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QUANTITATIVE ANALYSIS OF SWIMMERET BEATING IN THE LOBSTER

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INTRODUCTION

When an animal uses several body appendages simultaneously to achieve a single behavioural goal, the appendages are commonly recruited in succession from rear to front. Each appendage therefore passes through a given position slightly later than the immediately posterior one, giving the appearance of a wave of activity which moves along the animal's body. If the movement of each appendage is cyclic, then the wave of activity is generated repetitively, producing the so-called *metachronous rhythm*. In its simplest form the metachronous rhythm is quite stereotyped, and the movements of an individual limb are never purposefully uncoupled from the movements of ipsilateral neighbours. Examples include the movements of the locomotory appendages of polychaetes (Gray, 1939), onychophorans (Manton, 1950, 1952a), and many arthropods other than insects (Manton, 1950, 1952a, b). At the other and most complex extreme, metachronous coordination displays considerable variation in pattern, and the individual limbs which are involved can perform complicated, purposeful and independent movements. Examples include the locomotory movements of the walking legs of crayfish (Parrack, 1964) and many other crustaceans, spiders (Wilson, 1967), and many insects (e.g. Wilson, 1966).

The movements of the abdominal swimmerets (pleopods) of lobsters represent the simplest type of metachronous limb coordination (Davis, 1968a). Analysis of the underlying neural mechanisms is therefore an appropriate step toward a generalized understanding of the neural control of the metachronous rhythm. Swimmeret beating has several additional advantages for such an analysis. The swimmeret movements are relatively simple (Davis, 1968a), and therefore amenable to analysis, but their neural control is nevertheless interestingly complex. Each swimmeret is controlled by an endogeneous central nervous 'oscillator' which can produce cyclic bursts of motor nerve impulses even when isolated from the cyclic sensory feedback produced by the swimmeret movements (crayfish, Hughes & Wiersma, 1960; Ikeda & Wiersma, 1964; Wiersma & Ikeda, 1964; lobsters, W. J. Davis, unpublished data). Strong reflexes are nevertheless activated by proprioceptive feedback from the movements of the swimmeret (Davis, 1968b). Thus, the swimmeret system offers a good opportunity to study the interaction between purely central and reflex nervous activity. More important, however, the endogenous swimmeret oscillators can be activated in an isolated ventral nerve cord by stimulating the appropriate 'command' interneurones (Hughes & Wiersma 1960; Wiersma & Ikeda, 1964). Thus, the swimmeret system provides an excellent

preparation for investigating the way in which an isolated nervous system produces adaptively useful nervous discharge patterns.

In this paper a quantitative analysis of high-speed motion pictures of lobster swimmeret beating is described. The major goal of this analysis was to provide quantitative constraints for models of the neural mechanisms which underlie swimmeret beating. In addition, by analysing films produced before and after interfering with the sensory feedback from the swimmeret movements, it was possible to demonstrate that this feedback plays a supplemental role in the intersegmental co-ordination of the swimmeret movements.

MATERIALS AND METHODS

The abdomens of lobsters (*Homarus americanus*) were filmed from the side through the glass wall of an aquarium during swimmeret beating. The majority of the records which were analysed were filmed with a Hycam 16 mm. motion picture camera at 200 frames per second, providing adequate temporal resolution of the swimmeret movements. A timing light built into this camera produced a light spot on the lateral edge of the film every 10 msec., allowing calibration of the framing rate to within ± 0·5 %.

Table 1. *Standard form for recording motion picture data from each cycle of swimmeret beating*

	Swimmeret on abdominal segment			
	No. 5	No. 4	No. 3	No. 2
Begin powerstroke	$x(1, 1)$	$x(1, 2)$	$x(1, 3)$	$x(1, 4)$
End powerstoke	$x(2, 1)$	$x(2, 2)$	$x(2, 3)$	$x(2, 4)$
Begin returnstroke	$x(3, 1)$	$x(3, 2)$	$x(3, 3)$	$x(3, 4)$
End returnstroke	$x(4, 1)$	$x(4, 2)$	$x(4, 3)$	$x(4, 4)$
Powerstroke amplitude	$x(5, 1)$	$x(5, 2)$	$x(5, 3)$	$x(5, 4)$
Begin next powerstroke	$x(6, 1)$	$x(6, 2)$	$x(6, 3)$	$x(6, 4)$

Powerstroke amplitude was expressed in degrees of angular excursion. The remaining data, which took the form of the frame numbers corresponding to the indicated events, were converted by the computer to msec.

Typical records which were analysed contained 15–30 cycles of swimmeret beating. Measurements were usually made on sequential cycles, but occasionally two or three short sequences from one lobster were combined to make a single record long enough for correlation analysis. Since the movements of each member of a pair of swimmerets are normally identical, measurements were usually made only on the four swimmerets of one side. For each cycle of beating the frame numbers corresponding to the beginning and end of the powerstroke and returnstroke of each swimmeret were recorded, as was the angular excursion of each swimmeret during the powerstroke (the powerstroke amplitude). These data were recorded on a standardized form (Table 1) and later manually punched into IBM cards for machine analysis.

A general-purpose digital computer was programmed to convert the data from frame number to milliseconds and then to compute a number of 'movement parameters'. These parameters are defined in appropriate sections of the results. For each record the product moment correlation coefficient between each parameter and the swimmeret beat interval (the reciprocal of the beating frequency) was computed, as

was the mean and standard deviation of each parameter. The computer program is described in detail elsewhere (Davis, 1967).

Film records were produced before and after performing two kinds of operations on the swimmeret system: (1) ablation of the rami of one or more swimmerets by transecting the basipodite immediately above the joint with the rami; and (2) complete ablation of one or more swimmerets by severing the appendage at its joint with the abdomen and thoroughly cauterizing the wound with a hot soldering iron. As shown elsewhere (Davis, 1968 b), elastic stretch receptors span the joint between the abdomen and the coxopodite of each swimmeret, but are found nowhere else in the appendage. Therefore, only the complete removal of a swimmeret would be expected to interrupt proprioceptive feedback pathways which involve these stretch receptors.

RESULTS

Intact swimmeret system

Eleven film records of nine intact lobsters were analysed. The average record contained 20 cycles of beating. The results described below are averages computed from all records.

Table 2. *Whole-system parameters*

	Definition	$\bar{R}$	$\bar{X}$
Average beat interval	$\displaystyle\sum_{J=1}^{4} \frac{[x(6, J) - x(1, J)]}{4}$	$+1\cdot00$	577 msec.
Powerstoke component	$x(2, 4) - x(1, 1)$	$+0\cdot851$	427 msec.
Pause 1 component	$x(3, 4) - x(2, 1)$	$+0\cdot673$	288 msec.
Returnstroke component	$x(4, 4) - x(3, 1)$	$+0\cdot795$	415 msec.
Pause 2 component	$x(6, 4) - x(4, 1)$	$+0\cdot923$	323 msec.
Returnstroke component phase position	$\dfrac{x(3, 1)}{x(6, 4)}$	$-0\cdot384$	$0\cdot331$

In this table and those which follow, each parameter is defined in terms of the symbols introduced in Table 1. $\bar{R}$ is the mean correlation coefficient between the average beat interval and the indicated parameter, and $\bar{X}$ is the average mean value of the parameter. Both $\bar{R}$ and $\bar{X}$ are averaged values from eleven film records of nine lobsters (average record length, 20 cycles of swimmeret beating).

The movement parameters which were computed are conveniently described in four categories: (1) whole-system parameters, (2) between-segment parameters, (3) within-segment parameters, and (4) parameter gradients.

Whole-system parameters. The swimmerets are numbered according to the abdominal segments to which they are attached, 5, 4, 3 and 2, from rear to front. One complete cycle of swimmeret beating consists of the overlapping movements of all four pairs of swimmerets, in the sequence 5–4–3–2 (Davis, 1968 a). The movement of each swimmeret during one cycle of beating is divided into periods corresponding to the powerstroke, pause 1 (between the powerstroke and the returnstroke), the returnstroke and pause 2 (between the returnstroke and the next powerstroke). The powerstroke component of a cycle of swimmeret beating is defined as the time from the beginning of the powerstroke of swimmeret 5 to the end of the powerstroke of swimmeret 2. The pause 1, returnstroke and pause 2 components are analogously defined. These four components, and the returnstroke component phase position, comprise the whole-system parameters. Mathematical definitions of these and the other parameters are tabulated with the results.

Table 2 illustrates that each whole-system parameter was strongly and positively correlated with the average beat interval except the returnstroke component phase position, which showed a negative correlation. Thus, as the frequency of swimmeret beating (the reciprocal of beat interval) increased, each whole-system parameter decreased except the returnstroke component phase position, which increased. The same results and most other results pertaining to the intact swimmeret system were obtained even more strongly from one lobster from which the rami of all of the swimmerets had been removed. Therefore, mechanical damping of the movements in the intact swimmeret system was probably not a major source of interpretive error.

Table 3. *Powerstroke cross-latencies*

Swimmerets	Definition	$\bar{R}$	$\bar{X}$ (msec.)
5 to 4	$x(1, 2) - x(1, 1)$	+0·556	92
4 to 3	$x(1, 3) - x(1, 2)$	+0·523	86
3 to 2	$x(1, 4) - x(1, 3)$	+0 638	107
5 to 2	$x(1, 4) - x(1, 1)$	+0·796	282

In this table and those which follow, the swimmerets are numbered according to the abdominal segments on which they are located.

Table 4. *Returnstroke cross-latencies*

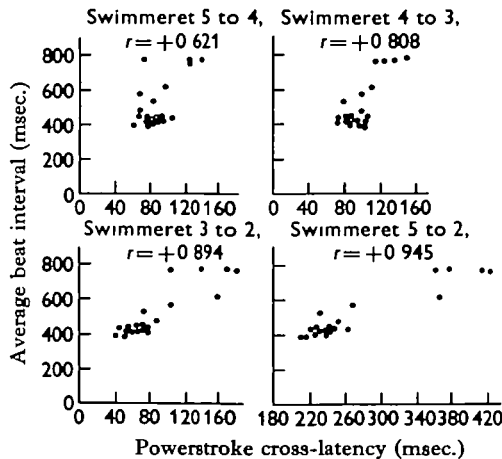| Swimmerets	Definition	$\bar{R}$	$\bar{X}$ (msec.)
5 to 4	$x(3, 2) - x(3, 1)$	+0·491	94
4 to 3	$x(3, 3) - x(3\ 2)$	+0·388	85
3 to 2	$x(3, 4) - x(3, 3)$	+0·405	92
5 to 2	$x(3, 4) - x(3, 1)$	+0 654	273

Fig. 1. Swimmeret beat interval against powerstroke cross-latencies (times between beginning of powerstrokes of different swimmerets on one side) for one representative film record. *r* is the correlation coefficient between the two variables plotted in each graph.

Between-segment parameters. Between-segment parameters include the powerstroke and returnstroke cross-latencies and phase positions. Powerstroke cross-latency, defined as the time from the beginning of the powerstroke of one swimmeret to the beginning of the powerstroke of a specified anterior swimmeret, is a measure of the

conduction time of the metachronous wave of activity between fixed points, and thus it is inversely proportional to the conduction velocity of the wave. Returnstroke cross-latency is analogously defined. Powerstroke and returnstroke phase positions, which are measures of the relative timing of the homologous movements of different swimmerets, were computed within the respective components of the whole cycle and within the entire cycle, in both cases relative to swimmeret 5.
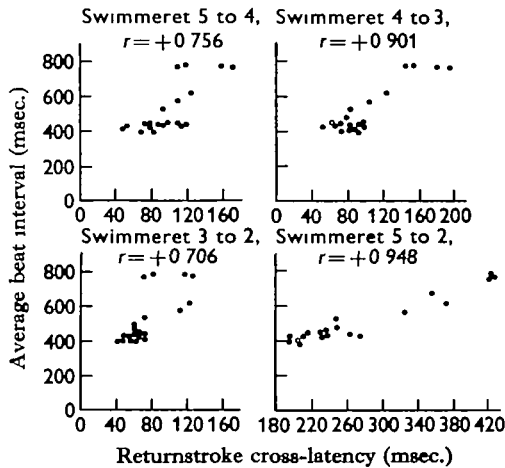

Fig. 2. Swimmeret beat interval against returnstroke cross-latencies (times between beginning of returnstrokes of different swimmerets on one side) for one representative film record. *r* is the correlation coefficient between the two variables plotted in each graph.

Table 5. *Powerstroke phase positions (within the powerstroke components)*

Swimmeret	Definition	$\bar{R}$	$\bar{X}$
4	$\dfrac{x(1, 2) - x(1, 1)}{x(2, 2) - x(1, 1)}$	+0·047	0·321
3	$\dfrac{x(1, 3) - x(1, 1)}{x(2, 3) - x(1, 1)}$	−0·108	0·457
2	$\dfrac{x(1, 4) - x(1, 1)}{x(2, 4) - x(1, 1)}$	+0·227	0·594

Table 6. *Returnstroke phase positions (within the returnstroke components)*

Swimmeret	Definition	R	$\bar{X}$
4	$\dfrac{x(3, 2) - x(3, 1)}{x(4, 4) - x(3, 1)}$	+0·115	0·183
3	$\dfrac{x(3, 3) - x(3, 1)}{x(4, 4) - x(3, 1)}$	+0·084	0·353
2	$\dfrac{x(3, 4) - x(3, 1)}{x(4, 4) - x(3, 1)}$	+0·031	0·535

Tables 3 and 4 and Figs. 1 and 2 illustrate that the powerstroke and returnstroke cross-latencies were strongly and positively correlated with beat interval. Therefore, as the frequency of swimmeret beating increased, so did the conduction velocity of the metachronous wave between each abdominal segment.

Tables 5 and 6 illustrate that the powerstroke and returnstroke phase positions with-

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in the respective whole-cycle components were not correlated with the frequency of swimmeret beating. Since the frequency of swimmeret beating within individual records varied from 30 to 200 %, the absence of significant correlation was not caused by the absence of frequency variation. In individual records an occasional significant positive or negative correlation occurred, but in no single record were the correlations for different swimmerets consistently significant and of one sign. Furthermore, the standard deviations of the phase positions were usually small, 10–30 % of the means. Therefore, the relative timing of the powerstrokes and returnstrokes of different swimmerets within the corresponding whole-cycle components was the same regardless of the frequency of beating. Phase positions computed within the entire cycle showed a weak and probably insignificant negative correlation with beat interval (Tables 7, 8).

Table 7. *Powerstroke phase positions (within the whole cycle)*

Swimmeret	Definition	$\bar{R}$	$\bar{X}$
4	$\dfrac{x(1, 2) - x(1, 1)}{x(6, 4) - x(1, 1)}$	−0·190	0·106
3	$\dfrac{x(1, 3) - x(1, 1)}{x(6, 4) - x(1, 1)}$	−0·367	0 199
2	$\dfrac{x(1, 4) - x(1, 1)}{x(6, 4) - x(1, 1)}$	−0·289	0·332

Table 8. *Returnstroke phase positions (within the whole cycle)*

Swimmeret	Definition	$\bar{R}$	$\bar{X}$
4	$\dfrac{x(3, 2) - x(3, 1)}{x(6, 4) - x(1, 1)}$	−0·085	0 107
3	$\dfrac{x(3, 3) - x(3, 1)}{x(6, 4) - x(1, 1)}$	−0·204	0·208
2	$\dfrac{x(3, 4) - x(3, 1)}{x(6, 4) - x(1, 1)}$	−0·275	0·314

Table 9. *Powerstroke durations*

Swimmeret	Definition	$\bar{R}$	$\bar{X}$ (msec.)
5	$x(2, 1) - x(1, 1)$	+0·679	187
4	$x(2, 2) - x(1, 2)$	+0·709	204
3	$x(2, 3) - x(1, 3)$	+0·776	206
2	$x(2, 4) - x(1, 4)$	+0·595	194

Within-segment parameters. Within-segment parameters include the durations of the powerstroke, pause 1, returnstroke and pause 2, the ratio of the powerstroke duration to the returnstroke duration, and the powerstroke amplitude (expressed in degrees of angular excursion of the swimmeret during the powerstroke) and the average powerstroke velocity per cycle (expressed in degrees per second).

The powerstroke duration of each swimmeret was positively correlated with beat interval (Table 9; Fig. 3). The durations of pause 1 showed either no correlation (swimmeret 3) or a weak positive correlation with beat interval (Table 10). The duration of pause 1 was small, however, so that it occupied only 5 to 10 frames at

Table 10. *Pause 1 durations*

Swimmeret	Definition	$\bar{R}$	$\bar{X}$ (msec.)
5	$x(3, 1) - x(2, 1)$	+0 292	56
4	$x(3, 2) - x(2, 2)$	+0 201	44
3	$x(3, 3) - x(2, 3)$	+0 065	32
2	$x(3, 4) - x(2, 4)$	+0·271	35

Table 11. *Returnstroke durations*

Swimmeret	Definition	$\bar{R}$	$\bar{X}$ (msec.)
5	$x(4, 1) - x(3, 1)$	+0 627	224
4	$x(4, 2) - x(3, 2)$	+0·659	233
3	$x(4, 3) - x(3, 3)$	+0·650	232
2	$x(4, 4) - x(3, 4)$	+0 595	233

Table 12. *Pause 2 durations*

Swimmeret	Definition	$\bar{R}$	$\bar{X}$ (msec.)
5	$x(6, 1) - x(4, 1)$	+0 796	102
4	$x(6, 2) - x(4, 2)$	+0·806	94
3	$x(6, 3) - x(4, 3)$	+0 821	92
2	$x(6, 4) - x(4, 4)$	+0·860	120

Table 13. *Powerstroke/returnstoke ratios*

Swimmeret	Definition	$\bar{R}$	$\bar{X}$
5	$\dfrac{x(2, 1) - x(1, 1)}{x(4, 1) - x(3, 1)}$	−0 069	0·86
4	$\dfrac{x(2, 2) - x(1, 2)}{x(4, 2) - x(3, 2)}$	−0·086	0·90
3	$\dfrac{x(2, 3) - x(1, 3)}{x(4, 3) - x(3, 3)}$	+0·067	0·90
2	$\dfrac{x(2, 4) - x(1, 4)}{x(4, 4) - x(3, 4)}$	−0·134	0 86

Table 14. *Powerstroke amplitudes*

Swimmeret	Definition	$\bar{R}$	$\bar{X}$ (deg.)
5	$x(5, 1)$	−0·305	67
4	$x(5, 2)$	−0·384	69
3	$x(5, 3)$	−0 441	72
2	$x(5, 4)$	−0·395	60

Table 15. *Average powerstroke velocities*

Swimmeret	Definition	$\bar{R}$	$\bar{X}$ (deg./sec.)
5	$\dfrac{x(5, 1) \times 10^3}{x(2, 1) - x(1, 1)}$	−0 618	367
4	$\dfrac{x(5, 2) \times 10^3}{x(2, 2) - x(1, 2)}$	−0·712	362
3	$\dfrac{x(5, 3) \times 10^3}{x(2, 3) - x(1, 3)}$	−0·774	335
2	$\dfrac{x(5, 4) \times 10^3}{x(2, 4) - x(1, 4)}$	−0·628	315

200 frames per second. Therefore, changes in the duration of pause 1 of the same relative magnitude as the changes in the other, longer-duration parameters, would not have been resolved as well, probably at least partially accounting for the relatively small
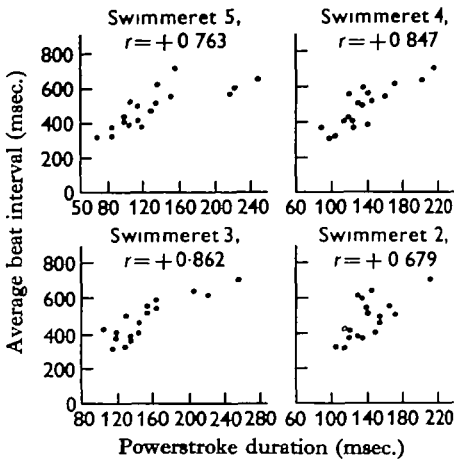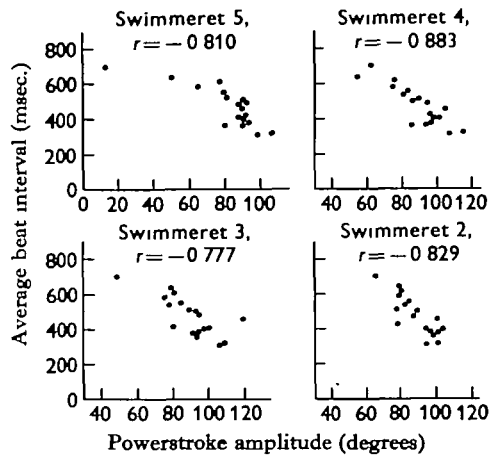

Fig. 3. Swimmeret beat interval against powerstroke durations for one representative record. The swimmeret movements of this lobster were undamped by removing all the rami. *r* is the correlation coefficient between the two variables plotted in each graph.

Fig. 4. Swimmeret beat interval against powerstroke amplitudes (the angular excursions of the swimmerets during the powerstrokes) for the same record as in Fig. 3. *r* is the correlation coefficient between the two variables plotted in each graph.
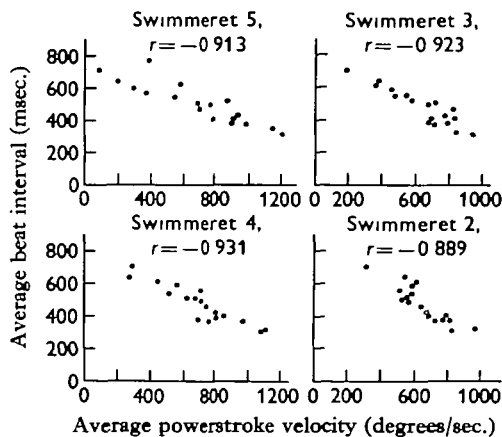

Fig. 5. Swimmeret beat interval against powerstroke velocities (powerstroke amplitudes/ powerstroke durations) for the same record as in Fig. 3. *r* is the correlation coefficient between the two variables plotted in each graph.

correlation coefficients with beat interval. Both the returnstroke and pause 2 durations were positively correlated with beat interval (Tables 11, 12). The ratio of the powerstroke duration to returnstroke duration was approximately 1:1 regardless of the frequency of swimmeret beating (Table 13). The powerstroke amplitudes and velocities were negatively correlated with beat interval (Tables 14, 15; Figs. 4, 5).

Therefore, as the frequency of swimmeret beating increased, so also did the power-stroke amplitudes and velocities of individual swimmerets.

Parameter gradients. The calculation of gradients was the same for each parameter described above. If $P(i)$ is the value of a given parameter for swimmeret i, the rear-to-front gradients for the paremeter, $G(i)$, are defined for each complete cycle of swimmeret beating as follows:

$$G(i) = \frac{100[P(i) - P(5)]}{P(5)} \quad (i = 4, 3 \text{ and } 2).$$

Therefore, if the value of a parameter was significantly larger for swimmeret i than for swimmeret 5, a positive mean gradient resulted for the entire recoid. Conversely, decreasing rear-to-front parameter values resulted in negative gradients.

Table 16. *Powerstroke cross-latency gradients*

	$\bar{R}$	$\bar{X}$ (%)
5–4 to 4–3	−0·060	+6
5–4 to 3–2	+0·122	+25
Total gradient	+0·040	+31

The computation of gradients is described in the text. In this table and those which follow, the numbers 5–4, etc., designate the swimmerets on abdominal segments 5, 4, etc.

Table 17. *Returnstroke cross-latency gradients*

	$\bar{R}$	$\bar{X}$ (%)
5–4 to 4–3	−0·093	+22
5–4 to 3–2	−0 096	+11
Total gradient	−0·067	+33

Table 18. *Powerstroke duration gradients*

	$\bar{R}$	$\bar{X}$ (%)
5 to 4	+0·039	+10
5 to 3	+0·158	+11
5 to 2	−0·188	+8
Total gradient	−0·002	+29

The average gradient correlations with beat interval were zero (Tables 16–24). In individual records, however, the gradients for certain parameters sometimes showed consistent positive or negative correlations with beat interval. Furthermore, in a given record, various combinations of positive, zero and negative correlations with beat interval sometimes occurred for gradients of the same parameter between different swimmerets. Therefore, while the average gradient correlations with beat interval were zero, considerable systematic and non-systematic variation characterized the correlation coefficients within individual records.

The mean values of the gradients were less variable than the correlation coefficients, but the gradients of some parameters in some records were consistently of the opposite sign from that of the mean values for all records. The powerstroke and returnstroke cross-latencies showed slight increasing gradients (Tables 16, 17). The powerstroke, returnstroke and pause 2 durations all showed positive gradients, i.e. the durations of

these parameters were greater in anterior segments (Tables 18, 20, 21). The durations of pause 1 therefore necessarily showed negative gradients (Table 19). The power-stroke/returnstroke ratios showed small positive gradients (Table 22). The power-stroke amplitude showed a positive gradient from swimmeret 5 to swimmeret 4 and from 5 to 3, but no gradient from swimmeret 5 to swimmeret 2 (Table 23).The powerstroke velocities showed small negative gradients (Table 24).

Table 19. *Pause 1 duration gradients*

	$\bar{R}$	$\bar{X}$ (%)
5 to 4	+0·022	−11
5 to 3	−0·060	−24
5 to 2	+0·013	−26
Total gradient	−0·023	−61

Table 20. *Returnstroke duration gradients*

	$\bar{R}$	$\bar{X}$ (%)
5 to 4	+0·027	+7
5 to 3	+0·001	+8
5 to 2	−0·070	+7
Total gradient	−0·023	+22

Table 21. *Pause 2 duration gradients*

	$\bar{R}$	$\bar{X}$ (%)
5 to 4	+0·088	0
5 to 3	+0 081	0
5 to 2	+0·161	+34
Total gradient	+0·115	+34

Table 22. *Powerstroke/returnstroke ratio gradients*

	$\bar{R}$	$\bar{X}$ (%)
5 to 4	+0·034	+8
5 to 3	+0·152	+6
5 to 2	−0·074	+4
Total gradient	+0·054	+18

Table 23. *Powerstroke amplitude gradients*

	$\bar{R}$	$\bar{X}$ (%)
5 to 4	−0·038	+11
5 to 3	+0·058	+16
5 to 2	−0·057	−1
Total gradient	−0·040	+26

Table 24. *Powerstroke velocity gradients*

	$\bar{R}$	$\bar{X}$ (%)
5 to 4	−0·027	+2
5 to 3	−0·088	−2
5 to 2	+0·058	−5
Total gradient	−0·038	−5

Ipsilateral effects of removing swimmeret 3

Seven film records of six lobsters were made before and after removing swimmeret 3 from one side. The pre-operative results were included in the averages presented in the preceding section on the intact swimmeret system. Those averages were compared to the post-operative results to determine the effects of the operation.

The average swimmeret beat interval was not significantly affected by removing swimmeret 3, nor were any of the average correlations between the beat interval and the individual movement parameters. The post-operative mean values of several parameters were different from the pre-operative values, but this is not a useful result by itself, since uncontrolled variables could have unselectively altered the means. Post-operative changes in the mean values of gradients, however, reflect a differential

Table 25. *Effect on powerstroke duration gradients of removing swimmeret 3*

	$\bar{R}$	$\bar{X}$ (%)
5 to 4	(+0 039), −0·084	(+10), +12
5 to 3	(+0·158), —	(+11), —
5 to 2	(−0·188), −0·148	(+8), +23
Total gradient	(−0·002), −0·176	(+29), +35

In this table and those which follow, values in parentheses pertain to the intact swimmeret system and are presented again for convenient comparison with the values without parentheses, which pertain to the operated system. Post-operative values are averages from seven film records of six animals (average record length, 22 cycles). $\bar{R}$ and $\bar{X}$ have their previous meanings.

Table 26. *Effect on powerstroke amplitude gradients of removing swimmeret 3*

	$\bar{R}$	$\bar{X}$ (%)
5 to 4	(−0 038), −0 150	(+11), 0
5 to 3	(+0·058), —	(+16), —
5 to 2	(−0·057), −0 123	(−1), −4
Total gradient	(−0 040), −0·161	(+26), −4

effect of the operation on the remaining swimmerets. It is not likely that uncontrolled variables could consistently affect individual swimmerets to different extents. Therefore, the changes in the mean values of certain gradients following removal of swimmeret 3 are presumed to be a specific result of the operation.

The parameters whose gradients were altered by removing swimmeret 3 were: (1) the powerstroke durations, (2) the powerstroke amplitudes, (3) the powerstroke velocities, and (4) the powerstroke/returnstroke ratios. The powerstroke duration gradients were larger after removing swimmeret 3 (Table 25), and the effect was greatest on swimmeret 2. That is, removing swimmeret 3 increased the powerstroke duration of swimmeret 2 relative to that of swimmeret 5. Since increased powerstroke durations are normally associated with the weaker movements which occur during low-frequency swimmeret beating, the operation weakened the powerstroke of swimmeret 2. The powerstroke amplitude gradients were decreased by removing swimmeret 3 (Table 26). The effect was strongest on swimmeret 4, immediately behind the removed swimmeret. In the intact system the powerstroke amplitude of swimmeret 4 is larger than that of swimmeret 5; removal of swimmeret 3, however,

reduced this difference to zero. Therefore, the powerstroke of swimmeret 4 was also weakened by removing swimmeret 3. The powerstroke velocity gradients, which are near zero in the intact swimmeret system, became large and negative after removing swimmeret 3 (Table 27), reflecting the weakening of the powerstrokes of swimmerets 4 and 2. Removing swimmeret 3 increased the powerstroke/returnstroke ratio gradients (Table 28), since the operation lengthened the powerstrokes of anterior swimmerets more than the returnstrokes.

Table 27. *Effect on powerstroke velocity gradients of removing swimmeret 3*

	$\bar{R}$		$\bar{X}$ (%)	
5 to 4	(-0.027),	$+0.018$	$(+2)$,	-8
5 to 3	(-0.088),	—	(-2),	—
5 to 2	$(+0.058)$,	$+0.071$	(-5),	-22
Total gradient	(-0.038),	$+0.057$	(-5),	-30

Table 28. *Effect on powerstroke/returnstroke ratios of removing swimmeret 3*

	$\bar{R}$		$\bar{X}$ (%)	
5 to 4	$(+0.034)$,	$+0.066$	$(+8)$,	$+12$
5 to 3	$(+0.152)$,	—	$(+6)$,	—
5 to 2	(-0.074),	-0.092	$(+4)$,	$+59$
Total gradient	$(+0.054)$,	-0.092	$(+18)$,	$+71$

The above effects might simply have resulted from elimination of the water currents which are normally produced by swimmeret 3. If this were the case, the effects would be expected to occur after removing only the rami of swimmeret 3, since the rami comprise about three-quarters of the swimmeret surface area, and therefore presumably produce most of the water currents. When only the rami of swimmeret 3 were removed from four lobsters, however, the average post-operative gradients were not significantly different from the gradients in an intact swimmeret system. In a fifth lobster, measurements, were made first after removing the rami from all swimmerets and then again after removing the remaining portion of swimmeret 3. Tables 29–32 illustrate that the gradients were indistinguishable from those of an intact swimmeret system until swimmeret 3 was completely removed, whereupon the effects were identical to those previously described for this operation. From these 'control' experiments, it can be concluded that the weakening of the swimmeret movements which followed removal of one swimmeret was not caused by the concomitant elimination of water currents. Instead, the weakening was presumably caused by the elimination of sensory feedback from the coxal proprioceptors described elsewhere (Davis, 1968b).

The following behavioural data are offered in support of the above interpretation. During low-frequency swimmeret beating the velocity curve of individual swimmerets occasionally showed two peak values during a single powerstroke. The second peak occurred at about the same time as the powerstroke of the immediately anterior swimmeret on the same side. This phenomenon, sometimes visible in several sequential cycles of swimmeret beating, was especially conspicuous in swimmeret 3, on the third abdominal segment (Fig. 6). The biphasic powerstroke was also seen after re-

moving the rami from all of the swimmerets, indicating that it was probably not caused by water currents.

The phenomenon described above would be expected if the powerstroke of a swimmeret caused reflex discharge to the powerstroke muscles of the immediately

Table 29. *Control for the effects of water currents*
(powerstroke duration gradients)

	R	X (%)
5 to 4	−0·327, +0·085	+11, +10
5 to 3	−0·254, —	+23, —
5 to 2	−0·565, −0·166	+16, +28
Total gradient	−0·412, −0·053	+50, +38

In this table and those which follow, *R* and *X* are the correlation coefficient and mean, respectively. The data was taken from one lobster whose rami had been removed from all swimmerets. The two values in each column correspond to before and after completely removing swimmeret 3.

Table 30. *Control for the effects of water currents*
(powerstoke amplitude gradients)

	R	X (%)
5 to 4	+0·484, −0·250	+29, 0
5 to 3	+0·547, —	+26, —
5 to 2	+0·542, −0·248	+31, −12
Total gradient	+0·525, −0·275	+86, −12

Table 31. *Control for the effects of water currents*
(powerstroke velocity gradients)

	R	X (%)
5 to 4	+0·648, −0·147	+19, −6
5 to 3	+0·724, —	+6, —
5 to 2	+0·755, +0·036	+22, −29
Total gradient	+0·734, −0·073	+47, −35

Table 32. *Control for the effects of water currents*
(powerstroke/returnstroke ratio gradients)

	R	X (%)
5 to 4	−0·293, +0·487	−3, −3
5 to 3	−0·250, —	+9, —
5 to 2	−0·446, +0·387	+7, +27
Total gradient	−0·365, +0·482	+13, +24

posterior swimmeret on the same side. Such an intersegmental reflex would represent a cycle-by-cycle phasing mechanism for the powerstroke movements of swimmerets on adjacent segments. Clearly, however, such a reflex could only passively amplify coordinating patterns which were produced by other means.

Indirect electrophysiological support for the postulated intersegmental reflex was obtained by recording from the mixed first abdominal nerve root, which contains both the motor and sensory innervation of the corresponding swimmeret, during electrical stimulation of the immediately anterior first root on the same side. At low and medium

stimulating frequencies a response was obtained which followed 1:1 with the stimulating pulses. When the stimulating intensity was increased, the number of motoneurones which responded was increased, some of the responding motoneurones discharged multiply, and the latency of the response decreased (Fig. 7).
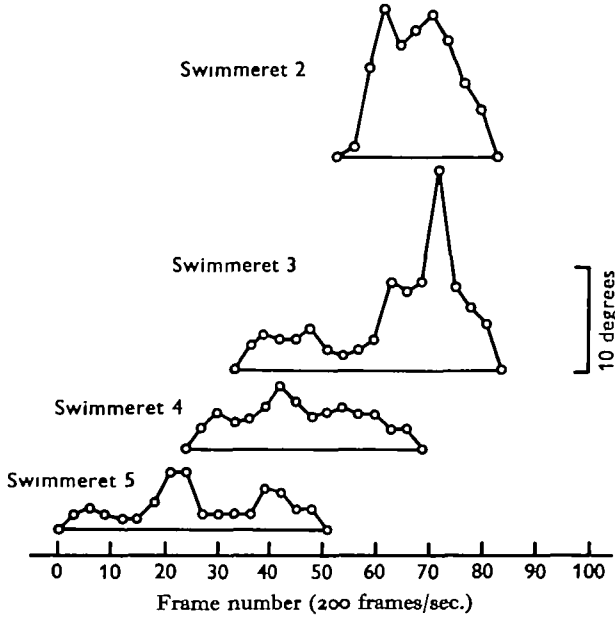

Fig. 6. Velocity of each swimmeret during the powerstroke of a long-duration cycle of swimmeret beating, as determined from high-speed motion pictures. Each point represents the angular excursion of the swimmeret during the preceding three frames (15 msec.). The vertical scale applies to all swimmerets. The rami of the swimmerets were removed.
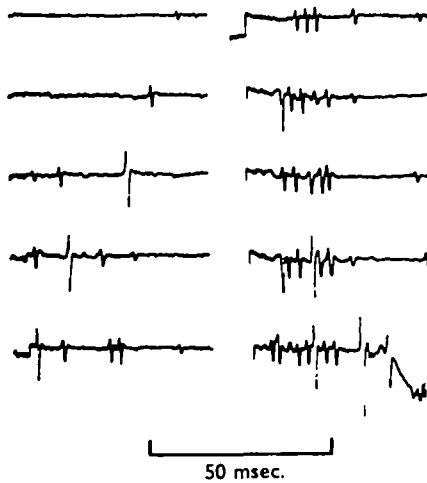
Fig. 7. Extracellular recordings from the mixed first abdominal nerve, which supplies the swimmeret, during progressively more intense electrical stimulation of the first root supplying the immediately anterior swimmeret on the same side. Each record is the response to a single shock applied at the beginning of the record. Records read from left to right, top to bottom, left column first.

Ipsilateral effects of removing swimmerets 3 and 4

The removal of swimmeret 3 from three of the six lobsters discussed above was followed by the removal also of swimmeret 4. The average beat interval was not significantly affected by this extra operation. The average parameter correlations with beat interval were still small, although the number of animals was probably insufficient for meaningful averaging. The mean values of the powerstroke amplitude and velocity gradients were even more negative after swimmeret 4 was removed, i.e. the effect on these gradients of removing swimmeret 3 was intensified by the removal also of swimmeret 4. The effect on the mean values of the other gradients was negligible.
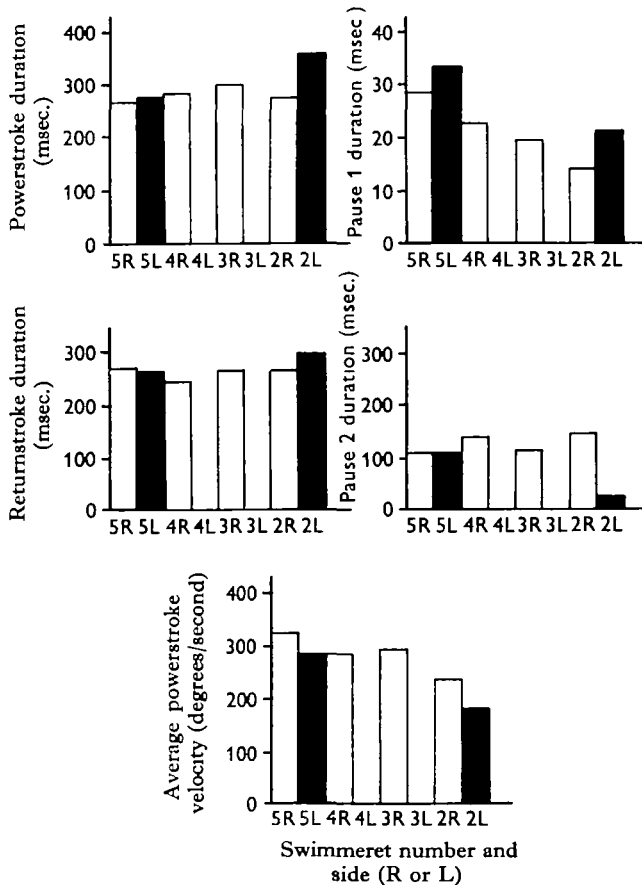
Fig. 8. Ipsilateral (solid bars) against contralateral (open bars) effects of removing the middle two swimmerets on the left side. Each histogram shows the mean values for the record of a given parameter of the movements of the remaining swimmerets. The operation weakened the movements of the remaining ipsilateral swimmerets relative to the movements of the contralateral swimmerets. This record was 12 cycles long.

Ipsilateral against contralateral effects of swimmeret removal

In an intact, upright lobster, the timing and amplitude of the movements of each member of a pair of swimmerets are normally the same. Removal of swimmerets

3 and 4 on one side differentially affected the members of the remaining pairs of swimmerets (Fig. 8). The durations of the powerstroke, pause 1 and returnstroke were greater on the operated side, while the pause 2 durations and powerstroke velocities were less. That is, the movements of ipsilateral swimmerets were weakened relative to the movements of the contralateral swimmerets. The powerstroke cross-latencies and phase positions were about the same on both sides, but the returnstroke cross-latencies and phase positions were greater on the operated side. These effects were visible on swimmerets 5 and 2, but stronger on 2. The effects were qualitatively visible in the films; the swimmerets on the operated side appeared lethargic compared to their partners on the unoperated side. The movements of the swimmerets on the unoperated side were largely indistinguishable from those of a normal, intact lobster.

DISCUSSION

Intact swimmeret system

Whole-system parameters. As shown in another paper (Davis, 1968a), the period of the cyclic force which is produced by the entire swimmeret system is inversely proportional to the maximum amplitude of the force during each cycle. The period is presumably directly related to the whole-system parameters computed here, and the amplitude of the force is proportional to the powerstroke velocities (Davis, 1968a). Therefore, it would be expected that the whole-system parameters are inversely related to the powerstroke velocities. This result was obtained, and together with the result that the timing of the movements of swimmerets on different abdominal segments (the phase positions) is constant despite changing frequencies of swimmeret beating, completely accounts for the forces produced by the entire swimmeret system in terms of the movements of individual swimmerets.

Between-segment parameters. The powerstroke and returnstroke cross-latencies decrease as the swimmeret beating frequency increases. Therefore, the conduction time of the metachronous wave between each abdominal segment is less at higher frequencies of swimmeret beating. Furthermore, the conduction time between adjacent swimmerets varied by as much as 600% in individual records. Therefore, homologous swimmeret muscles in different abdominal segments are undoubtedly not innervated exclusively by branches of the same motoneurones. It also seems unlikely that variation in monosynaptic delay could account for the large variation in intersegmental conduction time. The neural oscillators of different segments could be coupled monosynaptically, however, if an additional source of variation in the intersegmental conduction time were provided by the partial insertion of the oscillators themselves in the intersegmental coupling pathways. It seems more likely, however, that the oscillators of adjacent segments are coupled multisynaptically, and that the large variation in the intersegmental conduction time arises, at least in part, from variable temporal and spatial facilitation and summation at these coupling synapses.

Within-segment parameters. Many of the within-segment parameters show a strong, negative correlation with the frequency of swimmeret beating. For example, the durations of the powerstroke and returnstroke, as well as the short pauses between them, decrease for each swimmeret as the frequency of swimmeret beating increases. In addition, the powerstroke velocity of each swimmeret increases as the frequency of

beating increases. Therefore, the central nervous oscillator which controls the movements of each swimmeret behaves exactly like the force which is produced by the entire swimmeret system. That is, amplitude is inversely related to period.

Parameter gradients. The observed variability of the mean values of the parameter gradients, as well as their variable correlation coefficients with the swimmeret beating frequency, would be expected from a system which consists of synaptically-coupled oscillators of different and variable excitability. Since the relations between the beating frequency and the whole-system parameters, powerstroke velocities and powerstroke phase positions are relatively consistent, the variability of the parameter gradients need not interfere with the production of a useful average force by the entire swimmeret system.

The negative powerstroke velocity gradient is compensated by a positive powerstroke duration gradient, so that the power produced by individual swimmerets is about the same from the rear to the front of the abdomen. In the crayfish swimmeret system the preferred independent frequencies of the oscillators of different segments is about the same, but the inherent 'excitability' of the oscillators decreases from the rear to the front of the abdomen, an arrangement which permits the posterior oscillator to drive the anterior ones (Ikeda & Wiersma, 1964). A similar excitability decrease from the rear to the front of the abdomen may be presumed to occur in the lobster swimmeret system. To account for the constant power output from the rear to the front of the abdomen, it would seem that either the power produced by each swimmeret is independent of the inherent 'excitability' of the corresponding oscillator, or the efficacy of the interganglionic coupling signal increases as the signal passes forward. Such a hypothetical amplification could occur centrally, either by multiplication at intersegmental synapses, or by the delayed coupling of homologous halves of the oscillators of adjacent segments. Alternatively, the hypothetical amplification could occur peripherally, either by an increase from the rear to the front of the abdomen in the 'transfer functions' of the swimmeret muscles, or by the reflex mechanisms discussed below.

The decreasing rear-to-front gradient in the pause between the powerstroke and the returnstroke (pause 1) could be explained on the basis of the swimmeret intrasegmental limb reflexes. These reflexes are organized so that imposed movement of the appendage in one direction causes reflex motor discharge to the muscles which normally move the appendage in the opposite direction (Davis, 1968b). A rear-to-front increase in the strength of these 'resistance' reflexes would therefore account for the observed rear-to-front decrease in the pause between the powerstroke and the returnstroke. Such a gradient in the strength of the intrasegmental reflexes could also amplify the efficacy of the interganglionic coupling signal as it passes forward, accounting for the observation that the power produced by individual swimmerets is about the same from rear to front despite a presumable rear-to-front decrease in central 'excitability'. At present, however, there is no direct electrophysiological evidence for a segmental gradient in the strength of the swimmeret limb reflexes.

Operations on the swimmeret system

Removing all of swimmeret 3, including the stretch receptors which have been found in the coxal region (Davis, 1968b), reduces the relative power output of adjacent

swimmerets on the same side. Control experiments which were performed are considered to have reduced the possibility that these effects were caused by the elimination of water currents which are normally produced by the removed swimmeret. Therefore, although there is no doubt that the neural discharge patterns underlying coordinated swimmeret beating originate in appropriately 'wired' regions of the central nervous system (Wiersma & Ikeda, 1964), it appears that intersegmental proprioceptive pathways play a supplemental role. The results reported here suggest that proprioceptive information from the movement of a swimmeret is conveyed both anteriorly and posteriorly to supplement the strength of the movements of adjacent swimmerets on the same side, but that proprioceptive influences on the swimmerets of the opposite side are weak or absent.

The method by which the proprioceptive inflow from a swimmeret exerts its proposed influence on other swimmerets is not yet known. At least two possibilities should be considered. First, the proprioceptive inflow could influence the target motoneurones indirectly, by raising the 'level of excitation' of the corresponding central nervous oscillator. Secondly, the proprioceptive inflow could be transmitted directly to the target motoneurones, without affecting the corresponding oscillator. These two possibilities are not mutually exclusive, since the swimmeret motoneurones may themselves form part or all of the central oscillator. At present, however, I favour the latter view, largely because the frequency of the swimmeret oscillators is not significantly reduced by eliminating all proprioceptive feedback (crayfish, Ikeda & Wiersma (1964), Wiersma & Ikeda (1964); lobsters, W. J. Davis, unpublished data).

Speculation on a model

The analysis reported here provides quantitative constraints for models of the neural oscillator which controls the movements of each swimmeret. It is clear that these constraints, based only on analysis of the limb movements, cannot alone lead to restrictive models. To this end, considerable structural and additional functional data are required. It is worth noting, however, that a neural network which contains only random and unpolarized synaptic connexions can theoretically propagate a unidirectional wave of neural activity (Beurle, 1956). Refractory oscillation in such a network could convert a tonic input into a cyclic output. Owing to spatial and temporal facilitation and summation the amount of neural activity in any region of such a network should be inversely related to the conduction time of the activity through that region, i.e. the amplitude of a propagated wave should be inversely related to its period. If the network were homogeneous, the ratio of the conduction time through one half of the network to the conduction time through the opposite half should be 1:1 and independent of the frequency of the repetitive wave. Therefore, a model which utilizes the neuropilar network as the structural matrix of the oscillator, and propagates waves of neural activity through the neuropile as the source of the oscillation, can account for the major features of the movements of individual lobster swimmerets. Such a mechanism would of course require that the swimmeret motoneurones sample the neuropilar activity in the same sequence that they are recruited, a hypothesis which has obvious structural correlates.

Extension to complex metachronous rhythms

As discussed earlier, lobster swimmeret beating is a simplified version of the metachronous rhythm, the basis of limb coordination in many and diverse animal groups. To what extent can models developed from analysis of swimmeret beating account also for more complex metachronous rhythms? For a partial answer to this question, high-speed motion pictures of the relatively complex, metachronous walking gait of the cockroach were subjected to the same computer analysis which was used on swimmeret beating. The paired legs of cockroaches alternate exactly out of phase, of course, unlike the paired lobster swimmerets. Separate analysis of the movements of the intact walking legs of each side, however, gave essentially the same results as obtained from analysis of the movements of the intact swimmerets of one side. For example, the powerstroke and returnstroke durations and cross-latencies showed a strong, positive correlation with the duration of the stepping interval, as did all whole-system parameters except the phase position of the returnstroke component, which showed a negative correlation. The alternating tripod gait (Wilson, 1966) was used over the observed range of stepping frequency (4–22 cyc./sec.), and the phase positions of the legs showed no correlation with the duration of the stepping interval.* Therefore, judging only from quantitative comparison of the limb movements, it seems possible that the same basic mechanisms can account for metachronous coordination of different degrees of complexity, in which case neural models developed from analysis of swimmeret beating may be more generally applicable.

SUMMARY

1. High-speed motion pictures of the metachronous movements of the abdominal swimmerets of the lobster *Homarus americanus* were analysed. Measurements were made on films produced before and after removing part or all of individual swimmerets.

2. Analysis of the intact swimmeret system provided quantitative constraints for models of the neural mechanisms underlying swimmeret beating. For example, the conduction velocity of the anterior-moving, metachronous wave increases with increasing frequency of swimmeret beating, as does the powerstroke amplitude and velocity of each swimmeret. The phase positions of individual swimmerets in the movement cycle are the same regardless of the frequency of swimmeret beating, and so are the ratios of powerstoke duration to returnstroke duration. The durations of the powerstroke, returnstroke and the short pauses between them decrease as the frequency of swimmeret beating increases.

3. Removal of a swimmeret weakens the movements of ipsilateral swimmerets on adjacent segments, but does not affect the movements of contralateral swimmerets. Control experiments were performed to reduce the possibility that the effects were mechanical.

4. The results suggest that proprioceptive feedback from the movements of individual swimmerets plays a supplemental role in the intersegmental coordination of the swimmerets of one side, but that contralateral proprioceptive influences are weak or absent.

* Mr Fred Delcomyn, who filmed the cockroaches and made the required measurements, will fully report these results later. I thank him for permission to present this preliminary account.

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