

WHY DO CUBOMEDUSAE HAVE ONLY FOUR SWIM PACEMAKERS?

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Summary

The classic view of swimming control in scyphozoan and cubozoan jellyfish involves a diffuse motor nerve net activated by multiple pacemaker sites that interact in a simple resetting hierarchy. Earlier modeling studies of jellyfish swimming, utilizing resetting linkages of multiple pacemakers, indicated that increases in pacemaker number were correlated with increases in the rate and regularity of network activity. We conducted a similar study using the cubozoan jellyfish *Carybdea marsupialis*, concentrating not only on the adaptive features of multiple pacemaker networks but also on the mechanism of pacemaker interaction. The best fit for our experimental data is a model in which pacemakers express a degree of independence. Thus, our results challenge the idea that

pacemaker interactions in scyphozoan and cubozoan medusae are based on a strict resetting hierarchy. Furthermore, our data suggest that the combination of semi-independent linkage of pacemakers with the small pacemaker number characteristic of cubomedusae is important in (i) maintaining a biphasic modulatory capability in the swimming system, and (ii) allowing behaviorally appropriate directional responses to asymmetrical sensory inputs in the radially arranged jellyfish nervous system.

Key words: cubomedusa, jellyfish, *Carybdea marsupialis*, swimming, pacemaker, nerve net.

Introduction

An important feature of multicellular nervous systems is the provision for integrative sensing of environmental information so that appropriate reactions can follow. In most metazoans, specialized sensory systems make specific connections within integrative centers which, in turn, pass on sorted information to appropriate effectors. However, in the generalized cnidarian, integrative centers are considered to be poorly developed (in a comparative sense). In scyphozoan and cubozoan jellyfish, ganglion-like neuron accumulations are found in the marginal rhopalia; however, in most of these jellyfish, the conduction of information between rhopalia is by diffuse, non-polarized nerve nets (Pantin and Vianna Dias, 1952; Horridge, 1954; Horridge, 1956a; Horridge, 1956b; Passano, 1965; Passano, 1973; Satterlie, 1979; Anderson and Schwab, 1981; Anderson and Schwab, 1982; Anderson, 1985). This raises interesting questions concerning radial coordination of motor output in situations in which asymmetric sensory input produces directed locomotory movements. In particular, the lack of cephalization raises the question of how a series of such pacemakers interact to produce asymmetric locomotory responses to move the animal towards or away from environmental stimuli.

Swim pacemakers in cubomedusae and scyphomedusae are restricted to a finite number of distinct marginal neural structures (rhopalia). Removal of all the rhopalia leaves the

medusa unable to produce spontaneous contractions of the swimming musculature (Romanes, 1876; Romanes, 1877; Pantin and Vianna Dias, 1952; Passano, 1965; Passano, 1973; Passano, 1982; Satterlie, 1979). Transmission of electrical information throughout the muscle sheet is *via* subumbrellar nerve nets, which use symmetrical or reciprocal chemical synapses (Anderson, 1985; Anderson and Schwab, 1981; Satterlie, 1979; Satterlie and Spencer, 1987; Westfall, 1987). Coordination of rhopalial pacemakers is presumed to be due to a simple dominance hierarchy in which a discharge in one pacemaker not only triggers a through-conducted contraction of the swim musculature but also resets all the other pacemakers (Horridge, 1959; Passano, 1965; Passano, 1973; Passano, 1982).

Cubomedusae and scyphomedusae are under a developmental constraint of tetramerous symmetry, so the rhopalia occur in multiples of four (see Hyman, 1940). Cubomedusae have four rhopalia, while scyphomedusae have at least eight, with some species having up to 64 rhopalia. The resultant pacemaker redundancy was examined in three modeling studies of scyphomedusan jellyfish in which contractile activity in a piece of jellyfish containing a single rhopalium was used to construct models of multiple-pacemaker networks (Horridge, 1959; Lerner et al., 1971; Murray, 1977). In all three models, pacemakers were

connected to one another with resetting linkages similar to those described in earlier works. These modeling studies uncovered several advantages of using multiple pacemaker networks. First, with an increase in the number of pacemakers, the overall rhythmic output of the swimming system became more regular (less variation in interpulse intervals). Second, as pacemaker number was increased, the overall frequency of swimming increased. Third, the sensitivity of the system to sensory inputs was increased with increasing pacemaker number provided that the inputs to the pacemakers were equal and symmetrical (Murray, 1977).

We have conducted a similar study on the cubomedusan jellyfish *Carybdea marsupialis*, but our results are inconsistent with a model in which pacemakers interact *via* simple resetting linkages, thus challenging the decades-old idea of how pacemakers interact in cubozoan and scyphozoan jellyfish. In our study, electrophysiological data were compared with both resetting and independent model networks of pacemakers, and the real data fell between those of the two models, suggesting that pacemakers do not show strict resetting influences on one another, but instead show a degree of independence. Our modeling studies show that this type of semi-independent network may allow a greater sensitivity to asymmetrical stimuli and, thus, allow significant directional responses to these stimuli.

Materials and methods

Specimens of the cubomedusan *Carybdea marsupialis* (Linnaeus, 1758) (identified as *C. rastonii* in earlier publications) were collected by divers from the Santa Barbara channel (California, USA) and kept in running seawater tanks. Intracellular recordings were made with 3 mol l⁻¹ KCl-filled glass micropipette electrodes (40–80 Ω) and standard direct current amplification. Recordings were conducted on single-quadrant preparations pinned down firmly with cactus spines (*Opuntia* sp.; Satterlie, 1979; Satterlie and Spencer, 1979). For whole-animal experiments, polyethylene suction electrodes (Ag/AgCl, tip diameters 100–300 μm) were used to record from the rhopalia, nerve ring or immediately adjacent subumbrellar tissue to monitor the impulse traffic in the swimming system. Differential alternating current amplification and display electronics were used, and the data were recorded on chart paper. The signal-to-noise ratio was improved by low-pass filtering (typically at 0.3–1 kHz). Animals were minimally restrained and exhibited swimming frequencies and regularities that were similar to those observed in unrestrained animals. Recordings were conducted in intact animals and during sequential excision of rhopalia. In all animals ($N=5$), swimming was permanently abolished when the fourth (final) rhopalium was removed. One animal was collected with one missing rhopalium (animal 4, see below), but otherwise appeared normal behaviorally and electrophysiologically. A minimum of 45 min was allowed between rhopalial excision and initiation of a recording session. All recordings were conducted in a darkened room,

and all movements of the investigator ceased during the period of data collection. The recording period involved the collection of data from between 600 and 1000 swim cycles. Interpulse intervals between successive swim system spikes were measured by hand and sorted into 250 ms bins. For each animal, interpulse interval (IPI) means, standard deviations (S.D.) and coefficients of variation ($CV=S.D./\text{mean IPI}$) of observed electrophysiological data were plotted for one, two, three and four rhopalia. Similarly, the network output characteristics of resetting and independent models were compared for each experimental animal.

Model networks were programmed on a digital computer using Igor Pro 3.0 (Wavemetrics Inc.). Each model network contained a number of individual relaxation oscillators running concurrently. Each oscillator was designed to fire an output pulse with a probability, P , that cycled from baseline to threshold with a constant slope. To add more realistic variability, random increments and decrements were added to P (first component of 'Gaussian noise'). In this model, when P reached threshold, a pacemaker impulse was generated. At threshold, the function was then reset to baseline with a refractory period that approximated the shortest interpulse intervals observed for the single-rhopalium experimental preparations. Another element of variance, a slight and random variation in the absolute baseline value, was added (second component of 'Gaussian noise'). All noise generators (a function of Igor Pro) were reseeded for each iteration and produced a Gaussian output. The threshold value and noise levels could then be chosen to optimize the match between the IPI distributions and standard deviations for the model oscillator and those of the single-rhopalium data of an experimental animal. For each experimental run, the model sampled between 750 and 1000 IPIs (the number of cycles between oscillator output pulses) and provided an appropriate IPI distribution. Each time the model was run for each set of characteristics, the IPI distribution was different; however, the means and standard deviations of the IPI distributions were the same. This meant that for a given set of characteristics, including noise, the model would produce consistency in the IPI distributions, even though the raw data would be unique in each run. Similarly, in electrophysiological experiments, successive runs from an individual animal yielded similar IPI distributions, but with unique raw data in each run.

To construct network models, individual pacemaker characteristics were chosen to produce IPI distributions whose means and standard deviations were within 5% of those recorded experimentally from the one-rhopalium cases of each of the experimental animals. The independent network model consisted of the pooled output of 2–10 pacemakers with identical IPI characteristics that were allowed to run simultaneously without interaction. Similarly, the resetting network consisted of the output of 2–10 identical pacemakers running simultaneously; however, when any pacemaker generated an output pulse, all other pacemakers were reset to their average baseline value, plus or minus the second component of baseline noise. Interpulse interval histograms

were generated for the network outputs of the 2–10 pacemakers and compared with corresponding data derived from electrophysiological recordings of experimental animals.

In experimental animals, two pacemakers sometimes produced near-simultaneous impulses, each of which initiated a conducted impulse in the subumbrella. When the two impulses met, they cancelled because of mutual refractoriness in the nerve net. When this occurred, an electrode in the subumbrella recorded the event as a single pacemaker impulse. In the models, similar subumbrellar cancellation of near-simultaneous impulses cannot occur, so it is likely that both models slightly overestimate the number of short inter-pulse intervals.

Results

Our electrophysiological data from *Carybdea marsupialis* are in agreement with several of the observations made in earlier modeling studies (Horridge, 1959; Lerner et al., 1971;

Murray, 1977). Interpulse interval distributions for single-rhopalium preparations had long tails, showing that individual pacemakers are noisy, with a great deal of IPI variation (i.e. large standard deviations; Fig. 1). Adding pacemakers to the network reduced both the mean IPI and the standard deviation, reflecting an increase in the rate and regularity of the swimming rhythm (Figs 1, 2).

For both resetting and independent model networks, adding pacemakers decreased mean IPIs and reduced variance (i.e. standard deviation). But comparison of the model network outputs with the electrophysiological data from *Carybdea marsupialis* showed that the independent model network better predicted the change in both mean IPI and standard deviation with pacemaker number (Fig. 2). The best way to distinguish between the two models is to compare the coefficient of variation of their distributions as a function of pacemaker number. In the independent model networks, the coefficient of variation increased slightly as a function of pacemaker number with up to four pacemakers; however, with more than four

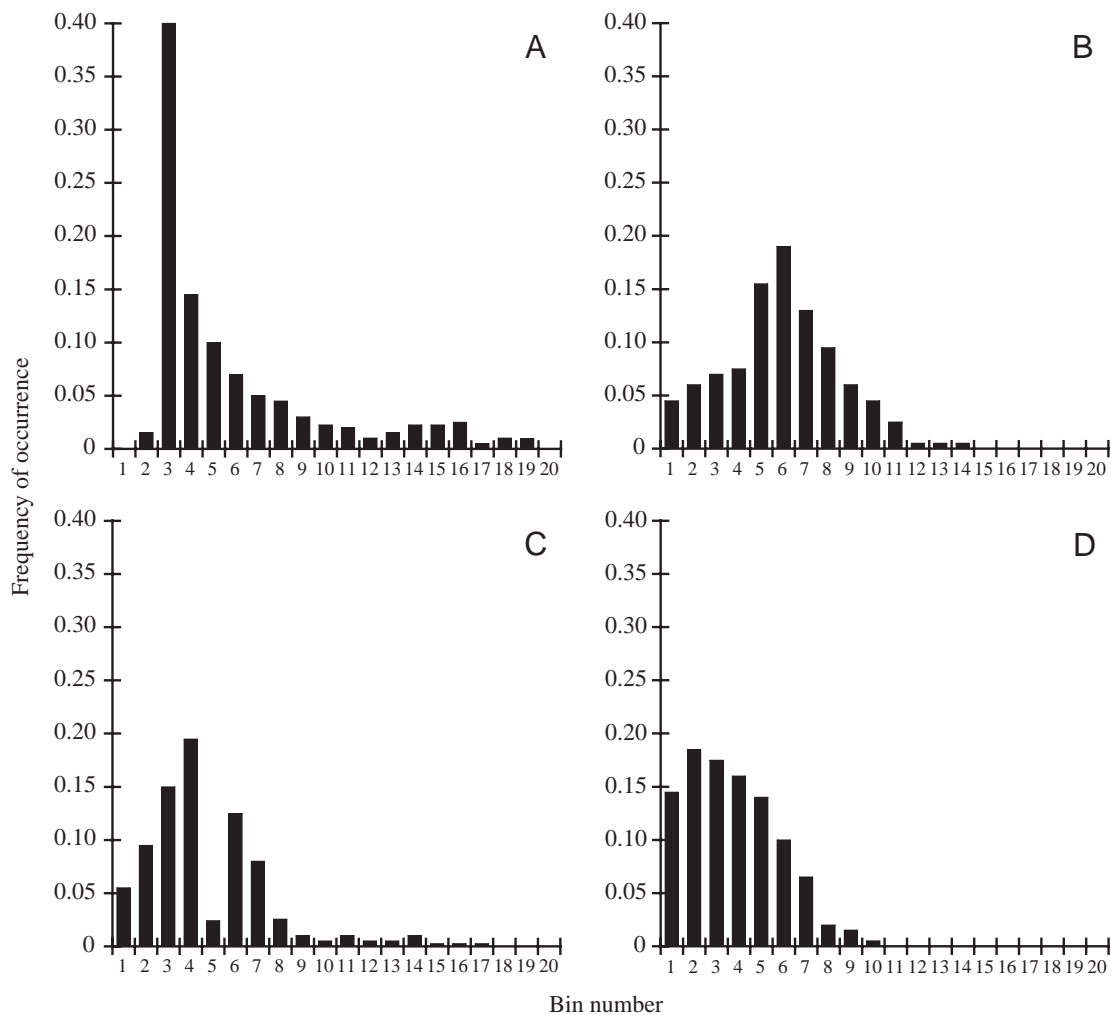


Fig. 1. Interpulse interval (IPI) data from experimental animal 2 for one- (A), two- (B), three- (C) and four- (D) pacemaker (rhopalia) conditions. The intervals were separated into 250 ms bins. Note that, with increasing pacemaker number, the distribution of inter-pulse intervals moves towards shorter intervals and narrows.

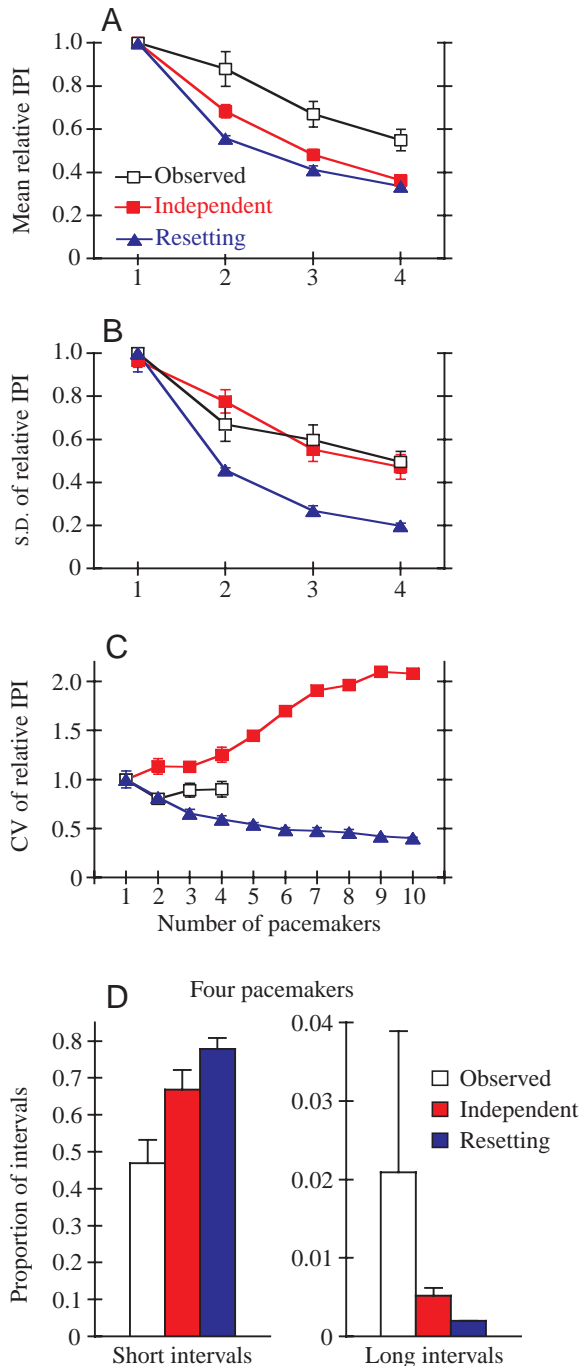


Fig. 2. Relationship between interpulse interval (IPI) (A), the standard deviation (S.D.) of the interpulse interval (B) and the coefficient of variation (CV) (C) and the number of pacemakers for observed data from experimental animals, a resetting network model and an independent network model. (D) A comparison of the proportion of short (<500 ms) and long (>2500 ms) intervals for the intact animals (observed) and the four-pacemaker models. For each model, the one-pacemaker data were adjusted to reflect the properties of one-pacemaker data from the five experimental animals. All data are normalized to the one-pacemaker cases. For coefficient of variation data, the models were extended to include 10 pacemakers. Values are presented as means \pm S.E.M.

pacemakers, the coefficient of variation increased to an asymptotic value twice that of individual pacemakers (Fig. 2C). In contrast, the coefficients of variation of resetting model networks decreased asymptotically to half that of the individual pacemakers.

With normalized data from the five experimental animals, the mean IPI plots for two, three and four pacemakers decreased less than that of the models, suggesting that, in intact animals, the increase in swimming rate was less than predicted by either model (Fig. 2A). Similarly, the variance (standard deviation) of experimental animals decreased less than predicted by the resetting model, suggesting that additional pacemakers increased their regularity less than originally predicted on the basis of the earlier work on scyphomedusae. The decrease in variance (standard deviation) of the independent model was similar to that observed in the experimental animals. A comparison of IPI distributions of the experimental animals with one *versus* four pacemakers showed that the latter contained relatively more short intervals and fewer long intervals (Table 1). In addition, the observed IPI distributions for the intact animals had a lower than expected proportion of short intervals and a larger than expected proportion of longer intervals (>2500 ms) in comparison with four-pacemaker model distributions (Fig. 2D). The combination of these two differences produced IPI distributions with larger than expected means for animals with four intact pacemakers compared with either model network (Fig. 2A).

In previous modeling studies, Murray (Murray, 1977) found that the addition of pacemakers with resetting linkages increased the sensitivity of the network to sensory inputs provided that the inputs were common (i.e. symmetrical) to all pacemakers. This seems counterintuitive for cubomedusae, since they have only four pacemakers, yet they have complex sensory structures that play significant modulatory roles in swimming. Our modeling of the experimental data suggests a resolution for this apparent anomaly. A comparison of coefficients of variation shows that the experimental data are intermediate between those of the two models (Figs 2, 3). This suggests that *Carybdea marsupialis* pacemakers do not interact *via* strict resetting linkages, but instead show some degree of independence. Furthermore, not all sensory inputs to the four rhopalia are either simultaneous or identical in strength. Asymmetric contractions of the subumbrella are important components of the behavioral repertoire of *Carybdea marsupialis*, allowing quick changes in direction in response to localized differences in sensory inputs to the four rhopalia.

The turning behavior of *Carybdea marsupialis* is due to asymmetric contractions in an annular flap of muscular tissue around the margin of the bell, termed a velarium, which creates a 'nozzle' effect, increasing the velocity of ejected water. The asymmetric contractions of the velarium result from enhanced contractions of the portion of the velarial circular muscle that forms the inside of the turn (Gladfelter, 1973). We found that asymmetric contractions of the subumbrella of *Carybdea marsupialis* follow 'double impulses' (80–250 ms apart) recorded in the rhopalial pacemaker region and subumbrella

Table 1. Comparison of one-pacemaker and intact (four-pacemaker) animals

Number of pacemakers	Proportion of short intervals	Proportion of long intervals	Mean of IPI distribution	s.d. of IPI distribution
One	0.100±0.039	0.216±0.082	1361.0±138.0 ms	852±156.1 ms
Four	0.469±0.063	0.021±0.018	767.5±66.8 ms	464.5±72.06 ms
One-tailed paired comparison	$P<0.0216^*$	$P<0.0337^*$	$P<0.004‡$	$P>0.016‡$

IPI, interpulse interval.
Short intervals, IPIs <500 ms; long intervals, IPIs >2500 ms.
Values are means ± s.e.m., $N=5$ animals.
*Wilcoxon signed-ranks test; ‡paired t -test.

(Fig. 4). The enhanced contractions of the swimming musculature are restricted to the quadrant initiating the double impulses. Our network models suggest that such double impulses would skew IPI distributions towards shorter mean IPIs. In contrast, inhibition of rhopalial pacemakers, as occurs with a shadow or a light-off stimulus, would serve both to increase the mean IPI and, together with double impulses, to increase the variance (standard deviation) of IPI distributions.

Discussion

Cubomedusae are probably best known for three characteristics. First, the sting of the tentacular nematocysts in some species is particularly virulent and, in some cases, is lethal to humans (Barnes, 1966). Second, they have a pair of lensed complex eyes on each rhopalium that rival in complexity the eyes of 'higher' animals (Berger, 1910; Hartwick, 1991). A great deal of attention has been paid to cubomedusan visual abilities, most centering on behavioral reactions to visual stimuli or the physical properties of the lens and retina of the complex eyes. For example, the complex eyes resemble the camera-lensed eyes of vertebrates and cephalopods (Land, 1990; Nilsson, 1990). Dark-adapted

cubomedusae swim towards a dim light and can distinguish between light and dark objects from a distance of up to 50 cm when the objects are as small as 1 cm wide (Hamner et al., 1995; Matsumoto, 1995). Third, cubomedusae are extremely agile swimmers, capable of changing swimming direction in only a few swimming contractions. The ability of cubomedusae to change direction rapidly in response to directional sensory input is of particular interest because of the radial arrangement of the multiple swim pacemakers and the relative simplicity of the neuromuscular system.

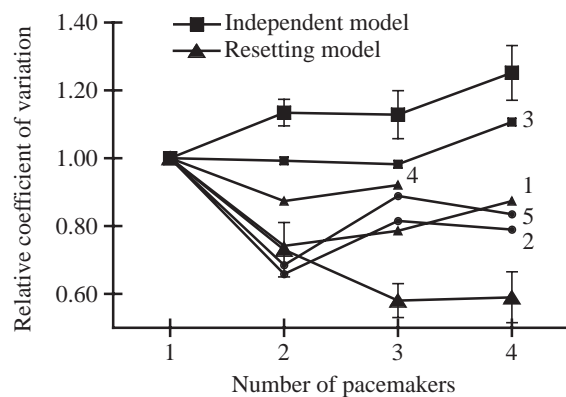


Fig. 3. Coefficient of variation (mean/standard deviation) for each experimental animal (indicated by the number next to the trace) and for the independent and resetting models. Animal 4 had only three rhopalia when collected. Note that, in the four-rhopalium cases, the values for all the experimental animals fall between the values for the two models.

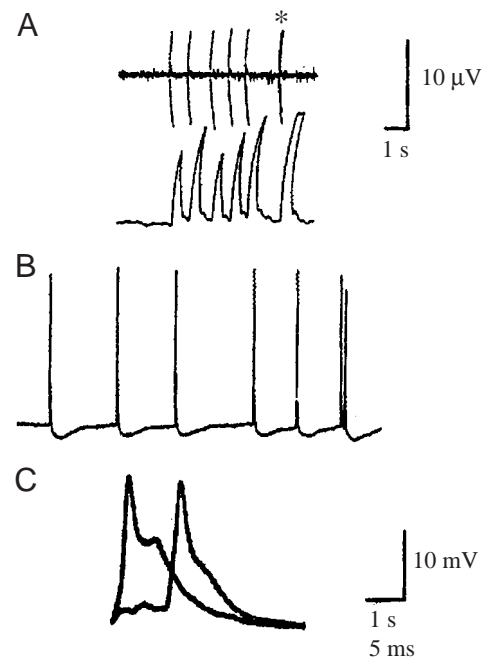


Fig. 4. (A) Extracellular recordings from a rhopalium (top trace) and a force transducer recording of subumbrellar contractions (bottom trace). The last rhopalial impulse is a 'double impulse', producing an extremely large, asymmetric contraction of the recorded quadrant. The contractile force in this last contraction exceeded the pen travel, so the peak is clipped. (B) Intracellular recording of action potentials in a subumbrellar motoneuron. An action potential doublet occurs at the end of the recording, and this has the same temporal characteristics as the 'double impulses' recorded with extracellular electrodes. (C) Superimposed traces of the two action potentials from a 'double impulse'. In such doublets, the second action potential always arises from a complex synaptic potential.

Our electrophysiological/modeling data on *Carybdea marsupialis* are in agreement with those of Horridge (Horridge, 1954), Lerner et al. (Lerner et al., 1971) and Murray (Murray, 1977), suggesting that multiple pacemakers increase both the overall swimming frequency and the regularity of swimming contractions. Since the contractile output of scyphomedusan and cubomedusan swimming musculature is heavily dependent upon frequency-dependent neuromuscular facilitation, regulation of a stable pacemaker output would be beneficial to efficient forward propulsion. Electrophysiological evidence from *Carybdea marsupialis* subumbrellar recordings indicate that the amplitude of extracellularly recorded muscle spikes varies with the interpulse intervals of swimming contractions in a predictable manner that is consistent with neuromuscular facilitation described for scyphomedusae (Bullock, 1943; Satterlie, 1979). The 'facilitation curve' derived from these data suggests that maximal spikes (muscle contractions) occur with IPIs of approximately 0.5 s and shorter. Furthermore, with IPIs that are equivalent to average swimming rates in unrestrained animals, the size of muscle spikes is approximately 80% of maximum (Satterlie, 1979). This suggests that a biphasic modulatory potential exists in the swim system, allowing enhanced contractions through a shortening of IPIs as well as a decrease in contractile strength through a lengthening of IPIs. The maintenance of this biphasic modulatory potential would be most critical for producing directional responses to asymmetrical stimuli. For example, turning behavior in *Carybdea marsupialis* is accomplished through localized enhanced contractions of the region of the velarium that forms the inside of the turn (Gladfelter, 1973). The asymmetrical velarial contraction directs the ejected water jet to that side, effectively propelling the animal into the turn.

So, why do cubomedusae have only four pacemakers? Localized responses to asymmetrical sensory inputs are important for the control of swimming in cubomedusae. Network properties, such as resetting linkages, that tend to limit deviations of the swimming rhythm from an average IPI by restraining variation could restrict the flexibility needed by a rapidly swimming predator such as *Carybdea marsupialis*. For example, while a purely resetting network would reduce the variance and produce more regularity in the swimming rhythm as the number of pacemakers was increased, it would do this at the expense of flexibility by selectively preventing (filtering out) longer IPIs. Furthermore, the IPI distribution would shift to shorter mean values, thus driving the facilitation level of the musculature towards maximal values and decreasing the potential for facilitation-based enhancement of contractile activity. Conversely, in a purely independent network, the coefficient of variation would increase with the addition of pacemakers. This could, in extreme cases, allow too much variation in bell contractions, which could be mechanically unfavorable for efficient forward locomotion. Moreover, in a large network of independent pacemakers, output would produce greater variation around shorter IPIs, creating a problem similar to that seen with the resetting network. Extending the independent model to include up to 10

pacemakers is instructive in this regard. The rise in the coefficient of variation is shallow for up to four pacemakers, but shows a steeper rise with four or more pacemakers (Fig. 2C).

In a semi-independent network, incoming impulses from an active pacemaker could have a significant resetting influence on all other pacemakers, although this input would not be absolute. Rather, it would be subject to modulation by a variety of external or internal inputs, conferring a semi-independence to the pacemaker linkage. Under this scheme, the overall system could act as a resetting network under some conditions and as an independent network at other times. Thus, asymmetric inputs could temporarily free one or more pacemakers from the resetting influence of the other pacemakers.

The hybrid network of *Carybdea marsupialis*, with a small number of semi-independently linked pacemakers, provides an effective compromise of reduced variance, but adequate flexibility. The use of multiple pacemakers produces an overall increase in contraction rate and regularity (shorter IPIs and smaller standard deviations); however, the hybrid network places limits on both. This is desirable since a significant increase in the contraction rate of the bell would bring the mean IPI close to the facilitatory limits of the swimming system and thus decrease the potential for biphasic modulation of swimming frequency and muscle contractility. Limiting the number of pacemakers preserves this biphasic modulatory potential with regard to swimming rate and specifically permits facilitation-based increases in contractile strength such as those seen during turning. The presence of four pacemakers in cubomedusae, as well as their semi-independent coupling, allows significant modulation of swimming by complex sensory systems and fast directionally accurate behavioral responses in a radially arranged, non-cephalized nervous system. Functionally, one could view the reduction in pacemaker number, and the resulting increase in responsiveness to asymmetrical stimuli, as a form of condensation of neural networks, analogous to cephalization in bilateral animals.

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