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Nonlinear Oscillations in Polyps of the Colonial Hydroid *Podocoryne carnea*

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Cnidarian colonies, while simple metazoans lacking true organs, all share one colony-wide system of physiological integration, the gastrovascular system. The circulation of gastrovascular fluid is responsible for the distribution of metabolites within a colony [6, 19, 23]. Recent experimental findings have shown that the physiological state of the gastrovascular system is a key determinant of colony morphology and life history [4, 7]. Yet, despite its apparent importance to colony morphogenesis, studies of gastrovascular circulation have been largely restricted to description of flow in localized regions of growth [1, 2, 5, 11, 20, 24, 26]. Given the complexity of gastrovascular flow dynamics, the relative paucity of colony-wide data is not surprising. Gastrovascular flow is generated by literally hundreds of individual pumping elements (polyps) connected by a complex anastomosed network of gastrovascular canals (stolons), within which flow velocity and direction varies in both space and time [10, 11]. As with any system of this complexity, one seeks to isolate individual components of the overall system and develop a simple, yet sufficient, description of the behavior of individual components. Here we present key observations which lead to a simple mathematical model qualitatively describing the behavior of the functional unit central to flow generation.

Our study organism is the colonial hydroid *Podocoryne carnea*. We have recently presented a detailed analysis of the feeding response of the *P. carnea* polyp [8]. Figure 1 illustrates the behavior documented and introduces the dynamic behavior that we seek to capture. Both length and volume of a polyp are effectively static prior to ingestion of a food item (Fig. 1a, c), and this ingestion is followed by the onset of regular oscillations in both length and volume (Fig. 1b, d). These features are repeatable and for the interval up to 100 min following ingestion of a food item are qualitatively similar for a single polyp isolated from a colony and one connected to a colony by a single stolon. It may also be mentioned that the time between feeding and cessation of polyp oscillations is proportional to the number of shrimp nauplii fed to the polyp (S.D., unpublished).

Several features of the observations deserve more comment. Hydroid polyps are known to periodically display a rapid contraction of the body column, the contraction pulse (CP). This behavior is characterized by a diagnostic conducting potential and, being restricted to ectodermal longitudinal muscle fibers, is distinct from digestive oscillations [12, 17, 21, 22]. CPs, an instance of which is shown in the prefeeding record of Fig. 1a, represent perturbations in the length (or width) of oscillating polyps. Figure 2 depicts three such length perturbations, and clearly demonstrates that the polyp rapidly approaches the oscillatory behavior it had before the perturbation. It may also be noted that mechanical stimulation alone is not sufficient to elicit polyp oscillations before feeding or to disturb them more than shown in a CP after feeding.

Figure 3 shows more detailed records of polyp behavior immediately after feeding. There is a period during which the polyp seems to be "unable to make up its mind" and then oscillations appear of increasing amplitude and frequency. It is also interesting to examine the oscillation data in the frequency domain. The spectral properties of the high-pass filtered time series for polyp length shortly after feeding is presented in Fig. 4 and shows (a) a dominant peak at $\omega/2\pi \approx 8$ mHz (corresponding to about

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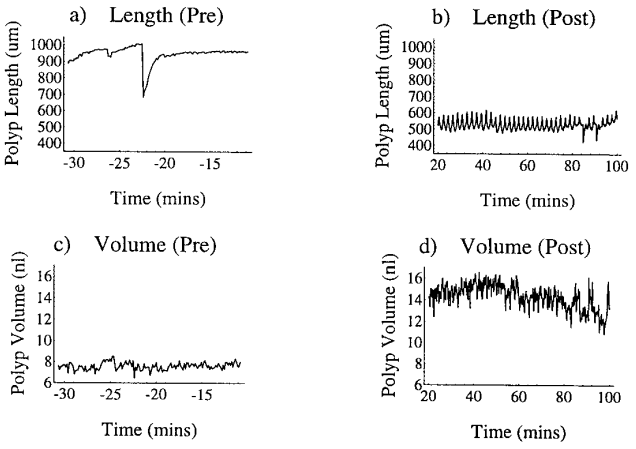

Fig. 1 a–d. Pre- and postfeeding behavior. Time series of length (a, b) and volume (c, d) of isolated polyp before (a, c) and after (b, d) ingestion of a single brine shrimp (*Artemia salina*) nauplius. Note the CP pulse in the prefeeding length record (*a*) and the absence of a corresponding response in the volume record (*c*). Polyp length and volume was measured every 8 s. *Abscissa*, minutes before feeding. See [8] for details of methods

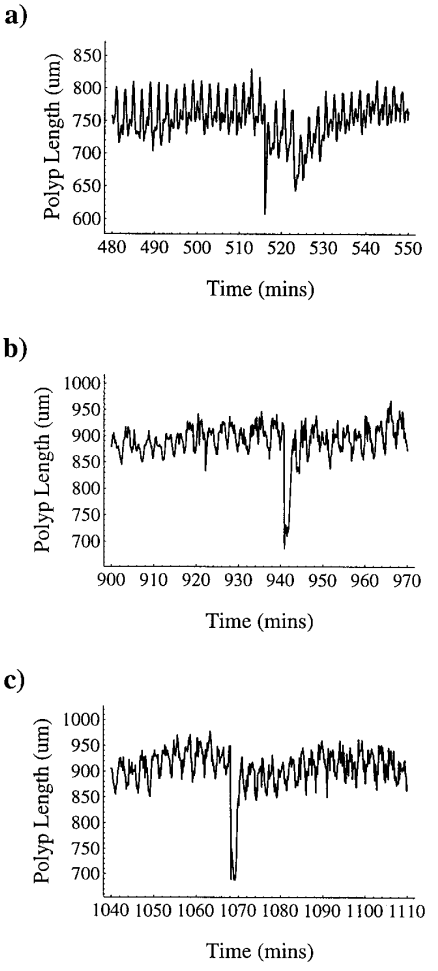

Fig. 2 a–c. Time-series of polyp length for three separate intervals during which a contraction pulse occurred. All three panels show that polyps rapidly return to the oscillation pattern they displayed prior to the contraction. *Abscissa*, minutes elapsed after feeding of polyp

one pumping cycle per 2 min), and (b) one much weaker harmonic at twice this frequency. Note that these properties are stable over time. This figure is based on power spectra calculated separately for 80 overlapping 20-min windows spanning a total of 100 min of postfeeding oscillations (see also [8]). Concatenation of the spectra for each window along the z-axis yields a three-dimensional graph that shows how polyp oscillations change over time. In Fig. 4b this three-dimensional graph is represented as a contour plot, i.e., viewed from above. It demonstrates the surprising stability of the frequency composition. Similar to frequency composition, amplitude does not vary dramatically, for example, the coefficient of variation of the power, ζ, in the dominant frequency peak is $\sigma_{\bar{\zeta}}/\bar{\zeta} \approx 0.21$. For an isolated polyp these qualitative features undergo little change over much larger time intervals than the 100 min shown here.

We posit that the behavior described above might be broken down into a sequence of more elementary events as follows: a food item captured by the polyp elicits the release of digestive enzymes, the action of which releases nutrients, and once the concentration of the nutrients reaches a threshold value, oscillations of the polyp wall ensue, observed as accompanying variations of length, shape, and volume. This conceptualization in turn may be expressed by the following system of differential equations:

$$\dot{s} = f_s(s, u) \tag{1a}$$

$$\dot{n} = f_n(s, n) \tag{1b}$$

$$\dot{x} = g_x(n, x, y) \tag{1c}$$

$$\dot{y} = g_y(n, x, y) \tag{1d}$$

Here, u represents the number of food items fed to the polyp. In the context of our experiment, where a polyp is fed once with a defined number of brine shrimp nauplii at t=0, one might think of u as an impulse function. The function $f_s(s,u)$ in Eq. 1a represents the dynamics of s, the amount of solid food substance remaining in the polyp after time t. Despite the relative transparency of the polyp it is not easy to obtain a quantitative characterization of s; for one, with natural food there is much nonnutritive masking material. However, qualitative observation of changes in polyp size after ingestion, of the amount of optical occlusion, of regurgitation products, as well as general knowledge of digestion processes allow us to state that s decreases monotonically with time. In a 0th iteration of a quantitative model, it makes sense to take $f_s(s,u)$ linear in s and u, subject to modification when quantitative observations become available.

In the above, n is a compound variable representing nutrients directly available to the polyp. The function $f_n(s,n)$ determines the net rate of nutrient generation: the difference between the rate at which the nutrients are generated by the digestion of solid food and the rate at which they are metabolized or exported by the polyp. It is not unreasonable to take the generation rate proportional to $f_s(s,u)$; when there is no export, the 0th assumption would be to make the metabolism rate linear in n. These assignments are consistent with the qualitative expectations for the behavior of n: The time course of n is expected to

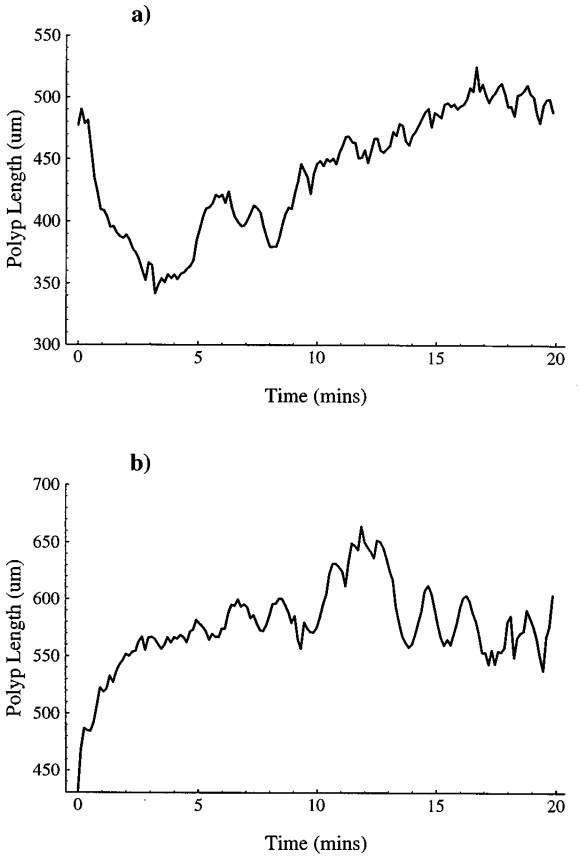

Fig. 3a, b. Immediate postfeeding behavior. Time-series of polyp length for 20 min immediately following feeding. Each panel shows an example of an isolated polyp fed at time zero with one brine shrimp (*Artemia salina*) nauplius. The large shifts in polyp lengths within the first 5 min after feeding occur due to repositioning of the food item inside the polyp. Note that 5–10 min elapse before the onset of polyp oscillations

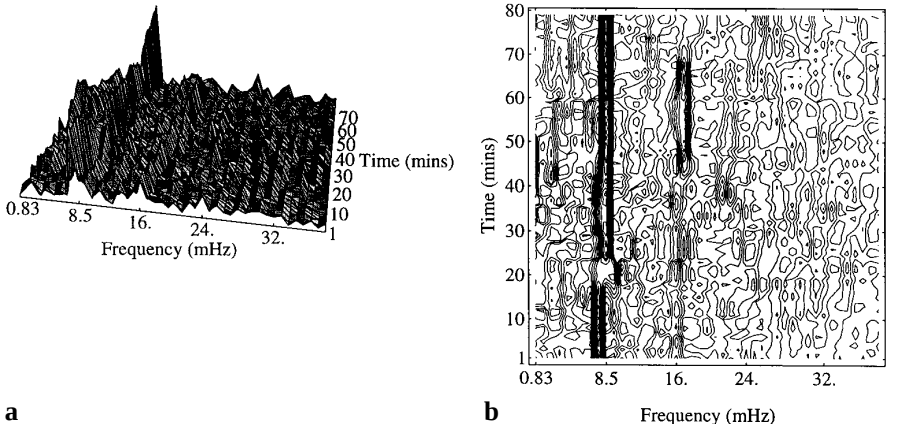

Fig. 4a, b. Sliding window power spectrum. a) Generated by concatenating spectra of 80 overlapping 20-min windows comprising minute 1 to minute 100 of a volume time series for an isolated *P. carnea* polyp. Raw data was de-trended by a high-pass filter, i.e., by subtracting a symmetric unweighted moving average covering a total of 200 data points from the time series. b) Same as a), but viewed from above as a contour plot. *Dense contour lines*, dominant frequency components at the time indicated on the ordinate axis. See [8] for details on numerical methods

start at zero at the time of feeding, rise as digestion commences, reach a plateau when a balance between production and utilization is reached, and subsequently decline towards 0 as the food source is depleted.

If s and n have the qualitative behavior described above, the observation that polyp length oscillates with time for a prolonged time period requires that there be at least one more dynamical variable in addition to the length itself; thus the two state variables x and y. To account qualitatively for the observed oscillations in polyp length it would be sufficient to make polyp length a linear function of the variable x; the presence of higher harmonics in the polyp length signal (see below) suggests that for quantitative agreement this function must be nonlinear, but monotonic, in x. At this point we would like to mention that one might argue that the proper way to model the polyp behavior would be to introduce an infinite dimensional state space, for example, one derived from modeling the polyp wall as an excitable shell-like structure in three-dimensional space. There are several reasons why we propose a much simpler model. First, for the longer range goals that we have of modeling fluid transport within a colony under the action of communicating polyps, it seems desirable to have as simple a model for an individual polyp as possible, as long as it can produce a useful estimate for the pressure within a polyp. Second, the observations that are available, or are likely to be available in the foreseeable future, are much too sparse to specify the parameters for a complex model, or to validate it. Third, even if such a detailed model were available, it would probably be explored by an appropriate expansion, which would be truncated at a low order and thus would reduce to a low dimensional model anyway. Thus we introduce the minimal model initially and are prepared to elaborate it if required when additional observations become available.

The functions $g_x(n,x,y)$ and $g_y(n,x,y)$ are independent of s because there is a delay of at least 5 min after the ingestion of a food item by the polyp before oscillations in polyp length begin. Note that prior to feeding, and

also prior to the onset of oscillations, the polyp does show some low amplitude irregular motions (as discussed above) but not oscillations of a defined frequency. We interpret this as motion excited by random perturbations about a stable equilibrium point. Thus we postulate that the linearizations of the two functions $g_x(n,x,y)$ and $g_y(n,x,y)$ in this regime would be characterized by negative real eigenvalues. Once oscillations are established they are distinctly periodic (as illustrated below) and on perturbation by mechanical or chemical means rapidly return to the same amplitude and frequency. Thus in this regime a linearization of the two functions would be expected to be characterized by an unstable equilibrium point with complex eigenvalues. In the transition regime, too short for the useful application of such techniques as Fourier analysis, the impression is of a smoothly increasing amplitude and frequency. The behavior described above, if we remain with a two-dimensional state space, can be modeled by a Hopf bifurcation, with the two functions expressible as:

$$g_x(n,x,y) = x \cdot g(n,x,y) - y$$
$$g_y(n,x,y) = y \cdot g(n,x,y) + x,$$

where for a minimally complicated model with an appropriately scaled period, $g(n,x,y)$ may be taken as $a+n-x^2-y^2$, the constant a fixing the threshold value of the nutrient concentration required to initiate oscillations, and thus determining the delay between polyp feeding and onset of polyp oscillation. To obtain a quantitative fit to the observed polyp behavior it may prove useful to replace n by a monotonic function of n, and to replace x^2+y^2 by a nonnegative function of x and y with a single global minimum, but the above simple form is in accord with the observations in all the qualitative aspects, including the observation that the polyp eventually returns to a quiescent state (when the nutrient level drops below the threshold level).

Our results show that a single hydroid polyp can be cast as a nonlinear oscillator and suggest by extension that a reasonable abstraction of a hydrozoan colony is that of a spatially distributed system of coupled nonlinear oscillators. Spatiotemporal nonlinear dynamic systems are mathematically challenging and unquestionably ubiquitous in natural systems [9, 13–16, 25]. The apparent empirical tractability of the hydroid gastrovascular system suggests that this system may prove a useful biological model for their analysis.

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