

UNILATERAL CILIARY REVERSAL AND MOTOR RESPONSES DURING PREY CAPTURE BY THE CTENOPHORE *PLEUROBRACHIA*

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SUMMARY

High-speed cinematography of feeding *Pleurobrachia* revealed a stereotyped sequence of ciliary motor responses underlying the feeding behaviour of this ctenophore. Prey capture by a tentacle first elicited high frequency beating in all comb rows, propelling the animal forward at a rapid speed for several seconds. This was followed by a brief period of inactivity on some or all comb rows. Then comb rows adjacent to the catching tentacle beat in the reverse direction, causing the ctenophore to spin rapidly toward this side and sweeping the prey-catching tentacle to the opened mouth, which bent towards it. After engulfing the prey, the animal slowly swam forward to re-set the relaxed tentacles as a fishing net. The patterns, timing, onset and coordination of these ciliary responses, particularly the unilateral reversal of comb rows on the catching side, are analysed with respect to possible conducting pathways mediating this behaviour.

INTRODUCTION

Ctenophores, or comb jellies, are among the most beautiful and voracious of the marine plankton, and play an important part in oceanic food chains (Hardy, 1956). It is characteristic of ctenophores that they have exploited both locomotory and sensory functions of cilia for much of their behaviour, including feeding responses.

In this report we describe the complete sequence of ciliary motor events responsible for the feeding behaviour of the cydippid ctenophore *Pleurobrachia*. Using high-speed cinematography, we document earlier reports that food is conveyed from the tentacles to the mouth by a localized reversal in the direction of ciliary beating on comb rows adjacent to the prey-carrying tentacle (Tamm, 1979, 1980, 1982; Moss & Tamm, 1981). We present new findings on the initiation, patterns and coordination of unilateral ciliary reversal, as well as on ciliary excitation and quiescent states which precede it. Finally, we discuss the possible pathways mediating ciliary motor responses during prey capture by *Pleurobrachia*.

Key words: Ctenophore, prey capture, ciliary reversal.

MATERIALS AND METHODS

Organism

Healthy specimens of *Pleurobrachia pileus* were carefully dipped from the surface of Great Harbor or Vineyard Sound near Woods Hole, MA. Ctenophores were maintained in perforated buckets immersed in fresh running sea water at 18–20°C.

Aquarium observations

The feeding behaviour of more than 40 free-swimming *Pleurobrachia* was observed individually in a large glass aquarium filled with sea water (18–20°C) using darkfield illumination. Single ctenophores were placed in the aquarium with fresh copepods as food organisms. The events leading to prey capture and ingestion were followed by eye and recorded vocally on a tape recorder using a verbal 'shorthand' code for specific behavioural acts. Extremely fast events and details of the ciliary responses could not be discerned by this method; nevertheless, timed transcription and analysis of the tapes provided an accurate description of the gross behaviour and body movements of the ctenophore during feeding.

High-speed cinematography of ciliary responses

Ctenophores were pinned to a clear Sylgard (184 Silicone Elastomer, Dow Corning, Midland, Mich.) disc in a Lucite viewing chamber filled with sea water, as shown in Fig. 1. Feeding responses to copepods were recorded on Kodak Plus X ciné film at speeds up to 400 frames s⁻¹, using a Locam 16 mm movie camera (Redlake Labs, Santa Clara, CA) with a 55 mm Nikon Micronikkor lens. More than 3000 feet of film were taken of the feeding behaviour of 39 different *Pleurobrachia*. Frame-by-frame tracing and analysis of the ciné films were done with a L-W Photo Optical projector (L-W International, Woodland Hills, CA).

Analysis of ciné films was based mainly on the activity of the five rows which directly faced the camera (Figs 1, 2), as well as additional rows on the far surface which happened to be visible (cf. Fig. 2). The pattern of comb row activity was represented by the four rows on the tentacular hemisphere facing the camera (Tables 1, 2). This pattern was a mirror-image representation of comb row activity on the opposite tentacular hemisphere, as judged by records of rows on this surface as well as occasional observations of animals pinned with a sagittal hemisphere facing the camera.

RESULTS

Aquarium observations

Pleurobrachia fishes by slowly swimming in gentle arcs, usually toward the surface, passively sweeping out its tentacles to form a long trailing net. Copepods making chance contact with the spread tentacles were caught and entangled by adhesive colloblast cells (Bargmann, Jacob & Rast, 1972; Franc, 1978) on the surface of the side-branches, or tentillae. Struggling of the prey resulted in brief local contractions of the tentillae and tentacle, followed by partial relaxation; the

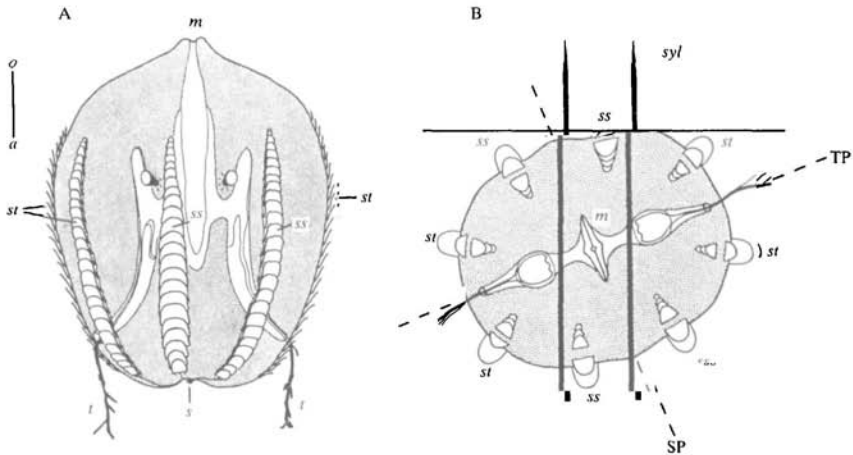


Fig. 1. *Pleurobrachia* pinned to a Sylgard disc (syl) for high-speed cinematography. (A) Surface facing camera; (B) oral view showing biradial body symmetry. The ctenophore is orientated in a vertical position with its mouth (*m*) uppermost and the tentacular plane (TP) at a $\sim 22^\circ$ angle to the disc surface. The flattened mouth and pharynx define the sagittal plane (SP) which lies perpendicular to the plane of the two tentacle pouches and tentacles (*t*). Each body quadrant formed by the intersection of the sagittal and tentacular planes contains two rows of ciliary comb plates termed subsagittal (*ss*) and subtentacular (*st*), according to the neighbouring plane. Each pair of subsagittal and subtentacular comb rows is connected by ciliated grooves to one of four pacemaker (balancer) cilia in the aboral statocyst (*s*). The two tentacles contract independently, so that only one tentacle and the four comb rows of its sagittal hemisphere are used to capture prey during any feeding episode (catching or reversal side). The opposite sagittal hemisphere with the relaxed tentacle is called the non-catching or normal side. The orientation of the pinned *Pleurobrachia* provides a profile view of a subtentacular row on either side, regardless of which tentacle captures prey. This orientation also allows simultaneous view of a pair of subsagittal and subtentacular rows on both catching and non-catching sides, as well as comparison of the two subtentacular rows on one side (left). *o-a*, oral-aboral axis.

cycle was repeated a number of times as the contractions became progressively stronger and spread over the tentacle, further entangling the prey. Because the two tentacles act independently, the other tentacle usually remained relaxed.

When the prey-bearing tentacle contracted vigorously over its entire length, *Pleurobrachia* swam rapidly forward, usually toward the surface, for 2–3 s. During this fast forward swimming the prey-carrying tentacle twitched violently with increasing frequency but did not shorten significantly further.

The ctenophore then suddenly halted and spun rapidly in the tentacular plane, always towards the tentacle carrying the prey. The ctenophore typically rotated 2–3 times at a rate of about $0.7\text{--}0.8 \text{ rev. s}^{-1}$, wrapping the tentacles around the body and over the opened lips of the mouth.

Spinning ceased abruptly when the prey contacted the opened lips, which reached toward the catching tentacle. The food was carried into the pharynx and ingested. *Pleurobrachia* slowly sank during this brief inactive period (~ 3 s), and assumed no

fixed orientation with respect to the vertical. The animal then vigorously righted itself, turning to point its mouth upward, and released the newly-unloaded tentacle from the mouth. The ctenophore swam quickly forward, stretching out the relaxed tentacle to re-set its fishing net for another feeding episode.

High-speed ciné recording of ciliary responses during feeding

Ctenophores pinned to a Sylgard disk (Figs 1, 2) exhibited ciliary responses which corresponded to the feeding behaviour of unrestrained animals. In addition, several ciliary responses not evident from visual observations of free-swimming animals were revealed by high-speed filming.

Fast forward period

Tentacles with entrapped copepods twitched progressively more violently until ciliary beat frequency suddenly increased for a brief period. This response corresponded to the rapid forward swimming of unrestrained animals. In 85% of the fast forward sequences analysed ($N = 70$), all eight comb rows beat at high frequency (10.8 ± 0.4 Hz; $N = 77$ rows) in the normal direction. In the remaining cases, one or two of the rows on the side facing the camera did not beat.

During high frequency beating, the lips opened and the mouth began to bend towards the prey-catching tentacle (Fig. 2A). However, if the fast forward period was not followed by a ciliary reversal (perhaps due to escape or insufficient quantity of prey), bending of the mouth did not occur. Consequently, mouth bending during

Fig. 2. Ciné prints of ciliary responses during prey capture by a *Pleurobrachia* pinned to a Sylgard disk as shown in Fig. 1. The comb rows directly facing the camera are indicated (subtentacular, *st*; subsagittal, *ss*); those on the far surface are not lettered. The two tentacles (*t*) hang down out of view. The tentacle on the left, emerging from its pouch between the two subtentacular rows, has already caught copepods and is partially contracted; the catching side is thus on the left in this example. The tentacle on the non-catching side (right) remains relaxed. The direction of the effective stroke (open arrows) is always opposite to the direction of metachronal wave propagation. (A) Fast forward. Normal antiplectic metachronal waves travel from the aboral statocyst (*s*) upward to the mouth (*m*) on all comb rows. The effective stroke is directed aborally. The mouth has already begun to bend towards the left side. (B) Quiescence begins on the left side as the last forward wave disappears at the oral end of the rows (solid arrow). Plates rest at the end of the recovery stroke with their distal ends inclined away from the body surface. Rows on the non-catching side (right) continue forward beating at the same frequency. (C) Laydown. Profile of the subtentacular row on the left shows that the plates have straightened against the body and are bent slightly upward near the base. Rows on the non-catching side (right) continue to beat in the normal direction. (D) Initiation of reversed beating begins synchronously at the oral ends of the two subtentacular rows on the left side, as a wave of reversed recovery strokes propagates in the aboral direction lifting adjacent plates away from the body surface (solid arrow). Plates at the oral end of these rows are already performing a reversed effective stroke towards the mouth (open arrow). The two subsagittal rows on the left side are still quiescent. Forward beating continues on the right side. (E) Reversed beating and reversed antiplectic metachronal waves are established along both subtentacular rows on the left side. The contracted tentacle (left) is being swept up toward the opened mouth, which has bent further to this side. Normal beating continues on the right side. Note that reversed waves are shorter than normal ones, reflecting the higher frequency of reversed beating. (F) Reversed beating has carried the contracted, prey-bearing tentacle further orally along the left side. The two subsagittal rows on the catching side are still inactive; reversed beating in these rows only begins 0.25 s later. Normal beating continues on the non-catching side. The patterns of quiescence and reversal in this example are thus 00/NN and RR/NN, respectively. Time intervals between prints A–F: 0.11 s, 0.36 s, 0.10 s, 0.29 s, 0.51 s. Scale bar, 1 mm.

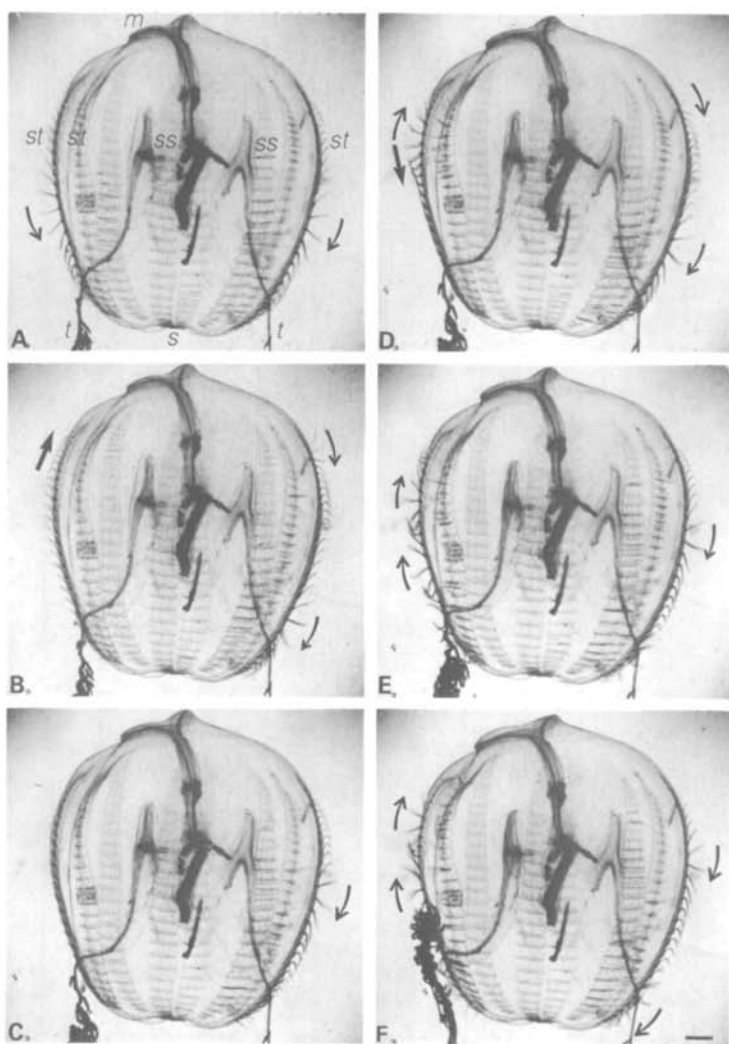
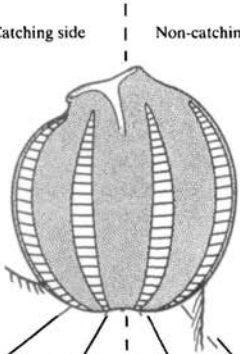


Table 1. *Patterns of comb row activity during ciliary quiescence and reversal*

		<div> <div>Catching side</div> <div>Non-catching side</div>  </div>					N	%
		st	ss	ss	st			
Quiescent patterns		0	0	1	N	46	38.0	
		0	0	1	0	51	42.2	
		0	0	1	0	5	4.1	
		0	0	1	N	1	0.8	
					0	103	85.1 %	
Reversal patterns		R	R	1	N	94	37.2	
		R	R	1	0	11	4.3	
		R	R	1	N	0	0	
		R	R	1	0	1	0.4	
						106	41.9 %	
		R	0	1	N	79	31.2	
		R	0	1	0	57	22.5	
		R	0	1	N	0	0	
		R	0	1	0	2	0.8	
						138	54.5 %	
		R	N	1	N	4	1.6	
		R	N	1	0	5	2.0	
		R	N	1	N	0	0	
		R	N	1	0	0	0	
						9	3.6 %	

Activity of subtentacular (*st*) and subsagittal (*ss*) rows on the tentacular hemisphere facing the camera. The sagittal hemisphere of the prey-catching tentacle is normalized to the left side; the non-catching sagittal hemisphere is depicted on the right. Activity of comb rows was scored as N, normal beat direction; R, reversed beat direction; or 0, quiescent.

Table 2. *Relation between activity patterns during ciliary quiescence and reversal*

Then reversal pattern is:	If quiescent pattern is:			
	0	0	0	0
	%		N	
R R - -	36		(18)	
R 0 - -	58		(29)	
	94			
	%		N	
R - N N	46		(23)	
R - 0 0	54		(27)	
	100			

Activity of comb rows is shown as in Table 1, with the catching (reversal) side normalized to the left. N, normal beat direction; R, reversed beat direction; 0, quiescence; -, any pattern.

high frequency beating was a reliable indicator of a forthcoming unilateral reversal, and served as a cue to begin high-speed filming.

Quiescence and laydown

In 96 % of the cases where a fast forward period was recorded prior to reversal ($N = 70$), rapid beating ended with a brief cessation of ciliary activity in some or all comb rows. This inactive period is called quiescence, because the plates simply remained at rest after the last fast forward wave had travelled to the oral end of the row and disappeared (Figs 2B, 3C-G). Inhibitory or arrest responses, in contrast, involve a sudden, almost instantaneous stoppage of all comb plates, triggered by a through-conducting pathway (see Discussion).

Two main patterns of quiescence were observed (Table 1): a global stoppage on all eight comb rows (42 % of cases, $N = 103$), or stoppage on the four rows of the prey-catching side only (38 % of cases). In 5 % of the cases, quiescence on the catching side was accompanied by a combination of quiescence and normal beating on the opposite side. In 85 % of the cases, therefore, both the subtentacular and subsagittal rows on the prey-catching side stopped. As judged by the time of disappearance of the last fast forward wave, quiescence began at approximately the same time in the subtentacular and subsagittal rows. In a small number of cases there was no detectable pause between fast forward and subsequent reversal on one or more of the rows of the catching side.

In contrast, rows on the non-catching side became quiescent only about half of the time (Table 1). When active, rows on this side beat at the same frequency as in the preceding fast forward period (~ 11 Hz).

The disappearance of the last fast forward wave at the oral end of a row left the plates in a position at the end of the recovery stroke with their distal regions slightly curved away from the body surface (Figs 2B, 3C,D, 4B). The distal part of the plate gradually straightened and approached the body surface during the next few

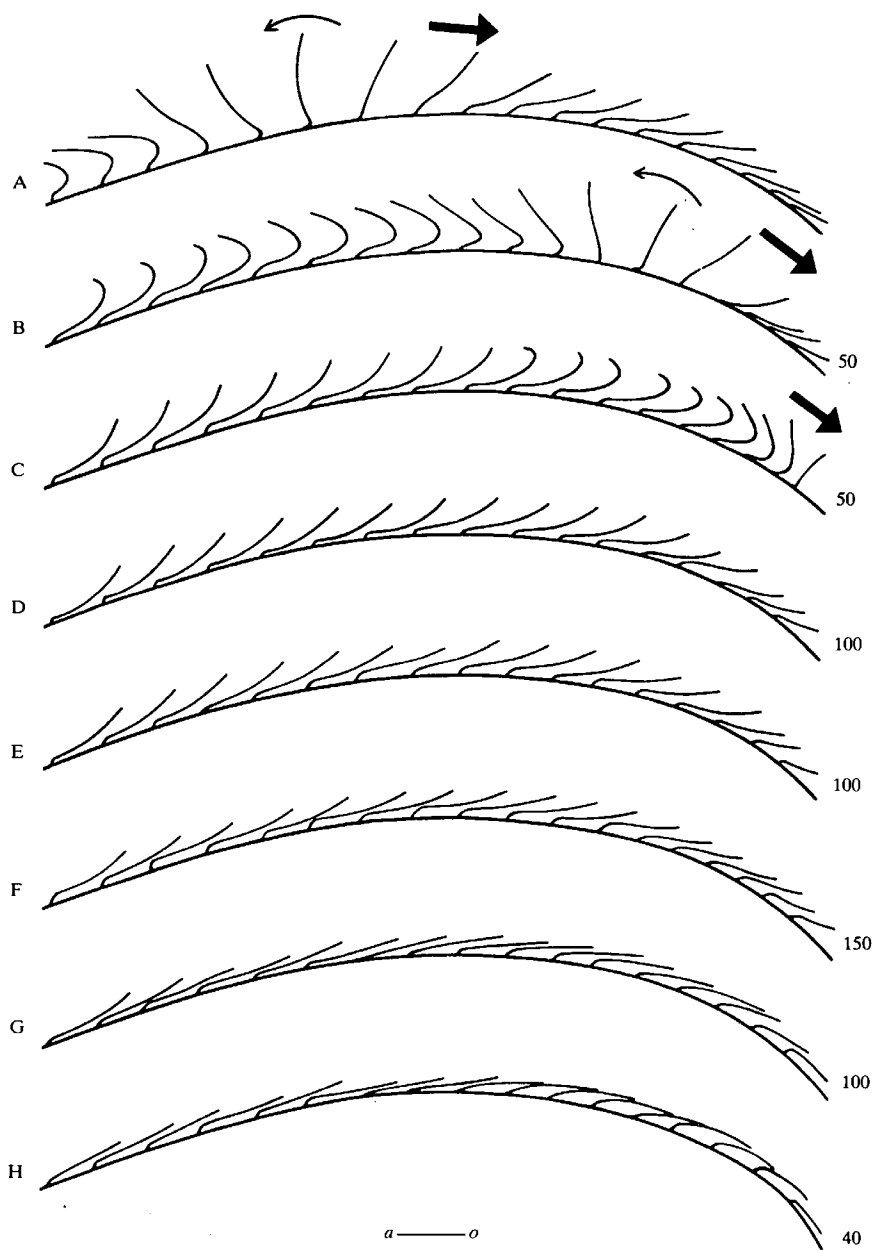


Fig. 3A-H

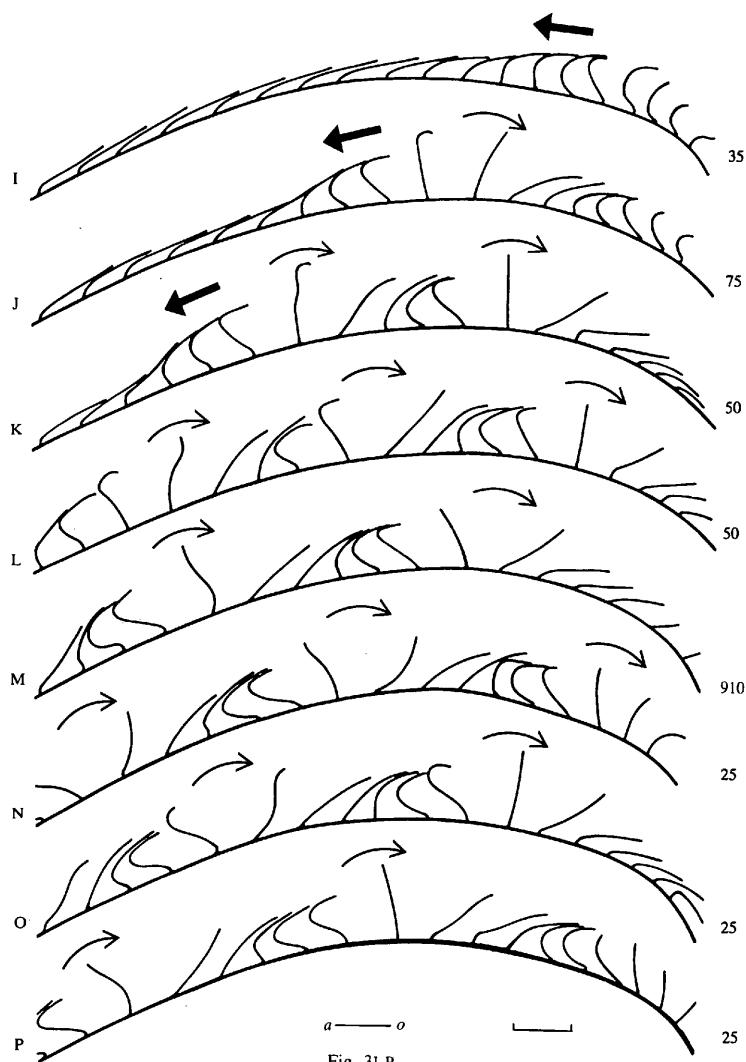


Fig. 31-P

hundred milliseconds (see Murakami, 1968), and remained in this flattened position for the duration of quiescence unless reversed beating followed (Figs 3E–G, 4C).

In 93 % of the rows which subsequently beat in the reverse direction ($N = 196$), the resting plates underwent a marked change in curvature. The basal portion of the plates moved away from the body surface with the formation of a slight upward bend, so that the plates became convex and arched over one another (Figs 2C, 3H,I, 4B). This posture, termed laydown, occurred 50 to several hundred milliseconds before the onset of reversed beating (Fig. 4B). Laydown often occurred first at the oral end of the row, and spread to the aboral end at $4\text{--}6\text{ cm s}^{-1}$ (Fig. 3G–I). In other cases, laydown began nearly simultaneously in all plates along the row.

Laydown seldom occurred in rows which beat in the normal direction after quiescence (i.e. rows on the non-catching side), and thus seemed to be preparatory to reversed beating. Indeed, the reversed beat cycle begins with an aborally-directed recovery stroke which is a continuation of the upward bend formed during the laydown (see Reversal).

The duration of the quiescent period, as measured by the time interval from the disappearance of the last fast forward wave to the onset of either reversed or forward beating, was shorter in the subtentacular rows (median, 0.28 s ; $N = 121$) than in the subsagittal rows (median, 0.69 s ; $N = 55$) on the catching side. This time difference

Fig. 3. Sequence of profiles of a subtentacular comb row during a feeding response, traced from a ciné film taken at 200 frames s^{-1} . Direction of effective stroke is indicated by open arrows; metachronal waves travel in the opposite direction (solid arrows). The plates near the oral end of the row (to right) are shorter and closer together ($a\text{--}o$, aboral–oral axis). Time intervals between successive tracings are indicated on the right in ms. Scale bar, 0.5 mm . (A–D) The last fast forward wave travels to the right and disappears at the oral end of the row, leaving plates at rest at the end of the recovery stroke. (E–G) Quiescent plates gradually straighten and lie closer to the body surface. (H) Laydown begins at the oral end with the formation of an upward bend near the base of the plates. (I) Initiation of reversed beating on the right. Oral-most plates perform a reversed recovery stroke to the left by propagating a bend up the cilia, lifting adjacent plates in the aboral direction and stimulating them to do likewise (solid arrow). Note that plates further to the left are now in the laydown position. (J–L) Propagation of the first wave of reversed beating to the left. Since the effective stroke is to the right (open arrows), metachronal coordination remains antiplectic. (M–P) Successive profiles of established waves of reversed beating travelling from right to left. A reversed metachronal wave consists of about six plates.

Fig. 4. Successive profiles of a subtentacular comb plate beating in the normal direction (A), during quiescence and laydown (B), and beating in reverse (C), traced from ciné films at 400 frames s^{-1} . A and C are profiles of the same plate at 5-ms intervals. $a\text{--}o$, aboral–oral axis. (A) In a normal beat cycle the plate rests at the end of the recovery stroke with a basal bend towards the mouth (profile 1). During the effective stroke this bend straightens out and the plate swings rapidly in the aboral direction (right) like a stiff paddle (arrow, profiles 2–9). By the end of the power stroke a bend of opposite sign forms near the base; during the slower recovery stroke this bend progressively enlarges and propagates toward the tip, unrolling the plate back to the resting position at the left (profiles 10–23). Beat frequency, 9 Hz . (B) Disappearance of the last fast forward wave leaves the plate inclined slightly away from the body surface at the end of the recovery stroke (profile 1). The distal part of the plate gradually straightens during quiescence (profiles 2 and 3). A slight bend then forms near the base, arching the plate upward to the laydown position (profiles 4 and 5) before reversed beating begins. Time interval between profiles is 0.1 s . (C) A reversed beat cycle begins with the formation and propagation of a recovery stroke bend toward the right (profiles 1–6). Before the recovery bend has reached the tip, the effective stroke starts as a bend forms in the opposite direction near the base, swinging the plate stiffly to the left (arrow, profiles 7–11). Beat frequency, 20 Hz .

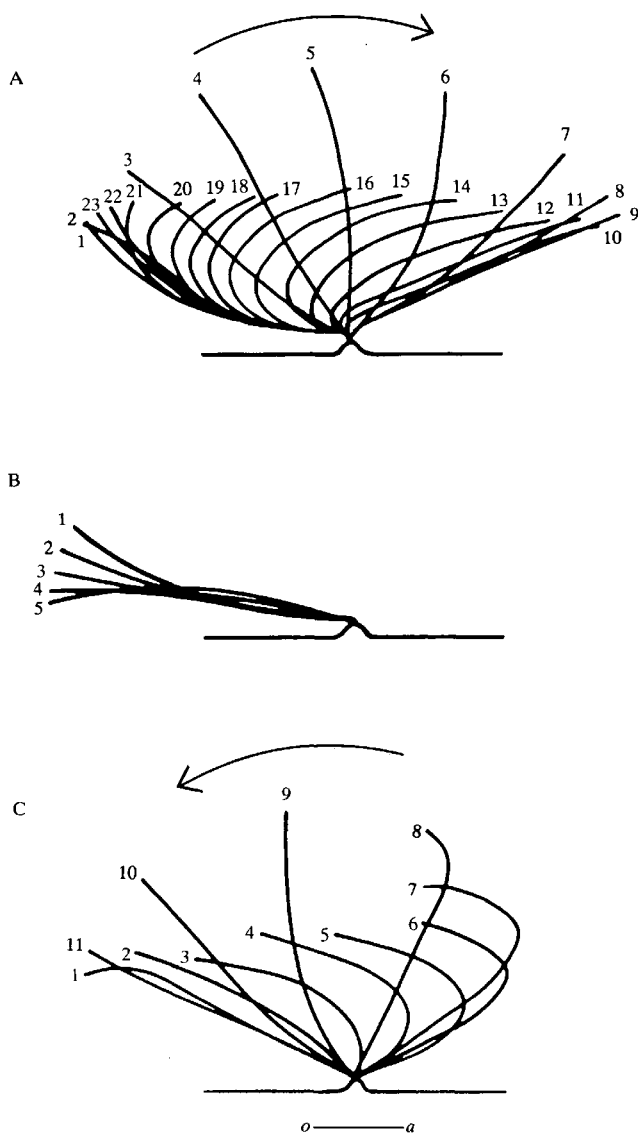


Fig. 4

reflects the earlier onset of reversed beating in the subtentacular rows (Fig. 2) (see Reversal). The duration of quiescence in the subtentacular and subsagittal rows on the non-catching side was similar to that of the subsagittal rows on the catching side. Since laydowns rarely occur in the former case, but do so almost half the time in the latter, the duration of quiescence was independent of the presence or absence of a laydown.

Reversal

A temporary reversal in the direction of effective stroke occurred exclusively in rows on the side of the prey-catching tentacle. In these rows the effective stroke of all plates was directed orally instead of aborally, and the direction of coordination was also reversed so that antiplectic metachronal waves travelled from the oral to the aboral end of the rows (Figs 2D-F, 3I-P, 4C).

Reversed beating commonly began at the oral end of the row (69% of rows, $N = 169$) (Figs 2D, 3I). The oral-most plate curved upward to perform a reversed recovery stroke towards the aboral pole, followed by an effective stroke towards the mouth. The distally propagated recovery bend resembled a continuation of the upward flexure near the base of the plate formed during the preceding laydown. Successive plates in the aboral direction were lifted away from the surface by the recovery strokes of their oral neighbours, stimulating them to perform reversed beat cycles in turn. Thus, antiplectic metachronal waves were propagated away from the mouth in the reverse direction (Figs 2D, 3J-P). Occasionally, reversed waves did not propagate very far from their origin at the oral end of the row, and only after several false starts did they travel the entire length of the row. In some cases (18% of rows) reversed recovery strokes began simultaneously over a limited region of a row; within a few beat cycles, however, the oral-most plates became pacemakers and antiplectic metachronism was established.

The frequency of reversed beating was 20.5 ± 0.3 Hz ($N = 250$), about twice the rate of forward beating on the non-catching side during this period (11.6 ± 0.6 Hz, $N = 229$) (Fig. 2E,F). The form of the reversed beat cycle closely resembled that of normal beating, except that the directions of the component movements were reversed (Fig. 4A,C). In both cases, the effective stroke was a rapid, stiff swing of the plate, which propelled water, and the recovery stroke was a slower unrolling of the plate in the opposite direction. The shorter metachronal wavelength during reversed beating (Figs 2E,F, 3M-P) is not related to reversal *per se*, but to the higher beat frequency associated with it.

Various patterns of activity were exhibited by different rows during the reversal period (Table 1). The two subtentacular rows adjacent to the prey-carrying tentacle beat in the reversed direction in all cases ($N = 253$). The two subsagittal rows on the catching side underwent reversal in 42% of the cases, and remained quiescent more than half the time. Rarely did these two rows beat in the normal direction. Only this latter pattern, now shown to be atypical, was described in earlier reports based on fewer examples (Tamm, 1979, 1980, 1982). On the non-catching side, all four rows usually beat in the forward direction (70% of cases).

When all four rows on the catching side underwent ciliary reversal, reversed beating was initiated earlier in the subtentacular rows than in the subsagittal rows (Fig. 2F). The subtentacular rows were first or second to begin reversed beating in 96% of their total responses, whereas the subsagittal rows were second, third or fourth in 94% of their reversals (Fig. 5).

The time delay between the onset of reversed beating in subtentacular *vs* subsagittal rows was 0.55 s (median value of the time interval for reversed beating to begin in a given row with respect to the first row to undergo reversal, whether subtentacular or subsagittal; $N = 60$). Reversal was initiated within 0.05 s (median value, $N = 57$) in the two subtentacular rows (Fig. 2D); likewise, reversed beating began at nearly the same time in the two subsagittal rows on the catching side (median, 0.05 s; $N = 11$). Thus, reversal was first initiated almost synchronously in the two subtentacular rows on either side of the prey-carrying tentacle; then, about 0.55 s later, reversal began nearly simultaneously in the two more distant subsagittal rows. This indicates a high degree of synchrony in the initiation of reversed beating in rows equidistant from the catching tentacle.

The mouth opened wider and continued to bend toward the catching tentacle during reversal (Fig. 2D–F), reaching a maximum excursion which was maintained for the remainder of the reversal period. The reversal current swept the prey-carrying tentacle toward the lips (Fig. 2F), where copepods were often successfully ingested even though the pinned animal could not spin.

In order to ascertain whether the patterns of comb row activity during reversal were related to the patterns of the preceding quiescence, we tabulated frequencies of various reversal patterns as a function of the two main patterns of quiescence (global *vs* catching side only). Table 2 shows that regardless of the preceding pattern of quiescence, reversal involving subtentacular as well as subsagittal rows occurred with about the same frequency as reversal in subtentacular rows only. Thus, the activity pattern on the non-catching side during quiescence did not influence whether or not reversal occurred in the subsagittal rows on the catching side.

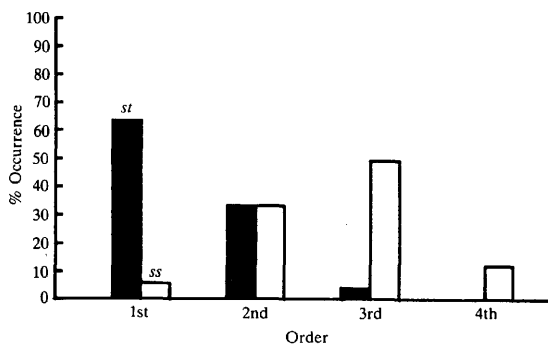


Fig. 5. Relative order of initiation of reversed beating in subtentacular (black bars, *st*) *vs* subsagittal (white bars, *ss*) rows on the catching side.

However, if rows on the non-catching side did not stop during quiescence, those rows almost always continued beating in the normal direction during the subsequent reversal period (Fig. 2D–F; Table 2). In contrast, after global quiescence, rows on the non-catching side remained inactive or resumed normal beating with about equal frequency during the reversal. Thus, active beating on the non-catching side during quiescence was followed by similar activity on that side during the subsequent reversal.

DISCUSSION

The impetus for this investigation came from an anecdotal account by Mrs M. A. Connell of how *Pleurobrachia* conveys food to its mouth: 'This is brought about by the rapid whirling of the *Pleurobrachia* towards the tentacle carrying the prey so that this is carried to the mouth in the current created by the comb plates and then the prey is sucked off by the cilia lining the inside of the lips.' (quoted in Hardy, 1956, p. 136).

To investigate the nature of the ciliary response causing this spinning behaviour, high-speed films were taken previously of immobilized *Pleurobrachia* (Tamm, 1979, 1980, 1982; Tamm & Tamm, 1981; Moss & Tamm, 1981). These earlier studies showed that spinning movements were caused by a unilateral reversal in beat direction of comb rows on the catching side, not by differences on opposite sides in the rate of beating in the normal direction, as assumed by Satterlie (1978).

In this report, more extensive analysis of a larger number of animals has provided a more detailed and complete description of the unilateral ciliary reversal response, including the initiation, patterns and coordination of reversed beating. In addition, we have characterized the other ciliary responses involved in the feeding behaviour of *Pleurobrachia*.

Fast forward period

The brief bout of rapid forward swimming that occurs in response to vigorous contractions of the prey-carrying tentacle resembles the global ciliary excitation induced in non-feeding *Pleurobrachia* by pinching either tentacle (Tamm, 1982). In the latter case, interruption of metachronal wave transmission by a mechanical block prevented conduction of high frequency beating, showing that the signal for ciliary excitation is not conducted to every comb plate directly, but only to pacemakers at the aboral end (Tamm, 1982). The increased rate of beating of these pacemakers is then propagated down the rows by the usual mechanism of hydromechanical coupling between plates (Tamm, 1973). Similar experiments performed on fast forward responses of feeding animals gave identical results (Moss & Tamm, 1981), suggesting that here too high frequency beating is triggered by excitation of aboral pacemakers. An increased rate of beating in the normal direction may thus be a general response to any mechanical stimulus causing strong contractions of a tentacle, whether it be struggling prey or other objects.

Quiescence

High frequency beating ceases when the last metachronal wave has disappeared at the oral end of a row. Because comb plates, unlike most other cilia, do not beat

unless stimulated to do so (Sleigh, 1974; Tamm, 1982), quiescence results from inactivity of pacemaker cilia at the aboral pole. If high frequency beating is caused by activation of these pacemaker cilia by an excitatory signal, quiescence may simply represent the turning off of this excitation.

In contrast to quiescence, ctenophores show an 'active' ciliary arrest following mechanical or electrical stimulation of the body surface (Göthlin, 1920; Horridge, 1966; Sleigh & Barlow, 1982). This inhibitory response is a sudden, temporary stoppage of all comb plates which is propagated rapidly by a diffuse through-conducting pathway to every plate directly, not just to aboral pacemakers. Ciliary arrest in other animals is also an abrupt, nearly synchronous stoppage, usually in a position distinct from that of the quiescent or resting state (Takahashi, Baba & Murakami, 1973; Mackie *et al.* 1974; Takahashi & Murakami, 1968).

The upward bend which forms near the base of quiescent plates during laydown anticipates the reversed recovery stroke which initiates the reversed 'eat cycle'. Sleigh & Barlow (1982) also noted that plates move into an upward curving position before beginning reversed beating. Laydown represents a shift from a resting position at the end of a normal recovery stroke to a 'primed' position poised at the start of a reversed recovery stroke. Laydown thus signals an internal change from forward to reverse states in non-beating comb plates, and in this respect resembles the 'silent reorientation' of resting *Stylonychia* cirri which occurs preparatory to depolarizing or hyperpolarizing activation of ciliary reversal and frequency responses (de Peyer & Machemer, 1983).

Reversal

Although changes in the direction of ciliary beat occur commonly in protozoa (Naitoh & Eckert, 1974; Machemer, 1974), reversal of beat direction in ctenophore comb plates has been claimed by some workers (Coonfield, 1936; Fedele, 1925; Chun, 1880; Verworn, 1891) but denied by others (Parker, 1905). Recently, ciliary reversal in ctenophores was documented directly for the first time by high-speed cinemicrography (Tamm & Tamm, 1981). In this study, a calcium-dependent global reversal of comb plates in *Pleurobrachia* cydippid larvae was induced by raising the KCl concentration of sea water (Tamm & Tamm, 1981). Further studies on *Mnemiopsis* larvae using calcium ionophores and ATP-reactivated ciliary models demonstrated that reversal in beat direction of comb plates, like ciliary reversal in protozoa (Naitoh & Kaneko, 1973), is triggered by an increase in intracellular calcium concentration (Tamm & Nakamura, 1983). Global ciliary reversal in adult ctenophores following chemical, electrical or mechanical stimuli has recently been reported in *Pleurobrachia* (Tamm & Tamm, 1981; Sleigh & Barlow, 1982), *Mnemiopsis* (Tamm & Tamm, 1981) and *Lampra pancerina* (Tamm & Tamm, 1981). In addition, local application of high K^+ or high K^+ -high Ca^{2+} sea water directly on to comb plates of adult *Pleurobrachia* or *Mnemiopsis* induces reversed beating of these plates (A. G. Moss, unpublished results).

The unilateral reversal of beat direction in specific comb rows of feeding *Pleurobrachia* reflects the bilateral arrangement of the tentacles, and is the best documented example of a localized ciliary reversal in metazoans (see Baba, 1968; Holley & Shelton, 1984). It seems likely that reversal is triggered by specific stimuli

associated with prey capture by the tentacles. The tentacle epidermis consists of sensory cells, mucus secretory cells and numerous adhesive colloblasts (Franc, 1978; Hernandez-Nicaise, 1973*b*, 1974; Bargmann *et al.* 1972). A central strand of nerves runs through the tentacle, with numerous nervous elements radiating outward to synapse on to muscle and the various types of epidermal cells; in addition, synaptic contacts between the sensory and glandular cells have been described (Hernandez-Nicaise, 1974). Chemical cues supplied by the prey, or activation of mucus secretion or colloblast discharge during prey capture may be involved in exciting a nervous pathway in the tentacle leading to activation of ciliary reversal on that side.

Comparison of the onset of reversal in the subtentacular and subsagittal rows on the catching side reveals a tight synchrony of response between rows equidistant from the catching tentacle, and a distinct order of activation with distance from this tentacle. The two subtentacular rows always undergo reversal and are the first rows to do so; the two subsagittal rows beat in the reversed direction only about half the time, and about 0.5 s after reversal begins in the subtentacular rows. This suggests that reversed beating is activated by a signal propagated rather slowly around the sagittal hemisphere in opposite directions from the catching tentacle, triggering the two adjacent subtentacular rows first, and reaching the more distant subsagittal rows later. Cases where only the subtentacular rows undergo reversal may be due to decrement or failure of the signal to spread a sufficient distance away from the catching tentacle.

The common finding of synapses onto comb plate cells (Horridge & Mackay, 1964; Horridge, 1965; Hernandez-Nicaise, 1973*a*; Tamm, 1982) suggests that ciliary reversal may be controlled by the nervous system. Romanes-type cutting experiments on *Pleurobrachia* show that the signal for unilateral reversal during feeding is conducted through the surface layer by a diffuse pathway from the tentacle base to every comb plate along a row (A. G. Moss, unpublished). These findings show that the 'tentacular nerve' tract, running from each tentacle sheath midway between the subtentacular comb rows (Hernandez-Nicaise, 1973*a*), is not the primary conducting pathway for unilateral reversal, but do not make it possible to distinguish between a nerve net and epithelial conduction. The apparent conduction velocity of the reversal signal from subtentacular to subsagittal rows (about 0.3 cm) is only about 0.5 cm s^{-1} , which is considerably slower than typical speeds of propagation in nerve-nets and conducting epithelia (Anderson, 1980; Spencer & Schwab, 1982; Bone & Mackie, 1982; Passano, 1982). In contrast, global ciliary reversals, or 'avoiding reactions', of ctenophores appear to be activated by a faster, through-conducting pathway not involving the tentacles.

Reversed beating is presumably caused by an increase in intracellular calcium concentration, as has been shown to be the case for ciliary reversal in protozoa (Naitoh & Eckert, 1974; Naitoh & Kaneko, 1973) and ctenophore larvae (Tamm & Tamm, 1981; Tamm & Nakamura, 1983). If so, it is likely that reversal is triggered by depolarization of the comb plate cells, thereby activating voltage-sensitive calcium channels which allow influx of calcium ions, as in *Paramecium* (Naitoh & Eckert, 1974). Ciliary arrests of lateral cilia on *Mytilus* gills and stigmatal cilia of tunicates are also calcium-dependent responses triggered by membrane depolarization, and are under the control of the nervous system (Murakami &

Takahashi, 1975; Mackie *et al.* 1974; Bone & Mackie, 1982; Takahashi *et al.* 1973; Tsuchiya, 1977; Saimi, Murakami & Takahashi, 1983). Recent intracellular recordings from *Pleurobrachia* show that ciliary laydown and reversal, elicited by electrical stimulation of a tentacle, are accompanied by action potentials in the comb plate cells (A. G. Moss & S. L. Tamm, in preparation).

Once plates are 'primed' for reversed beating in the laydown, the oral-most plate performs a reversed recovery stroke, lifting up neighbouring plates in the aboral direction and stimulating them to make reversed recovery strokes in turn. A wave of reversed beating thus propagates to the aboral end of the row, establishing antiplectic metachronal coordination in the reversed direction. Mechanical blocks prevent transmission of reversed waves; however, new reversed waves are initiated independently at the aboral side of the block, sometimes before the reversed wave from the oral end reaches the block (Moss & Tamm, 1981; S. L. Tamm, in preparation). These observations indicate that initiation and coordination of reversed beating are due to hydromechanical interaction between the plates, as shown previously for beating in the normal direction (Tamm, 1973). In addition, comb plates primed for reversed beating seem to possess a heightened level of mechanosensitivity, as shown by the ability of very small vibrations, transmitted by contact with the mechanical block, to stimulate reversed waves (Moss & Tamm, 1981). This increased mechanosensitivity, together with muscular movements of the oral end associated with bending of the mouth toward the catching tentacle, may explain how the first recovery stroke of the oral-most plate is triggered.

During normal beating in *Pleurobrachia*, lifting of a plate by the effective stroke of its aboral neighbour triggers a power stroke in the aboral direction (Sleigh, 1972; Tamm, 1973). In reversed beating, lifting of a plate (from the laydown position) in the same direction – in this case by the recovery stroke of its neighbour orally – triggers a recovery stroke in the aboral direction. Thus, mechanical stimuli applied in the aboral direction activate either an effective or a recovery stroke in this direction, depending on whether the plate will beat normally or in reverse. The nature of the motile response – effective or recovery stroke – is clearly independent of the direction of stimulation, and may depend upon a programmed switch from normal to reversed states inside the comb plate.

In conclusion, our description of the sequence of ciliary motor responses involved in prey capture by *Pleurobrachia* provides a mechanistic explanation for the feeding behaviour of this important planktonic predator. By analysing the patterns and timing of the unilateral ciliary reversal underlying this behaviour, we have characterized an unusually favourable system for investigating the nervous and ionic control of ciliary beat direction in metazoans.

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