possible with multiple-cycle LC cell recordings.

The reciprocal interaction model for sleep cycle control is explicit and testable. It helps to order a confusing pharmacological literature and suggests critical experiments to test its postulates. For example, the model predicts that suppression of LC activity or its postsynaptic effects will produce augmented FTG activity and hence more desynchronized sleep. Indeed, more desynchronized sleep has been found to result from administration of substances blocking alpha-adrenergic receptors (*17*) and norepinephrine synthesis (*18*). These results run counter to the theory that desynchronized sleep phenomena are actively generated by the LC, but are entirely consonant with our model. An interesting but so far untested corollary prediction about cellular events is that the LC cells normally showing a marked decrease in discharge activity with the advent of desynchronized sleep should show a less marked decline following the administration of these drugs, since the inhibitory feedback will be less potent. The model further predicts that another approach to desynchronized sleep enhancement—through direct increase of FTG activity—would be to administer compounds that simulate the effect of acetylcholine in the FTG; this prediction of the model is also confirmed by several experiments (*19*). The parallel prediction that injection of such cholinomimetic compounds into the LC should result in less FTG activity and thus less desynchronized sleep because cells inhibitory to the FTG are being stimulated has not been tested. We conclude that the model offers a good first approximation to the discharge activity curves of FTG and LC cells and is consonant with anatomical, physiological, and pharmacological data.

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14. An important temporal feature postulated by the model and present in the data is the phase lag between the FTG and LC activity peaks; this is on the order of several minutes in duration in the cat's usual cycle. The mechanisms of this phase lag are not explicitly included in the model, but the duration of the phase lag suggests the presence of transmitter effects whose duration extends into the minute range. Such long-duration effects for the transmitters postulated in our model have been reported to occur at several synapses. M. Segal and F. E. Bloom, *Brain Res.* **72**, 79 (1974); F. Weight, in *The Neurosciences, Third Study Program*, F. O. Schmitt and F. G. Worden, Eds. (MIT Press, Cambridge, 1974), p. 929.
15. Numerical integration of the second-order nonlinear differential equations derived from the text equations was done by the method of continuous analytic continuation, as outlined in (*12*). With the start of the curve set at the end of the desynchronized sleep cycle, $x(0)$ is fixed at the equilibrium value and $dy/dt = 0$ at $t = 0$. The values of $y(0)$ (or, alternatively, dx/dt at $t = 0$) and the constants a and c were set to match the observed modulation during the sleep cycle and scaled for the appropriate duration. The constants b and d scale the amplitude of the FTG and LC activity curves.
16. Note that, unlike the onset and end of desynchronized sleep periods defined by crossing of the FTG equilibrium values, the portions of the theoretical cycles to be identified with the behavioral states of waking and synchronized sleep are more fuzzy, since the model attempts only to show the control mechanisms for desynchronized sleep. On a probabilistic basis, the first fifth of the cycle is most often associated with waking, and synchronized sleep includes the rest of the cycle up to desynchronized sleep onset, although arousals may sometimes occur during this period.
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Colonial Nervous Control of Lophophore Retraction in Cheilostome Bryozoa

Abstract. *Nervous impulses causing lophophore retraction over large areas of* Membranipora membranacea *and* Electra pilosa *were recorded with external electrodes. The response propagates at about 100 centimeters per second, presumably through the colonial nerve plexus of Hiller and Lutaud. Impulses are rapid up to 200 per second. A second impulse was recorded from individual zooids, probably generated by the polypide's nervous system. The retractor muscle shortens at more than 20 times its own length per second and is apparently the most rapidly contracting muscle known.*

Various authors have investigated the control of behavior by simply organized nervous systems in colonial invertebrates [for example, see (*1, 2*)]. Except for recordings of the Hydrozoa (*2, 3*), however, no direct electrophysiological recordings of colonial nervous activity have been made. Marcus (*4*) claimed that no colonial coordination existed in the gymnolaemate Bryozoa. This view, supported by Silen (*5*) and others, has been widely accepted in the last 50 years. Hiller (*6*) and more recently Lutaud (*7*) presented histological evidence for a colonial nervous plexus in *Electra* (formerly *Membranipora*) *pilosa* (L.) to support the behavioral data of Bronstein (*8*).

Our work has shown that there is a high degree of coordination between zooids in the two species we have studied—*Membranipora membranacea* and *Electra pilosa*. Furthermore, electrophysiological recordings indicate that a highly active colonial nervous system is involved.

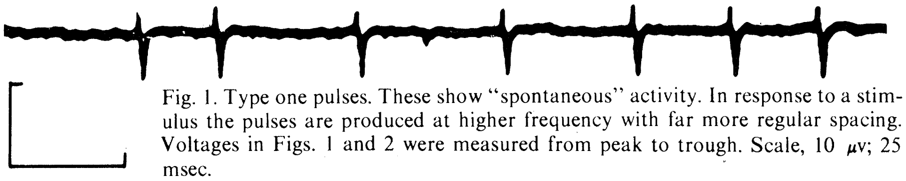

Fig. 1. Type one pulses. These show "spontaneous" activity. In response to a stimulus the pulses are produced at higher frequency with far more regular spacing. Voltages in Figs. 1 and 2 were measured from peak to trough. Scale, 10 μv; 25 msec.

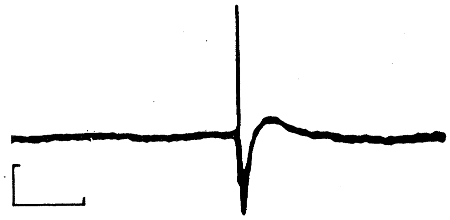

Fig. 2. Type two pulse. This pulse was not produced in response to type one activity, which would normally be superimposed upon it. Scale, 20 μv; 50 msec.

A colonial retraction of zooids is evoked by a single, above-threshold, mechanical or electrical stimulus to the surface membrane of an individual. Stimuli applied to the extended tentacles of a single animal in a colony produce a retraction response in that animal only. During a colonial response, all extended lophophores within a few centimeters of the zooid stimulated are involved in an almost simultaneous withdrawal. Those nearest the point of stimulation retract for a longer period than those on the edge of the retracting area. Second and third stimuli applied a few seconds after the first one may produce small increases in the area of spread, but the response can never be made to spread over the entire colony. The response to subsequent stimuli shows marked habituation (measured by the response area). Retractions and extensions of one or more lophophores were monitored with a narrow light beam and a photodiode (Texas Instruments, type H-38 NPN photoduodiode) connected to an oscilloscope and pen recorder. This apparatus was also used to measure the delays between stimulus and response at varying distances from the point of stimulation. The response spreads at a velocity of about 100 cm sec^{-1}. The protective lophophore withdrawal response takes place very rapidly (60 to 80 msec) and corresponds to a peak contraction rate (the greatest velocity reached by the muscle during a single contraction) of more than 20 muscle lengths per second in the lophophore retractor muscle, which is probably the fastest contracting muscle known [compare other extremely fast muscles—locust flight muscle, 13 lengths per second (*9*); rat diaphragm, 11 lengths (*10*); and frog sartorius, 10 lengths (*11*)]. In view of this, the muscle might be expected to show interesting ultrastructural adaptations to contractions at great velocity.

Electrophysiological recordings, in which extracellular suction electrodes were used (*12*), showed two distinct types of electrical pulses within the colony. "Type one" pulses (Fig. 1) are of about 2 msec duration and up to 10 μv in amplitude. They are conducted between zooids at a velocity of about 100 cm sec^{-1}. These data indicate probably nervous (or possibly neuroid) origin. As no other suitable nervous or neuroid pathway has been described, the pulses may emanate from the tiny neurites in the colonial nervous system described by Lutaud (*6*). If so, their conduction velocity is surprisingly rapid. A single above-threshold stimulus causes a burst of type one activity, the size of the response depending upon the magnitude of the stimulus. These pulses show three features of particular interest. (i) They are very regularly spaced, which suggests pacemaker control. (ii) Their peak frequency during a burst is often extremely high (more than 200 sec^{-1}), and they often continue to fire at high frequency for long periods of time. (iii) A single burst may contain more than 1000 pulses in the first 10 seconds. This probably unique property suggests that the nerves involved may have a most unusual degree of tolerance to changes in internal ionic concentration. The threshold, conduction velocity, and habituation of the type one response correspond with those of the colonial withdrawal of polypides.

Type two pulses (Fig. 2) are not conducted between zooids but occur whenever the lophophore retractor muscle of an animal contracts beneath the recording electrode; they are of two parts. The first is of large amplitude (up to 200 μv) and short duration (10 msec); this is followed by a much longer duration component probably related to the muscular activity. The first part could be nervous activity in a giant axon system innervating the muscle and possibly coming from the main ganglion of the zooid. There is a frequency-dependent relation between type one and type two pulses, although type two pulses can be recorded without type ones (see Fig. 2). In this case they are probably not the result of colonial activity.

The nonlinear increases in the size of the colonial retraction response following repetitive stimulation closely resemble the behavior of certain coral polyps (*13*). Since, however, the type one pulses can be shown to travel outside the immediate area covered by the colonial response, Horridge's theoretical explanation of coral behavior in terms of the density of active neurites in a nerve net will not explain the observed results in the Bryozoa.

These results represent the first electrophysiological evidence for a functional colonial nervous system in gymnolaemate Bryozoa. The nerve plexus is anatomically simple (*7*), but allows versatility in the control of colonial behavior.

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Allometry and Early Hominids

We applaud the use of allometry which allows Pilbeam and Gould (*1*) to treat the welter of early hominid finds in an orderly and integrated manner. In passing, we note that the same approach could profitably be applied to testing possible male-female dimorphism at early hominid sites (*2*).

Our purpose here, however, is not to question the treatment of the australopithecines per se, but to question the validity of the taxon which Pilbeam and Gould place as the first recognized member of the lineage leading to *Homo sapiens.* The very existence of the taxon "*Homo habilis*" owes more to an extraordinarily wide press, such as that to which Pilbeam and Gould correctly attributed the enshrinement of the killer ape image, than to actual data (*3*).

Homo habilis was one of the last crea-