases the tension developed by the excitatory motoneurons (*8*).

Centrally generated patterns of activity in these motoneurons have been investigated. The common inhibitor (axon 3) and two excitors (axons 5 and 6) discharge regularly with the locomotor-like bursting seen in deafferented preparations. Nonspiking interneurons that can generate these patterns and set a bursting rhythm have been identified; they affect only the same three flexor motoneurons (*9*). Axon 4 is only irregularly active in locomotor-like bursting, and its inputs have not been determined.

We studied reflex effects on flexor motoneurons of two groups of leg proprioceptive sense organs, the coxal chordotonal organ (*10*), which responds to extension of the coxotrochanteral joint, and the distal tibial campaniform sensilla (*11*), which monitor cuticular strain generated by muscle contractions. Adult cockroaches were briefly anesthetized with CO_2, pinned ventral surface up on a resin-coated block, and dissected to expose the trochanteral flexor nerve and another small motor nerve containing a branch of the common inhibitor (*8*). These nerves were lifted onto chloridized silver hook electrodes (diameter, 75 μm) for conventional recordings.

Stimulation of the coxal chordotonal organ by extending the coxotrochanteral joint with a wire mounted to a piezoelectric crystal elicited vigorous reflex activity in one flexor motoneuron, axon 4, and had no discernible effects on other flexor motoneurons (Fig. 1A). Stimulation of individual distal tibial campaniform sensilla with a fine etched tungsten wire driven by a piezoelectric crystal elicited bursting from the same flexor motoneuron (Fig. 1B). Thus, both of these proprioceptive sense organs reflexly excite a single flexor motoneuron not driven by central locomotor interneurons.

What is the function of this subdivision of flexor motoneurons? In their study of the distribution of flexor axons to muscle cells, Pearson and Bergman (*8*) observed that excitatory axon 4 and inhibitory axon 3 invariably accompany each other when they innervate flexor muscle cells. The other flexor excitatory axons innervate many muscle cells unaccompanied by the inhibitor.

To determine whether muscle tensions developed in postural reflexes can be inhibited at the muscle cell, we monitored tension developed in the posterior flexor trochanter muscle tendon in response to repetitive stimulation of the coxal chordotonal organ and also stimulated the common inhibitory axon. Stimulation of the common inhibitor at 50 Hz (less than half the rate seen in spontaneous bursting) completely inhibited re-

Table 1. Axon 4 spikes in the flexor nerve with and without stimulation of the common inhibitor. Values are means ± standard deviations.

Leg extension (degrees per second)	Axon 4 discharge (N = 4) (Hz)	Axon 4 discharge with common inhibitor stimulation (N = 4) (Hz)	
		At 10 Hz	At 60 Hz
25	8.2 ± 2.2	8.7 ± 2.8	8.0 ± 1.9
150	63.6 ± 13.1	68.0 ± 14.6	64.1 ± 15.3

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flexly developed tension (Fig. 1C). Lower rates of inhibitor stimulation effectively modulated tension development. To ensure that these interactions were occurring at the muscle cell and not in the central nervous system, we counted axon 4 spikes in the flexor nerve with and without stimulation of the common inhibitor (Table 1). No significant difference was observed. Thus, the common inhibitor has no direct effect on the discharging of axon 4 and must act directly on the muscle.

A variety of spontaneous muscle contractions were recorded as tensions at the flexor muscle tendon. Common inhibitor stimulation had no regular discernible effect on these contractions (Fig. 1D). While spontaneous contractions were generally rapid and ballistic and all the possible rates of tension development were not examined, it is apparent that the common inhibitor does not affect all flexor muscle tensions equally.

A hypothesis that accounts for the peripheral location of these interactions is that the common inhibitor overrides proprioceptively developed muscle tensions in preparation for rapid movements. One pathway for the initiation of rapid locomotion is the escape response: air movement stimulates receptors on the cercus (an abdominal appendage), producing excitation of abdominal nerve cord fibers and subsequent rapid leg movements (*12*). Fourtner and Drewes (*13*) recorded from a number of leg nerves and found that the common inhibitor is the first neuron excited in the escape response. We have found that this discharge can eliminate flexor muscle tensions reflexly developed in response to activity in proprioceptive sense organs. This interaction at the initiation of escape would substantially relax postural muscle tensions in some legs before the activation of motoneurons generating rapid locomotion. These muscles would be rapidly reset to the same starting condition for escape, regardless of prior postural tension.

In summary, our findings indicate that one role of peripheral inhibition in insects is the modulation or suppression of postural reflex tension (Fig. 1E). Inhibition of postural reflexes by central and peripheral inhibitory connections was recently shown to occur in crayfish prior to escape tail flips (*14*). Many animals may use similar mechanisms to acquire rapidity in the initiation of centrally programmed behaviors.

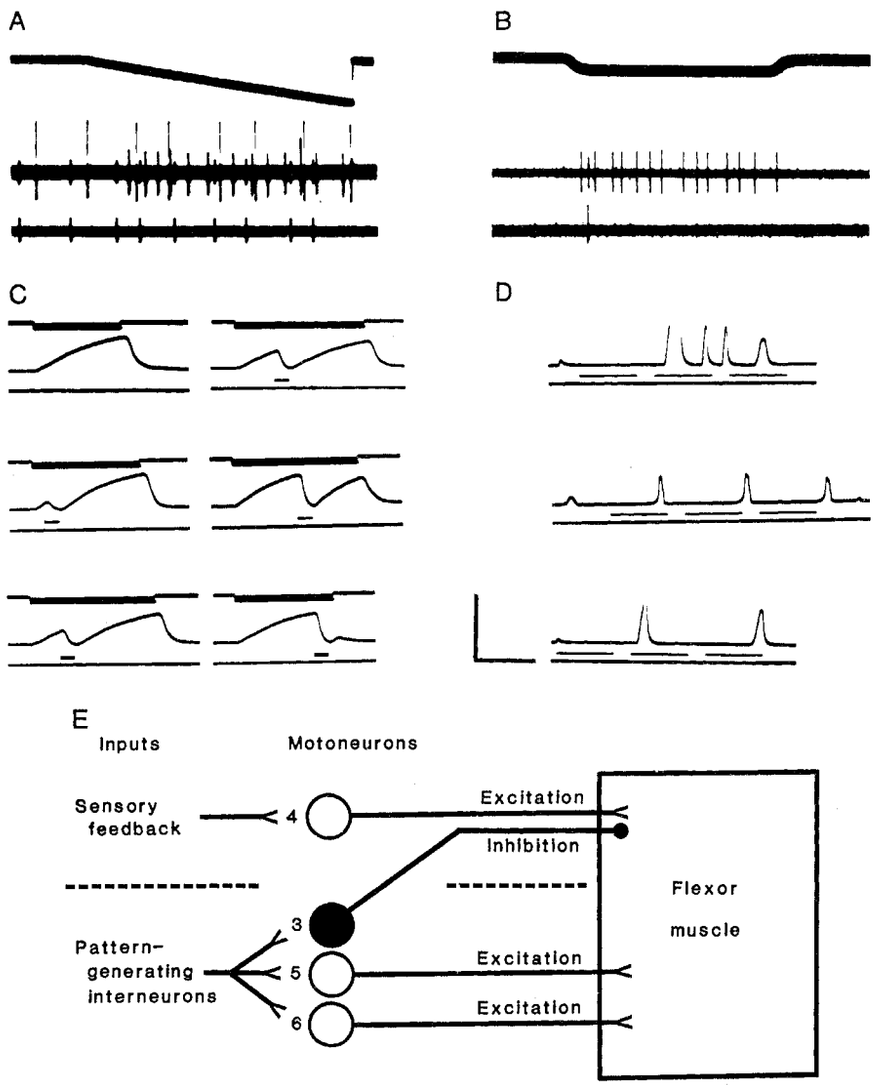

Fig. 1. (A) Reflex effect of stimulation of the coxal chordotonal organ. The joint between the coxa and trochanter was extended at a constant rate over a 10° arc (upper trace). This produced a uniform discharge from a single axon in the flexor motor nerve (middle trace). This axon was not the common inhibitory neuron that was also monitored in another leg nerve (lower trace). (B) Reflex effect of tibial campaniform sensillum stimulation. A single distal tibial campaniform sensillum was stimulated with a fine tungsten wire probe (upper trace). The flexor nerve recording (middle trace) shows reflex activation of a single flexor axon (axon 4) that was not the common inhibitor (lower trace). (C) Stimulation of the common inhibitor suppresses reflexly developed tensions. Reflex tensions were produced by repeatedly extending the leg over a 10° arc with a ramp function [see (A)]. The duration of this repetitive stimulation is indicated in the upper trace. The graded increase in tension that developed was monitored by a tension transducer clamped to the severed flexor muscle tendon (middle trace). Introduction of common inhibitory neuron stimulation at 50 Hz (bar in lower trace) inhibited all levels of reflexly developed tension. (D) Stimulation of the common inhibitor does not affect many spontaneously generated muscle tensions. Spontaneous movements were monitored as tensions in the flexor muscle (upper trace). These tensions were not affected by stimulation of the common inhibitor at 50 Hz (bar in lower trace). Equal tensions could be developed before, during, and after common inhibitor stimulation. (E) Summary of connections of flexor motoneurons and their interactions at muscle cells. Sensory inputs reflexly excite the smallest excitatory flexor motoneuron, axon 4. Previous studies by Pearson and colleagues (*5*, *7*–*8*) showed that pattern-generating interneurons excite other flexor motoneurons. One of these, the common inhibitory neuron, has its major peripheral inhibitory effect on axon 4. The present study shows that the common inhibitor can modulate or override reflexly developed muscle tensions. Calibration: (A and B) horizontal, 100 msec; (C and D) vertical, 2.0 g; (C) horizontal, 3 sec; (D) horizontal, 800 msec.

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Is Sperm Cheap? Limited Male Fertility and Female Choice in the Lemon Tetra (Pisces, Characidae)

Abstract. *In the laboratory, fertilization rates achieved by male lemon tetras decline with spawning frequency. Even when the number of females is not limited, males can produce only four times as many offspring as females. Females show a preference for males that have not recently spawned as opposed to those that have. The cost of producing sufficient sperm to maximize fertilization rates may therefore reduce the intensity of sexual selection in this polygamous fish species.*

The massive difference in the size of the egg and the sperm forms the basis of much contemporary theory concerning sexual dimorphism and social behavior. A case in point is the theory of sexual selection developed by Darwin (*1*) to explain the evolution of characters, seen especially in males, that seemed unlikely to have evolved by natural selection but could offer a reproductive advantage either in competing with the same sex or in courting the opposite sex. For polygamous species in which paternal care is absent, Bateman (*2*) argued that since males invest so much less in each zygote than do females, males are potentially capable of producing many more offspring than are females. The reproductive success of females is limited by their ability to produce eggs, and the reproductive success of males is limited by their ability to obtain mates. Competition between males and female choice cause some males to achieve more of their potential reproduction at the expense of others, resulting in a higher variance of reproductive success among males than among females. This results in a greater intensity of sexual selection on males (*2, 3*). Trivers (*4*) generalized this argument to include investment in parental care, concluding that the sex that invests less in each offspring is limited by the availability of the sex that invests more and is subject to a greater intensity of sexual selection. This conclusion has been advanced in recent discussions of the evolution of social behavior (*5*).

These theoretical arguments do not take into account the number of sperm produced to fertilize each egg. The rate of external fertilization is maximized only at sperm concentrations of about 10^6 sperm per milliliter, and similar concentrations are required in the ejaculates of internal fertilizers (*6*), potentially reducing the upper limit to male fertility (*7*). A decline in sperm concentrations or fertilization rates with successive ejaculations in internal fertilizers (*8*) may indicate the high cost of producing adequate sperm concentrations (*7*). However, many investigators (*9*), in field studies, assume that males are not limited by sperm supply (*10*). Although laboratory observations of sperm depletion may be artifacts resulting from matings at frequencies that do not occur in nature, we noted indications of fertility limitation in a small, tropical fish at mating frequencies that could occur in nature. Our study documents male fertility limitation in an external fertilizer; we investigated the mating frequencies at which males would be limited by mates and by sperm supply and compared maximal offspring production of males and females. We found that mate selection by females supports the argument that sperm limitation may occur in nature. The data call into question the assumption that "sperm is cheap" and show that the reproductive success of the sex that invests less in each gamete is not necessarily limited exclusively by the availability of the opposite sex.

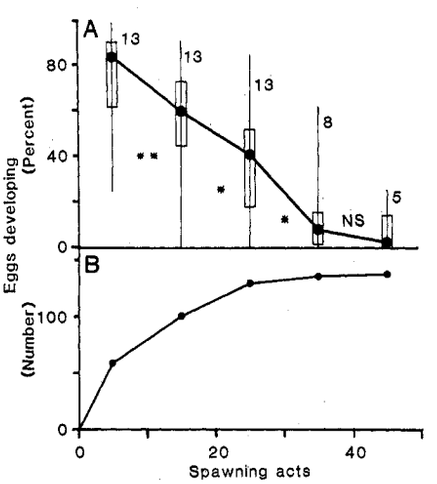

Fig. 1. The relation between total daily spawning acts and fertility (A) or estimated, total number of offspring (B) in male lemon tetras. The graph in (A) is based on 13 different tests carried out on six individual males. Eggs were removed after each ten spawning acts and incubated to determine fertility, but the total number of spawning acts achieved by each male varied as a function of female availability and fecundity on the test day. Dots show medians, open rectangles are upper and lower quartiles, and vertical lines represent ranges. Sample sizes are indicated, as is the statistical significance of the differences between adjacent means (Wilcoxon matched-pairs test; $^{**}P < .01$; $^{*}P < .05$; *NS*, not significant). The graph in (B) is based on the median fertility in (A) and an average production of seven eggs per spawning act.

The lemon tetra *Hyphessobrycon pulchripinnis* is a small (31 to 38 mm), characid fish native to the Amazon Basin. In our laboratory, spawning takes place during the first 2 hours of the morning. At this time males defend spawning sites while females school. A female ready to spawn enters a male's territory, is briefly courted, and approaches a spawning site such as a clump of plants. The male positions himself beside her. After a period of quivering, the pair leap forward releasing eggs and presumably sperm. On the average, ovulation occurs once every 4 days, and on this day each female spawns an average of 23 times, producing a total of 160 eggs. Mating is promiscuous, and males spawn every day that receptive females are available. Parental care is absent; both sexes school together after spawning (*11*). Male fertility as a function of the number of spawning acts was determined by placing one at a time females that had ovulated with an isolated male and observing the spawning frequency (*12*). Egg traps used as spawning sites (*13*) were replaced after each series of ten spawning acts. When a female stopped spawning she was replaced. Each egg collection was incubated separately for at least 4 hours, and the percentage of developing eggs was used as an index of the fertilization rate.

The percentage of eggs developing declines, nearly linearly, as a function of the number of spawning acts by the male (Fig. 1A). The decline is most easily explained by a reduction in the quantity or quality of sperm released at successive spawnings (*14*). A statistically significant difference in the rate of fertiliza-

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