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16 July 1980

Conduction System in a Sponge

Abstract. *The hexactinellid sponge* Rhabdocalyptus dawsoni *is capable of arresting its exhalant water current in response to mechanical and electrical stimuli. The arrest is coordinated by a conduction system with a precise threshold of excitability and a chronaxie of 38 milliseconds. The response is propagated throughout the sponge at a mean velocity of 0.22 centimeter per second, and conduction is unpolarized.*

Sponges show little behavior in the usual sense. Oscular contractions and slow changes in shape have been described in several species, but these usually appear as local responses confined to a few millimeters of tissue (*1*, *2*). Conduction of contractile responses over longer distances occurs in a few cases (*3*, *4*), and an ability to regulate overall water flow has been demonstrated in certain tropical demosponges (*5*). In the latter case, flagellar pumping activity and oscular movements seem to be coordinated, but the conduction system involved has never been demonstrated or characterized physiologically. We present here the first such evidence.

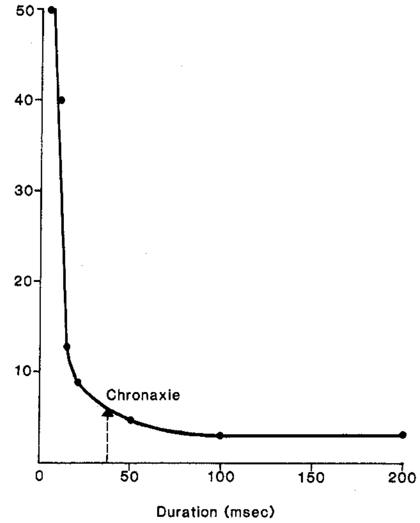

Fig. 1. Intensity plotted as a function of duration showing that the exhalant current of the sponge is arrested by a conduction system with a precise threshold. For most stimulus durations, there is a minimum intensity that will produce a response: the classical "all-or-none" response of excitable tissue. The chronaxie (38 msec) is high compared with that of nerve and muscle, an indication that the conduction system of the sponge may have a low excitability.

Field observations on *Rhabdocalyptus dawsoni* (Lambe, 1892), a large hexactinellid sponge from coastal waters of British Columbia, involved monitoring the exhalant water current with a compensated, thermistor flow-meter (*6*). Arrests occurred in response to local disturbances such as mechanical jarring. Further, as noted in certain demosponges (*5*), periodic arrests were seen in the absence of such stimuli and were assumed to be of endogenous origin. The osculum of *Rhabdocalyptus* cannot change shape, and therefore sudden stoppage of the exhalant current must be due to a coordinated arrest of the individual currents passing through the body wall. This in itself suggests that a diffuse conduction system is present in the sponge.

After being transferred to laboratory tanks, the sponges were maintained in slowly running seawater (11°C) for 2 days before observations were made. Steady pumping activity interrupted by occasional arrests took place as in the natural environment. Mechanical stimulation also induced arrests; a sharp tap

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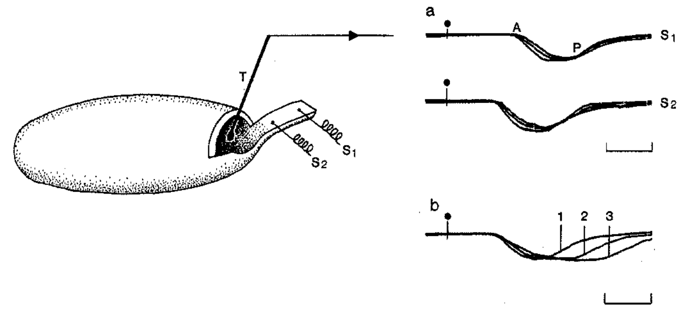

Fig. 2. Conduction in the sponge tissue. A thermistor flowmeter (*T*) is used to detect fluctuations in the exhalant water current, and two stimulating electrodes are placed on a flap of tissue cut at the margin of the osculum. The accompanying traces from the flowmeter show the response of the exhalant current to single shocks (denoted by dots) applied to the flap. In each record, three responses have been superimposed: the start of an arrest (*A*) appears as a downward deflection of the trace, and the reverse occurs when pumping resumes (*P*). (a) Evidence that the latent period varies with the site of stimulation. Shocks applied through the distal electrode (S_1) take longer to initiate an arrest than those applied through the proximal one (S_2). (b) Records showing that the duration of the arrest is increased by repetitive stimulation. A series of shocks is applied through S_2 at a frequency of one every 5 minutes. Traces show the arrests produced by shock 1 (1), shock 8 (2), and shock 16 (3) of the series. The constant durations seen in (a) were assured by resting the sponge sufficiently between tests. Time scales in all records are equal to 30 seconds.

on the side of the tank or gentle prodding of the sponge usually produced an arrest after a latent period of 20 to 50 seconds (measured to the first sign of a decrease in flow). The most interesting finding, however, was that electrical stimulation could be used to evoke arrests. This made it possible to study responses by means of precisely measurable stimuli.

A single shock delivered through an electrode applied to any part of the body wall produces an arrest with a latent period again in the range of 20 to 50 seconds. The arrests may last for 30 to 100 seconds before pumping is resumed. By varying the intensity and duration of the applied stimulus, a precise threshold of excitability was detected, below which arrests could not be elicited. Occasionally, incomplete arrests would occur, but these were rare; responses were usually "all-or-none." Plotting the intensity as a function of duration for electrodes placed close to the osculum (Fig. 1) shows that the conduction system responsible for the arrests has a chronaxie of 38 msec at 11°C (the chronaxie is a convenient measure of excitability and represents the duration of a threshold stimulus at twice the minimum intensity capable of eliciting a response). Such empirical results, however, should be treated cautiously in comparison with other systems (*7*); in this instance, the shunting effect of the seawater and the difficulty in obtaining a close contact between the electrodes and the sponge tissue may produce an artificially high value for the chronaxie. The excitability of the tissue may therefore be greater than the chronaxie suggests.

Conduction velocity was measured by cutting a flap (4 cm long and 1 cm wide) in the body wall at the margin of the osculum (Fig. 2). Two stimulating electrodes were placed on the long axis of the flap with a gap of 3 cm between them and single shocks were applied, first to the distal electrode and then to the proximal one. The resulting arrests, as recorded by a compensated, thermistor flowmeter, are shown in Fig. 2a. The difference between the latent periods produced by stimulation at either site represents the time taken for the propagated activity to bridge the distance between them. From these values, conduction velocities of 0.17 to 0.3 cm/sec (mean = 0.22) at 11°C were calculated for ten sponges. Although this is slow in terms of nervous conduction in higher animals, it is much too fast for conduction by simple chemical diffusion (*8*) and is only an order of magnitude lower than some conduction velocities reported in sea anemones (*9*). It also exceeds, by at least an order of magnitude, the values quoted for contraction waves in sponges (*3*, *10*).

Attempts to record electrical activity either with intracellular or extracellular electrodes were unsuccessful, a situation previously encountered by other workers (*2*). Repetitive stimulation of the body wall had the effect of increasing the duration of the arrest without altering the latent period (Fig. 2b). At a frequency of one shock every 5 minutes, the 8th shock of the series increased the duration by 57 percent (trace 2) and by the 16th shock it was increased by 100 percent (trace 3).

All regions of the sponge seem to be responsive to electrical stimulation and capable of serving as conduction pathways to other regions. Experiments with flaps cut in various parts of the body wall show that conduction is unpolarized. One sponge had a bud attached in which the spongocoel was continuous with that of the parent. Simultaneous recordings with two thermistors showed that the arrests occurred at the same time in both the parent and the bud.

We conclude from the evidence presented here that electrical shocks or local tactile stimuli elicit some kind of propagated signal or impulse which travels from the site of stimulation to widely dispersed effectors. These are responsible for controlling the flow of water through the body wall, but the direct cause of the arrests remains unclear. Microscopic examination of the lining of the spongocoel during arrest indicated that contraction and occlusion of the exhalant apertures did not occur, contrary to the situation reported in the demosponge *Verongia gigantea* (*5*). Likewise, the inhalant openings on the dermal surface of the sponge showed no changes during arrests. While contraction in some part of the canal system inaccessible to direct observation remains a possibility, the lack of any known network of contractile cells suggests that this is unlikely. It is more probable that the sponge turns off its feeding current by stopping the beating flagella in the choanocyte chambers. Other filter-feeding animals, including bivalve mollusks (*11*) and tunicates (*12*), use such ciliary control systems and this would seem to be a predictable adaptation in any animal where cilia or flagella were the principal effectors. Observation of the choanocytes in situ, however, is difficult in *Rhabdocalyptus* owing to the thickness of the body wall so that there is no direct evidence that the flagella are capable of arrest. The microscopic anatomy of hexactinellids is too poorly known at present for any physiological deductions to be made on the basis of histology (*13*), but recent findings that all surfaces in hexactinellids may be syncytial (*14*) suggest that the entire conduction system could act as a single neuron.

The existence in sponges of a rapid, diffuse conduction system with a precise threshold, one that is capable of coordinating effectors spread over the entire body, is a novel concept for biologists and implies that present views concerning the evolution of conduction systems and the basis of animal behavior will have to be modified. This investigation, however, has not demonstrated the existence of a nervous system in a sponge and, despite some suggestive histological (*15*) and pharmacological (*16*) evidence, it is doubtful that true nerve cells exist in the phylum (*17*). Impulse conduction by nonnervous, noncontractile tissues plays a significant behavioral role in several groups of animals (*18*) and may be the basis for coordination in sponges. Electrical coupling has been demonstrated between sponge cells in vitro (*19*), and structures resembling gap junctions have been reported in certain sponges (*20*). Failure to record electrical signals from *Rhabdocalyptus* may be due to purely technical difficulties inherent in the material and need not imply that impulse propagation does not occur (*21*). If impulses must pass by circuitous routes through the porous body of the sponge, conduction velocities measured along strips of body wall would be much lower than those in the primary conducting elements. While it seems most likely that conduction is electrical, as in other excitable tissues, we cannot at present exclude the possibility that conduction in *Rhabdocalyptus* involves some quite novel, nonelectrical signaling mechanism.

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11 February 1980; revised 7 July 1980

Prenatal Exposure to Synthetic Progestins Increases Potential for Aggression in Humans

Abstract. *Seventeen females and eight males exposed during gestation to synthetic progestins showed a significantly higher potential for physical aggression than their sex-matched unexposed siblings. Exposure to androgen-based compounds appeared to be most closely associated with aggressive responses. There were no differences in verbal aggression or IQ between exposed and unexposed siblings.*

The presence or absence of gonadal hormones early in development affects the expression of a wide variety of sexually dimorphic behaviors in mammals (*1*). For most mammalian species, the organism, regardless of genetic sex, must experience early androgenic stimulation in order to develop many of the behaviors characteristic of males in adulthood, whereas behavior more characteristic of females depends on the relative absence of these gonadal hormones during early development. Reproductive and aggressive behaviors have been clearly documented as hormonally mediated (*1-3*). Evidence is given in this report that human aggression, like aggression in lower mammals, may also be influenced by exposure to steroid hormones early in ontogeny.

In most mammalian species, including humans, males display more intraspecific aggressive behavior under a wider variety of conditions than do females (*4, 5*). Data, particularly from studies of rodents, indicate that exposure to gonadal hormones early in development is linked to a greater likelihood of aggressive display in response to adult testosterone stimulation and to an increased sensitivity to the aggression-promoting property of androgens in adulthood (*2, 3, 6*). Female rhesus monkeys exposed to testosterone during fetal development showed increased frequencies of male-like threat and rough-and-tumble play during the juvenile period (*7*). When these prenatally androgenized females were ovariectomized in adulthood, they displayed significantly more aggressive behavior toward normal females than did animals that had not been exposed to testosterone (*8*). Thus, for many mammals, exposure to gonadal steroids early in ontogeny, whether from an endogenous or exogenous source, appears to be a primary factor in the development of increased aggressive behavior in adulthood.

During the past three decades millions of pregnant women have been treated for threatened abortion with progestins and estrogens (*9*). Evidence that the synthetic progestins administered orally during pregnancy may have some androgenic potential includes reports of (i) masculinization of the genitalia of as many as 18 percent of human female offspring of progestin-treated mothers (*10, 11*) and (ii) virilizing effects on genital morphology of rats treated with both progesterone- and androgen-based synthetic

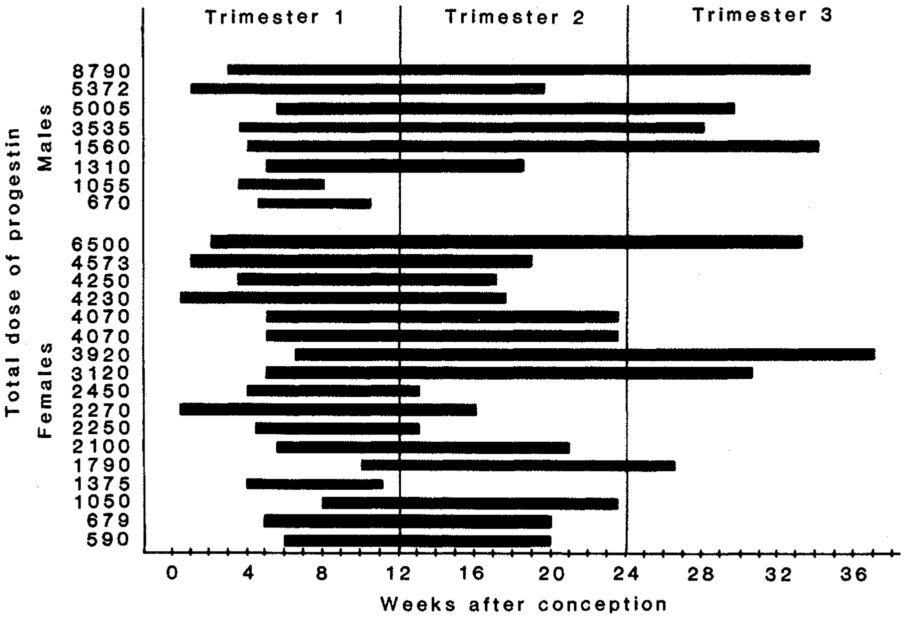

Fig. 1. Duration, timing, and total dose (in milligrams) of exposure to synthetic progestins for male and female human offspring.