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TRANSIENT RHYTHMS IN THE SWIMMING ACTIVITY OF *SARSIA TUBULOSA* (HYDROZOA)

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SUMMARY

Maximum entropy spectral analysis (MESA) was used to assess the contribution of endogenous rhythms to the timing of swim bouts in a hydrozoan jellyfish, *Sarsia tubulosa* M. Sars. The results show that the high degree of variability in *Sarsia* swimming activity is due largely to the number of rhythms which may contribute to the behaviour and to the transient nature of these rhythms. I conclude that the ability to 'choose' among behavioural rhythms may be a widespread behavioural mechanism in cnidarians and I suggest that, in *Sarsia*, these transient behavioural rhythms may originate in activity of the marginal pacemaker system.

INTRODUCTION

The goal of much of behavioural physiology is to explain how animal behaviour is organized. There have been two major avenues of approach to the problem. One is to obtain precise quantitative descriptions of the occurrence of the behaviour in time and then to attempt to formulate 'soft-ware explanations' of animal behaviour (Dawkins, 1976). The alternative is to obtain 'hard-ware' or neuronal explanations of animal behaviour by means of studies of the structure and function of the neural pathways involved in particular behaviours. Recently the field of neuroethology has attempted to combine these two approaches. The current study relates new findings from a quantitative study of the occurrence of swimming behaviour in a hydrozoan jellyfish (*Sarsia tubulosa*) to the results of earlier neurophysiological studies. Testable hypotheses about the nervous system and feeding behaviour of this and other hydromedusae are then developed from this synthesis.

Sarsia tubulosa is a marine hydrozoan with a circumboreal distribution. It has both a colonial hydroid and a sexual medusa stage in its life-history. *Sarsia* medusae grow to a maximum bell height of 1 cm and are abundant in the spring and early summer plankton in inshore waters of the North Pacific. They have separate sexes and release their gametes directly into the water. *Sarsia* are usually buoyant and they are able to adjust their density to become buoyant in a dilute medium (Leonard, 1980*a*).

During the day, *Sarsia* float motionlessly with extended tentacles and manubria.

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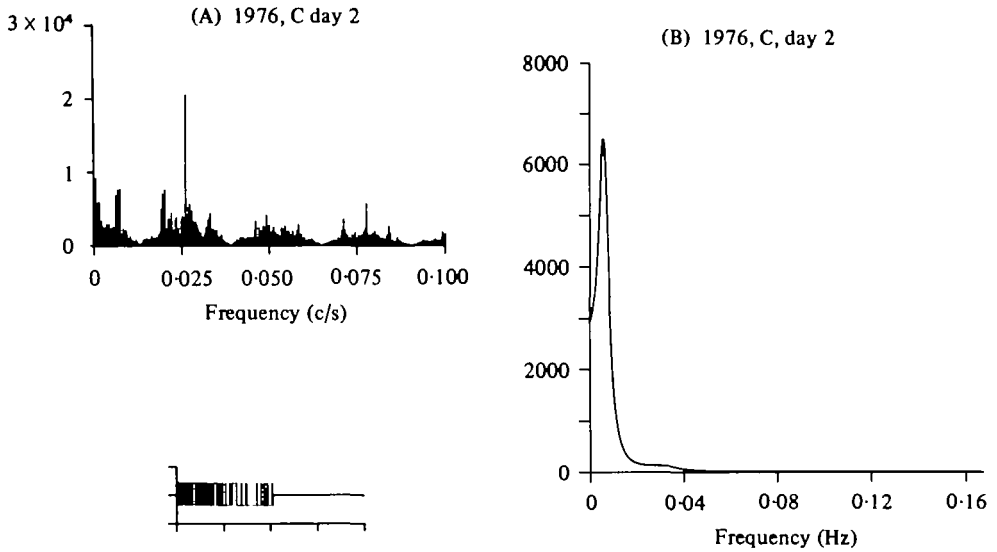

Fig. 1. (A) FFT spectrogram of chunk 1 of the activity record of animal C on the second day of observation. The mean has been removed and the ordinate is the square root of the power spectrum. The abscissa has been truncated at 0·1 Hz. The spectrogram indicates a single rhythm with a frequency of 0·012–0·037 Hz. The other sets of peaks are harmonics. (B) MESA spectrogram of the same chunk of data plotted as in Fig. 1. The chunk was truncated at 4000 samples after decimation. The MESA spectrogram shows a strong rhythm, precisely located at 0·007 Hz, a substantial amount of trend (0 Hz) and a very small peak near 0·035 Hz.

They are 'sit-and-wait' (Schoener, 1969) or 'ambush' predators (Gerritsen & Stickler, 1977) and feed on 'any small animals of appropriate size that happen to come into contact with the tentacles' (Hyman, 1940, p. 448). The prey transfer behaviour of *Sarsia* has been described by Hernandez-Nicaise & Passano (1967). Motionless 'fishing' is interrupted by periods of swimming by means of a series of bell contractions (swim bouts).

Bouts of swimming contractions in *Sarsia* may be elicited by such stimuli as illumination (Passano, 1973), touch, or they may occur spontaneously. Spontaneous activity is common in coelenterates and there is good evidence to indicate that it is generated at least in part by endogenous pacemakers (Josephson, 1974). Such activity may or may not show an obvious rhythm (in the sense of Broom, 1980).

Swim bouts in *Sarsia* occur at very irregular intervals even in aquaria (Leonard, 1978; Romanes, 1877). As part of an analysis of the organization of swimming activity in *Sarsia* (Leonard, 1980*b*, *c*), I reported that several factors contribute to the variability of the timing of swim bouts. First, the length of a swim bout is important in determining when subsequent swim bouts will start, in all but very active animals. Secondly, individual *Sarsia* show strongly idiosyncratic patterns in spectrograms derived from Fast Fourier Transforms (FFT). This implies each individual uses a particular set of frequencies in its swimming behaviour. Thirdly, the FFT spectra showed a clear rhythm in the swimming activity of some (7/23) animals. A problem with the FFT spectrograms used in the previous study was that the bulk of the power spectrum, in all cases, was concentrated at low frequencies. It was not possible to determine whether the concentrations of peaks at low frequencies were due to a trend in the data or to rhythms with very long periods (Leonard, 1980*b*).

In the current study, the contribution of rhythms to the temporal organization of bouts of swimming was examined further. Maximum entropy spectral analysis (MESA) (Childers, 1978) was used to provide better resolution of rhythms for a given length of data than had the FFT (Fig. 1). Fourier analysis by MESA is mathematically equivalent to using maximum-likelihood criteria to fit an nth order Markov process to the data (van den Bos, 1971). An nth order Markov process exists where the value of a parameter at point X in a series of discrete events determines the value of the parameter at point $X+n$. The results of the MESA analysis show that the very variable timing of spontaneous swim bouts in *Sarsia* medusae (Romanes, 1877; Leonard, 1978, 1980*b*) is largely a result of the wide variety of rhythms that can occur in the behaviour and of the animals' ability to change from one rhythm to another.

MATERIALS AND METHODS

The data used in this study were obtained from observations made at Friday Harbor Laboratories, Friday Harbor, Washington, during 1976 and 1977. An analysis of the serial organization (the extent to which the duration of an event predicts the durations of past or future events) and a preliminary analysis of the temporal organization (the regularity with which events occur in time) of swimming bouts in *Sarsia* derived from these observations were reported elsewhere (Leonard, 1980*b*).

Individual animals in aquaria were observed over 6 h observation periods using a time-lapse videotape system. Since confinement to small aquaria is known to increase the swimming activity of *Sarsia* medusae (Leonard, 1980*c*), observations were made in the largest chamber within which the animal could be kept in focus (Leonard, 1980*b*). Details of the methods used to obtain and hold animals have appeared elsewhere (Leonard, 1980*a*). A description of the way in which observations were made and data recorded was published with the analysis of serial organization (Leonard, 1980*b*) along with definitions of the behavioural categories used. Activity records from a total of 33 animals were used in this study. An activity record is a plot of the occurrence of swim bouts and pauses during an observation period (fig. 1 in Leonard, 1980*b*). The activity record is binary with swimming represented by a '1' and not-swimming represented by a '0' in the data. In most cases, an activity record was broken into a series of 'chunks'. A 'chunk' is a section of an activity record during which the animal was continuously under observation.

The original sampling rate was 3·3 samples/s. Many of the 'chunks' used in the original analysis contained more than 60000 samples (time points) (Leonard, 1980*b*). In order to increase the ease of computation of MESA spectra, the data in each chunk were decimated. Every tenth sample (point) in the chunk was retained for use in computing a MESA spectrogram. The other points (9 out of 10) were discarded. Since pause and swim-bout durations were always more than 10 samples (3·03 s) long, no behavioural events were lost by decimating the data. Only chunks which were at least 200 samples long after decimation and included at least 20 transitions between swimming and non-swimming were included. Twenty transitions were required because of the possibility of spurious rhythms appearing in MESA spectra in cases where the signal (data record) is very simple (Radoski, Zawalick & Fougere, 1976). The subroutines used to compute the MESA spectra, PRDFLT and MESA,

were written for use on small computers by the author and Bruce D. Karsh of the Geophysics and Polar Research Center, University of Wisconsin – Madison, based on algorithms by Andersen (1974). PRDFLT uses Akaike's information criterion (Akaike, 1974; Tong, 1975) to determine the order of the Markov process used in computing the MESA spectrum. The length of the Markov process is limited to half the length of the data to avoid possible spectral instability (Ulrych & Bishop, 1975; Radoski *et al.* 1976). The MESA subroutine computes the spectrum. Copies of these subroutines are available from the author on request. Because of the memory limitations of the computer used for this work, a maximum of 4000 samples could be analysed as one chunk. In cases where a chunk contained more than 4000 samples after decimation, the first 4000 samples were treated as one chunk, and the remaining samples were treated as a second chunk. In some cases, chunks were divided into halves or quarters for further analysis and spectrograms were calculated for each part. This was done by changing the upper limit (4000 samples) on chunk size to a lower value. For each MESA spectrogram, a time-plot of the data in that chunk was made. For the purposes of this descriptive study, any peak, visible in a MESA spectrogram was considered to represent a behavioural rhythm. A peak which is so small as to seem insignificant in one spectrogram may be an important feature of the animal's behaviour at a different time (compare Fig. 3*b–d* and Fig. 4*a–d*).

While this study represents the first application of MESA to behavioural data, there is an extensive body of recent literature on the technique. General discussions of the technique are found in Burg (1967, 1978) and Ables (1974). Childers (1978) provides a handy compilation of important papers on this and other new methods of spectral analysis. The underlying principles of MESA have been reviewed by Ulrych & Bishop (1975). Radoski *et al.* (1976) compared MESA's performance in describing geophysical data to that of a variety of other techniques for spectral analysis.

RESULTS

There are three striking features of the MESA spectrograms. The first is the large number of animals and records that show rhythms (Table 1). Rhythms are detectable in half (48/98) of the MESA spectrograms. Most (28/33) individuals show rhythms in at least one spectrum. The second striking feature of the MESA spectrograms is the presence of more than one rhythm in many spectrograms (Table 1, Examples Fig. 2, 3*a*, *b* and *c* and 4*b* and *d*). Multiple rhythms are present in 28% (27/98) of the MESA spectrograms and they are found in records from 64% (27/33) of the individuals. Multiple rhythms are an important source of the variability so characteristic of the swimming activity of *Sarsia* (Romanes, 1877; Leonard, 1978, 1980*b*) since they explain almost all of the variance in some records (Figs. 2, 3*a*). Thirdly the rhythms detected are transient, in at least some cases. Dividing a given chunk of data into halves or quarters, and plotting a MESA spectrogram for each part shows that a rhythm or a set of rhythms that appear in the spectrograms of the whole chunk may not be present in the spectrograms of some parts of the chunk (examples, Figs. 3*b*, *c*, *d*; 4*a–d*). Features that are not apparent in the spectrogram of the whole chunk may show up in spectrograms of smaller parts of the chunk. For example, Fig. 4 shows that the small peak present in the spectrogram of the whole chunk (4*a*) repre-

Table 1. *Summary of MESA spectrograms*

Individuals	
No rhythms detectable in any record	5
Single but not multiple rhythms detectable	7
Multiple rhythms detectable	21
	$N = 33$
Chunks	
No rhythms detectable	50
A single rhythm detectable	21
Multiple rhythms detectable	27
	$N = 98$

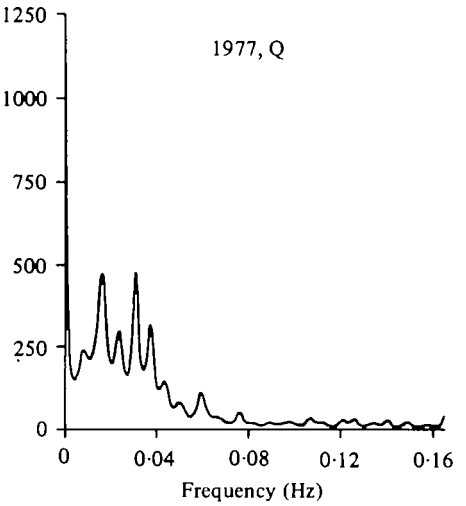

Fig. 2. MESA spectrogram of chunk 11 of the activity record of animal Q in the 1977 observations. The area under the curve equals the variance of the data. The ordinate is the power spectrum.

sents a strong rhythm present only in the first 25 min of the whole (100 min) chunk. Small peaks which do not appear in the spectrogram of the whole chunk, are detectable in the first 25 min of the chunk (Fig. 4*d*). Since a reduction in the length of data used to calculate a spectrogram, results in a loss of resolution of peaks, one would expect the disappearance but not the appearance of peaks to be an artefact of truncation of the data.

The transient nature of the rhythms found in *Sarsia's* swimming behaviour makes the results of the serial correlation analysis in the previous study (Leonard, 1980*b*) less perplexing. In that study, serial autocorrelograms of swim bout durations, interonset intervals, and pause durations often showed patterns, but the patterns varied from animal to animal, and from day to day for the same animal. In many cases the patterns seemed very complex (examples in table 2 of Leonard, 1980*b*). If there is a regular rhythm in the swimming behaviour, there should be a regular pattern in the serial autocorrelograms for swim-bout duration or interonset intervals, since the swim bout durations determine when subsequent swim bouts will start. However, if the rhythm is only present for part of the record or more than one rhythm

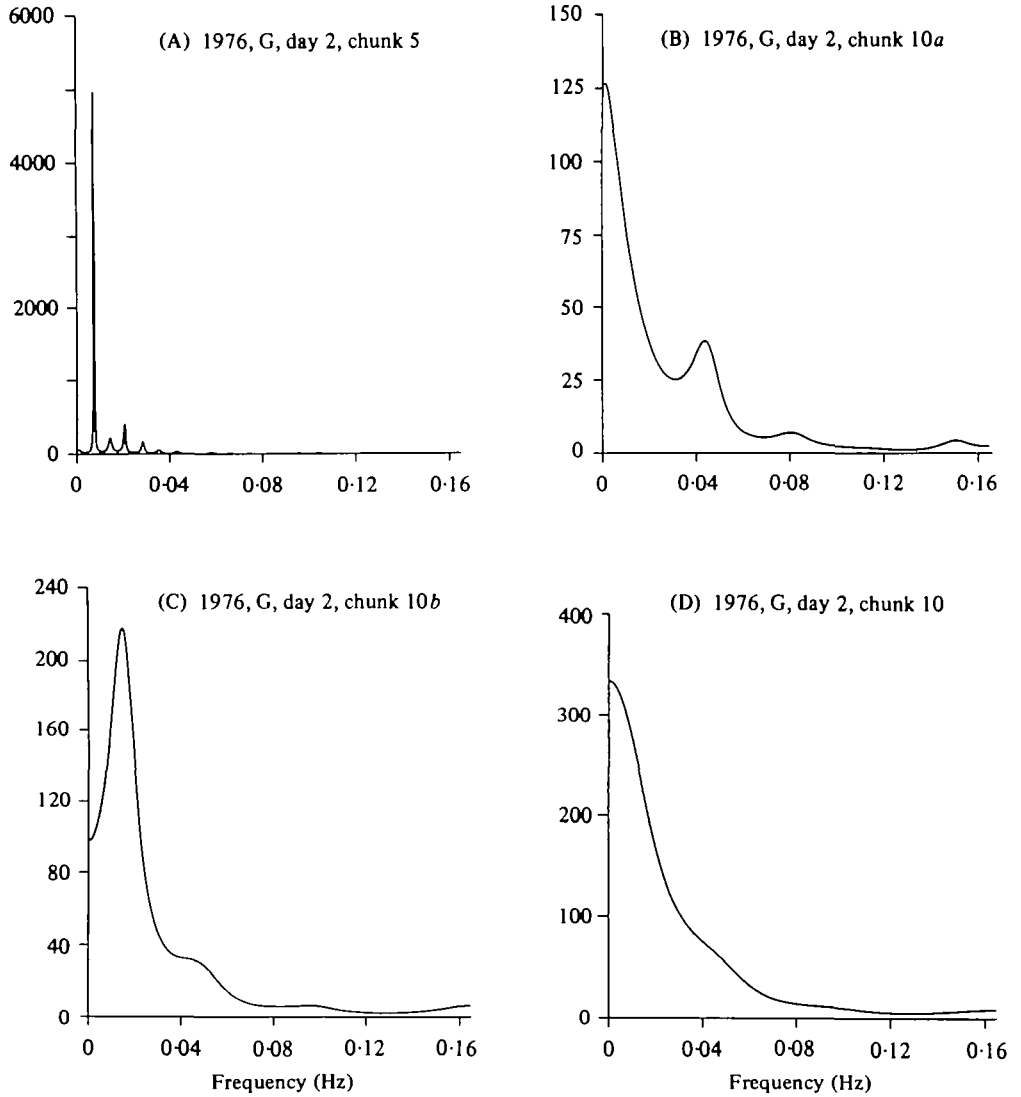

Fig. 3. (A) MESA spectrogram of the first 500 samples after decimation of chunk 5 of the activity record of animal G on the second day of observation, plotted as in Fig. 1. (B) MESA spectrogram of the first 500 samples after decimation of chunk 10 in the same activity record, plotted as in Fig. 1. (C) MESA spectrogram of the remaining 679 samples (after decimation) of chunk 10, plotted as in Fig. 1. (D) MESA spectrogram of the entire chunk 10, plotted as in Fig. 1.

is present during the record, the serial autocorrelograms will be more complicated. Swim-bout durations will change abruptly as rhythms appear and disappear, since the swim-bout durations are related to the periods of the rhythms. This could explain the very complex serial autocorrelograms seen in the previous study (Leonard, 1980*b*).

I have not been able to determine whether or not spectrograms contain multiple rhythms because of a succession of rhythms over time or the simultaneous presence of a number of different rhythms. In some cases a rhythm appears suddenly, such as

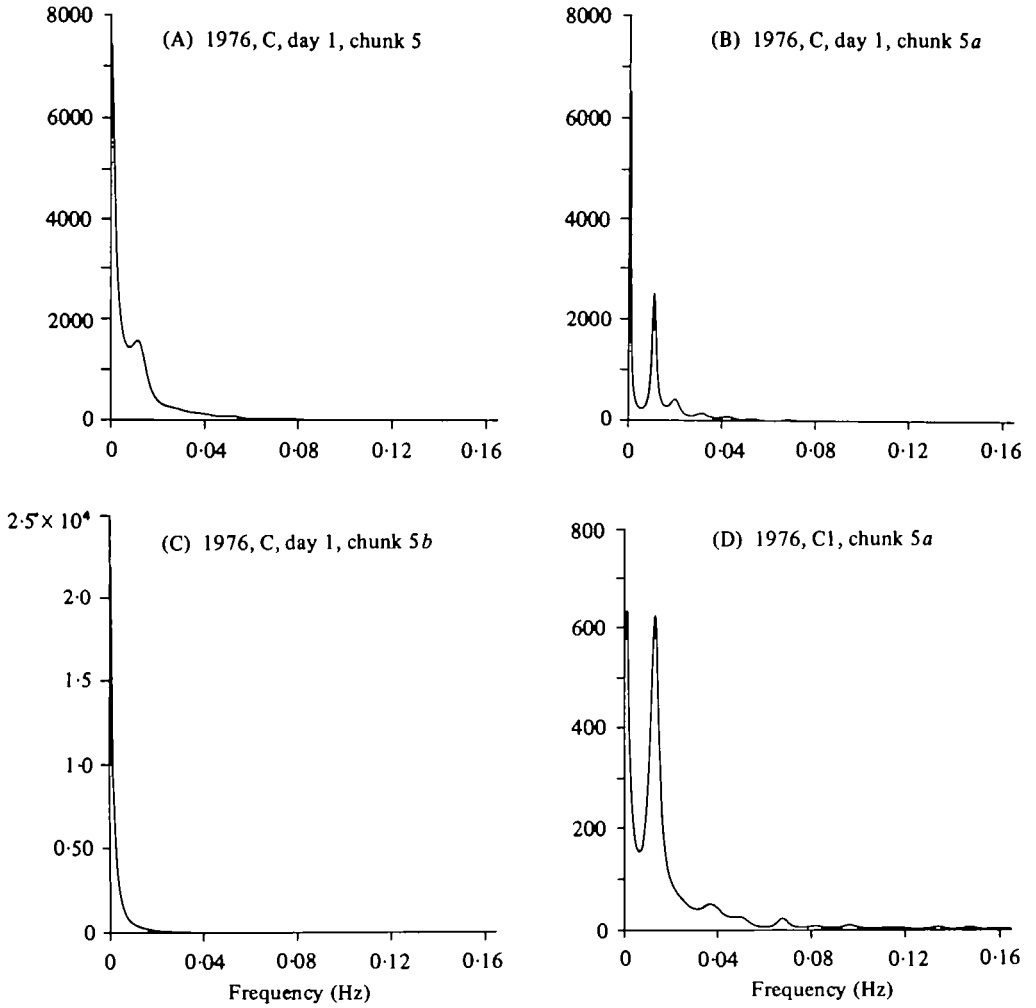

Fig. 4. (A) MESA spectrogram of chunk 5 of the activity record of animal C on the first day of observation, plotted as in Fig. 1. (B) MESA spectrogram of the first half (1000 points after decimation) of chunk 5, plotted as in Fig. 1. (C) MESA spectrogram of the second half (955 points after decimation) of chunk 5, plotted as in Fig. 1. (D) MESA spectrogram of the first quarter of chunk 5 (the first 500 points of B above), plotted as in Fig. 1.

the main peak in Fig. 3(*c*). In other cases, a whole pattern seems to appear at once. Since subdividing chunks leads to a loss of resolution in the spectrograms, it is impossible to determine with MESA whether multiple rhythms occur successively or simultaneously. It may be that all the same rhythms are present, but they cannot all be detected in such a short record. Another approach is necessary to determine whether or not rhythms can occur simultaneously and how swimming activity is organized in the remaining spectrograms; i.e. those that do not show rhythms (50/98).

The previous study also showed that although the relative heights of peaks might change from record to record, the overall shape of the spectrogram was characteristic of the individual animal (Leonard, 1980*b*). MESA spectrograms do not reflect this;

probably because of the loss of detail in the MESA spectra. For a given data chunk, one-tenth as many sine waves were used to match the data for the MESA spectra as were used for the FFT spectra (due to decimation of the data (see Materials and Methods)). The idiosyncratic nature of the FFT spectrograms implies each animal uses a characteristic, endogenous set of frequencies in its swimming behaviour.

DISCUSSION

The results of this study offer an important insight into the organization of cnidarian behaviour and, perhaps, into the function of cnidarian pacemaker systems. Spontaneous, repetitive movements that occur with variable regularity in time, such as the swim bouts of *Sarsia*, are characteristic of cnidarian behaviour. For example, Taddei-Ferretti & Cordella (1976) observed that spontaneous column contractions in *Hydra attenuata* can occur with a regular rhythm or be apparently arrhythmic. Batham & Pantin (1950), working with the sea anemone *Metridium senile*, found that the spontaneous column activity of an individual animal was sometimes rhythmic and sometimes arrhythmic. More recently, cycles of swimming activity that may or may not be rhythmic have been described for another hydromedusa, *Aglantha digitale* (Mackie, 1980). The results of the present study, which show that the very variable timing of spontaneous swim bouts in *Sarsia* medusae (Romanes, 1877; Leonard, 1978, 1980*b*) is largely due to the wide variety of rhythms which can occur in the behaviour and the animal's ability to change from one activity rhythm to another, may reveal a general feature of the organization of the behaviour of cnidarians. 'Choosing' from among a set of available activity rhythms may allow these 'nervously lowly' animals (Bullock & Horridge, 1965) to respond behaviourally to changes in environmental and physiological conditions. What is the physiological basis of this behavioural mechanism?

Physiological basis of swimming rhythms

The swimming rhythms of *Sarsia* probably originate in the activity of endogenous pacemakers. Pacemakers in coelenterates typically occur as multiple potential pacemakers, which are functionally similar. These potential pacemakers are then co-ordinated by a common conducting system to form a pacemaker system (Josephson, 1974). *Sarsia* has two such pacemaker systems involved in swimming; the marginal pacemaker (MP) system and the swim pacemaker (SP or PSP) system (Passano, 1965, 1973, 1976). Anderson & Mackie (1977) found that all members of a population of large neurones in the inner nerve ring of another anthomedusan, *Polyorchis*, were potential swim pacemakers. Two of the questions which need to be answered in order to understand the way in which *Sarsia*'s pacemaker systems coordinate swimming are: what is the function of pacemaker redundancy? and what is the function of each of the two pacemaker systems?

Neurophysiological evidence suggests that the PSP system in *Sarsia* acts only to determine the timing of individual swimming contraction within a swim bout (Passano, 1973). A similar swim pacemaker or pre-swim-pulse system has been found in a number of hydromedusae (Mackie, 1975; Ohtsu & Yoshida, 1973; Passano, 1965, 1976; Spencer, 1975). These studies also found systems similar to *Sarsia's* (MP)

system. The MP system apparently has no parallel in the scyphomedusae (Passano, 1973).

The output of *Sarsia's* MP system is 'cryptic', in that activity in the MP system may have no obvious behavioural correlates (Passano, 1965, 1973). Spencer (1971) suggested for a limnomedusan, *Proboscidactyla*, that the MP system may determine the timing of bouts of swimming contractions. The need for a mechanism to generate bursts of contractions, as opposed to single contractions, was also recognized for the hydroid *Tubularia* by Josephson (1962). In *Sarsia*, the MP system may act to generate bouts of swimming by turning the PSP system on and off. The PSP system then activates the swimming musculature. The MP system is clearly also involved in behaviour other than swimming (Passano, 1965, 1973).

What function could multiple potential marginal pacemakers serve in such a system? The classical explanation for pacemaker redundancy is that of Horridge (1959), who suggested, on the basis of his studies of *Aurelia*, a scyphomedusan, that pacemaker redundancy serves to increase the regularity of the rhythm. Horridge's explanation would adequately explain the multiplicity of pacemakers in the PSP system but not in the MP system in *Sarsia*. In *Sarsia*, the timing of individual swim contractions within a swim bout is mediated by the SP system (Passano, 1973) and is very regular (Romanes, 1877). This regularity may serve to prevent the bell from completely relaxing after each contraction within a swim bout and thus increase swimming efficiency (Donaldson, Mackie & Roberts, 1980; T. L. Daniel, pers. comm.).

It seems unlikely that pacemaker redundancy in the MP system, which according to Spencer's model generates bouts of swimming, functions to increase the regularity of the occurrence of swim bouts, because the occurrence of swim bouts is so variable (Romanes, 1877; Leonard, 1978, 1980*b*). Passano (1976) emphasized that the generation of variability *per se* is a basic feature of *Sarsia's* 'brain'. Surely this variability must have some function. The results of the current study indicate that the function of the variability is to generate multiple, transient rhythms of swimming activity. This leads to two more questions: how does *Sarsia's* 'brain' generate transient rhythms? and what is the biological function of transient behavioural rhythms?

A model for the generation of transient rhythms

Lerner *et al.* (1971) observed that individual pacemaker ganglia of a scyphomedusa (*Aurelia*) have different patterns of output. The idiosyncratic nature of the FFT spectrograms of *Sarsia* swimming activity (Leonard, 1980*b*) suggests that each animal has a marginal pacemaker system which generates swimming activity with a unique set of frequencies. These sets of frequencies may reflect individual differences in potential marginal pacemakers. Lerner *et al.* (1971) also suggested that the redundancy of pacemakers in *Aurelia* may allow the animal to respond to local stimuli with a change in the swimming rhythm of the whole animal. A variety of factors influence the pacemakers of medusae (Bullock & Horridge, 1965; Josephson, 1974). Anderson & Mackie (1977) demonstrated that the individual potential swim pacemakers in *Polyorchis* become actual swim pacemakers when they are stimulated by light. The marginal pacemaker system in *Sarsia* is influenced by such factors as light and input from other parts of the nervous system (Passano, 1973).

In *Sarsia*, stimuli or neural input to a local area (one tentacle bulb or part of one tentacle bulb) might cause synchronization of the marginal pacemakers in that area. That is, a number of marginal pacemakers would start firing at once. Synchronization could create an overall rhythm of activity in the MP system which would then activate the PSP system rhythmically, generating a rhythm in the occurrence of swim bouts. If marginal pacemakers differ even slightly in their firing patterns, the MP system rhythm would have a frequency which was either the average of the frequencies of the pacemakers involved or the product of the frequencies. If a large number of pacemakers are synchronized, the resultant behavioural rhythm will have a frequency equal to the average of the frequencies present in the synchronized population. If a small number of rhythms are involved, the frequency of the resultant behavioural rhythm may be the product of the individual pacemaker frequencies. This would explain the generation of slow rhythms by a system of pacemakers all of which have relatively fast rhythms. For example, if pacemaker A fires every 5 s, and pacemaker B fires every 6 s, they will fire simultaneously every 30 s, once they have been synchronized. If the simultaneous firing of two pacemakers were necessary and sufficient for a behavioural response, synchronization of the pacemakers would create a behavioural rhythm with a frequency of 1/30 Hz (period = 30 s). A change in the number or identity of pacemakers which were involved in the synchronization could change the frequency of the resultant behavioural rhythm, whether the rhythm represents the average or the product of the rhythms of the pacemakers.

If each marginal pacemaker has some variability in its firing rhythm, pacemakers that have been synchronized will gradually drift out of phase with one another and the resultant behavioural rhythm will change or disappear. This might explain transience in behavioural rhythms. A change in the input to the site of the synchronization could change the behavioural rhythm abruptly. Synchronization of a different part of the MP system might change the rhythm or add on a second rhythm. Mackie (1975) found that stimulation of the TP system in *Stomotoca* (analogous to the MP system in *Sarsia*) at rates faster than its usual rhythm sometimes resulted in long periods of quiesence.

The behaviour of the animal may also be changed by factors which affect the PSP system directly. Mackie (1975) described feedback inhibition of the PSP system in *Stomotoca* by the swimming contractions themselves. Anderson and Mackie (1977) described changes in the membrane potential of the potential PSP pacemakers in *Polyorchis* as a result of illumination. Passano (1973) described a variety of environmental and physiological influences on *Sarsia's* PSP system. Since the influence of the MP system on the PSP system is one-way (Passano, 1978), direct effects on the PSP system would cause changes in behaviour but not changes in the activity of the MP system.

The model presented above suggests that the marginal pacemaker system in *Sarsia* behaves in a manner analogous to that of the system of coupled electronic relaxation oscillators analysed by Gollub, Brunner & Danly (1978). They found that changes in the nature of the coupling of the oscillators resulted in the system showing a variety of complex periodic or non-periodic states. An alternative to the model which I have presented would be an extension of Horridge's (1959; Bullock & Horridge, 1965) idea that the rhythm of a pacemaker system is set by the rhythm of the fastest individu

pacemaker. That is, local stimulation of, or physiological input to, part of the MP system may act to create or change the behavioural rhythm, in that pacemakers in that area begin to fire and the fastest one sets a rhythm for the whole MP system which then generates the behavioural rhythm. The first model better explains why variability is important to the system. In order to distinguish between these two models, one must first know the frequencies of individual marginal pacemakers. If the MP pacemaker frequencies are similar to those of the behavioural rhythms, then the second model must be given serious consideration. Josephson (1961) described single pulses in the hydranth or distal stalk of *Tubularia* as occurring at frequencies of from 1 every 1·5 s to 1 every 30 s, with bursts of pulses occurring at frequencies of once every 10 s to once every several minutes. The burst frequencies Josephson observed fall within the range of behavioural rhythms detected in *Sarsia* by this study. Spectral analysis of the activity in the marginal pacemaker system of *Sarsia* is needed to help in designing experiments to distinguish between the two models and between various possibilities included in the first model.

The importance of transient rhythms

Transient swimming rhythms may serve to allow *Sarsia* to respond to brief, local stimuli or transient physiological states. H. S. Jennings, a forefather of ethology, emphasized that the behaviour of even the simplest animal must be variable if it is to be adaptive. Behaviour must reconcile the physiological states of the animal with the states of the environment (Jennings, 1906). Since both physiological and environmental states vary, the behaviour of the animal must be capable of varying. Some centre of *Sarsia's* 'brain', presumably the marginal pacemaker system, integrates environmental and physiological information and generates patterns of swimming activity as a result of this integration.

Why might variability in swimming activity be more important to *Sarsia* than to the scyphomedusae? The answer to this question lies in the difference in feeding strategy between *Sarsia* and the scyphomedusae. Gerritsen & Strickler (1977) described two optimal foraging strategies for planktonic predators. One of these, the ambush strategy, consists of floating motionless, waiting for prey to swim into capture range. The other strategy, cruising, involves capturing prey while swimming. The scyphomedusae are cruising predators. They swim almost continuously, catching prey as they swim. With this foraging strategy there is little need for elaborate organization of the swimming system. A regular rhythm is important to swimming efficiency, and this rhythm may need to be modulated in response to environmental stimuli, but there is no need for variable patterns of swimming bouts. *Cassiopea* may be the exception which proves this rule. *Cassiopea* is a sedentary scyphomedusa which lies upside down on the substrate, using currents generated by contractions of the swimming bell to draw food onto its oral arms. *Cassiopea* then, feeds by swimming continuously, but against the substrate. A single redundant pacemaker system, modulated by environmental stimuli and physiological input, is adequate to generate this kind of swimming behaviour (Horridge, 1959; Lerner *et al.* 1971; Passano, 1973).

Sarsia, on the other hand, is an ambush predator. It catches prey that swim into its tentacles while it floats motionless in the water. If there are few prey in the area in which *Sarsia* is floating, then the animal should change location. The marginal

pacemaker system in *Sarsia* may serve to make decisions as to when the animal should start swimming in order to reach a different location, and how long it should spend swimming. *Stomotoca* offers an interesting comparison to *Sarsia*. Like *Sarsia*, it is an anthomedusan, and has both an PSP and an MP system (Mackie, 1975). Unlike *Sarsia*, it is a cruising predator, feeding on other small hydromedusae. Since *Stomotoca* is a cruising predator, it should not require the variability in swim-bout organization that *Sarsia* has. In fact, *Stomotoca's* swimming behaviour is less variable than *Sarsia's*. Mackie & Singla (1975) found that the intervals between swim bouts in *Stomotoca* are about 1·5–2·0 s long. Swim bouts in *Stomotoca* contain 3–8 swimming contractions (Hyman, 1940).

The model of behavioural organization presented above and the suggested relationship between behavioural organization and feeding ecology can be used to generate a number of testable hypotheses. For example, one would predict that swim bouts in *Phialidium*, a leptomedusan with a PSP system, a MP system (Passano, 1976) and a cruising strategy, would be organized more like those of *Stomotoca* than those of *Sarsia*. Since most leptomedusae seem to be cruising, and most anthomedusae ambush predators, one would predict that the organization of the MP system differs in the two orders. Comparative studies of the behaviour, neurophysiology and feeding ecology of the hydrozoan medusae offer an exciting opportunity for understanding how the nervous system works to generate adaptive behaviour.

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