Marine Biology (1999) 133: 249–258

P. H. Lenz · D. K. Hartline

Reaction times and force production during escape behavior of a calanoid copepod, *Undinula vulgaris*

Received: 25 November 1997 / Accepted: 8 October 1998

Abstract Effective escape behavior contributes to the success of copepods in planktonic communities. The kinematics of escape were studied in tethered *Undinula vulgaris* (Calanoida) by analyzing the timing and magnitude of their power strokes to a precisely controlled, sudden mechanical perturbation in the surrounding water. Copepods responded with rapid swims to water velocities of 36 to 86 μm s^{-1}. Reaction times were under 2.5 ms following stimulus onset. The time course of force exerted was complex, but reproducible from stimulus to stimulus. Multiple power strokes (''kicks'') were frequently observed in response to single stimuli. Time intervals of 5 ms were observed between the end of one escape kick and the beginning of the next. *U. vulgaris* developed maximum forces of 40 to over 100 dynes (dyn) during a rapid swim. The behavioral reaction times and intervals between multiple responses observed in this calanoid are among the shortest reported in aquatic invertebrates.

Introduction

Copepods are preyed upon by a wide range of predators, including whales, fishes, squid, jellyfish, chaetognaths and other copepods. Planktonic organisms, including the copepods, have evolved a variety of strategies to decrease predation pressure. Diel vertical migration, transparency and small size are among these strategies (for review see Hamner 1996). In addition, copepods have a spectacular escape behavior (Singarajah 1969, 1975; Strickler 1975; Fields and Yen 1996). During escape, the copepods are propelled forward in a rapid swim by the metachronal power strokes of the 4 or 5 pairs of pereiopods, starting with the most posterior (Storch 1929; Strickler 1975). Each pair of pereiopods is powered by antagonistic promotor and remotor muscle groups (Boxshall 1992). High-speed cinematographic methods have shown that by employing this rapid swim, copepods can achieve rates of 200 to 500 body lengths per second (Strickler 1975; Fields 1996). The effectiveness of this rapid swim in escaping from predators has been demonstrated experimentally in reduced capture rates for copepods compared to other planktonic prey organisms of comparable size (e.g. Browman et al. 1989; Trager et al. 1994).

Mechanoreception appears to be the predominant sensory modality in predator detection (Singarajah 1969; Strickler 1975; Gill 1985; Gill and Crisp 1985). Copepods detect and respond physiologically and behaviorally to very small (10 nm) and brief hydrodynamic signals (Yen et al. 1992; Lenz and Yen 1993; Hartline et al. 1996). High sensitivity to a potential threat is a key capability for an effective escape; however, a successful escape response requires much more. After the detection of a hydrodynamic disturbance, the copepod needs to decide rapidly if the signal was generated by a threat and not by noise. Then, it must determine whether the threat is sufficiently imminent to necessitate initiation of an escape, and which of various possible responses is appropriate. Once initiated, a locomotor reaction needs to generate enough force to provide a timely removal from the potential predator. To understand how copepods achieve successful escapes, direct measurements of reaction times and force development are needed. Using electrical stimulation to elicit rapid swims, Svetlichnyy (1987) measured maximum forces of 48 dynes generated during the power strokes of *Calanus helgolandicus*. In our study, we used hydrodynamic stimuli to elicit escapes by a sub-tropical calanoid, *Undinula vulgaris*, and

Communicated by M.F. Strathmann, Friday Harbor

P.H. Lenz (✉) · D.K. Hartline
Békésy Laboratory of Neurobiology,
Pacific Biomedical Research Center,
University of Hawaii at Manoa,
1993 East-West Road, Honolulu,
Hawaii 96822-2359, USA
Fax: 001 (0)808 956-6984 e-mail: petra@hawaii.edu

we measured the temporal sequence and force development during the rapid swim. The behavioral performance of *U. vulgaris* approaches the limits set by physiological constraints.

Materials and methods

The calanoid copepod *Undinula vulgaris*, which has been described as a warm-water analog to *Calanus* spp. (Park and Landry 1993), is abundant in the coastal waters around Oahu, Hawaii. Specimens of two varieties of *U. vulgaris*, *typica* and *giesbrechti*, were routinely collected in Kaneohe Bay by 5 to 10-min net-tows (50 cm diam, 1 m length, 333 μm mesh). The varieties were identified according to descriptions by Kasturirangan (1963). Adult females (2.2 mm prosome length) of both varieties and one adult male (variety unknown) were used in the experiments. No consistent differences were noted in results from the two varieties. In the laboratory, the copepods were sorted into jars filled with filtered seawater, maintained at room temperature (21 to 24 °C), and fed an algal mixture of *Nannochloris* spp. and *Isochrysis galbana* (Tahitian strain).

The experimental apparatus (Fig. 1) was adapted from the physiological set-up described by Gassie et al. (1993; also see Hartline et al. 1996). Copepods were glued with cyanoacrylate adhesive (Krazy Glue) to a stiff wire tether. They were positioned ~7 mm below the water surface, at least 10 mm from the nearest wall of a glass aquarium measuring 10 × 10 × 5 cm. They were allowed to rest for 1 to 2 h prior to the experiment. Not all specimens survived the gluing and manipulation in good condition (although success rate increased as we gained experience). However, the copepods used in the experiments typically survived for one to several days on the tether. Specimens which did not generate strong forces (> 20 dyn) or which were insensitive to hydrodynamic disturbances were not used in our measurements of forces or threshold sensitivities, even if they were otherwise apparently healthy. The use of tethered copepods in behavioral studies has the advantage of working with a stationary object, but such tethering has trade-offs (e.g. Svetlichnyy and Svetlichnyy 1986; Hwang et al. 1993; Bundy and Paffenhöfer 1996). It results in slower pereiopod movements, and perhaps in alterations in force because the copepod is restrained from being propelled through the water. In addition, mechanotransduction depends on small displacements of the setae in relation to the first antenna (A1). In a free-swimming copepod, a local deformation is required to produce a relative movement of water past the sensory setae (Haury et al. 1980), whereas in our experiments tethering permitted stimulation with precisely-controlled near-field water movements generated by a fixed dipole source.

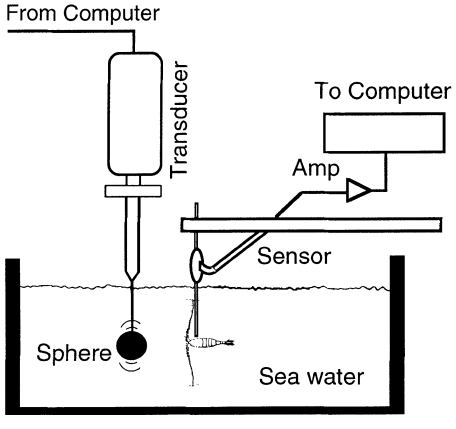


Fig. 1 Experimental set-up. Copepod (*Undinula vulgaris*) is glued to aluminum wire clamped to a rod; rod is mounted on a micromanipulator (not shown). 3 mm sphere is driven by piezoelectric transducer. Force produced by copepod is monitored by fiberoptic displacement sensor, which measures movement of reflector mounted near base of wire tether. Diagrammatic (not to scale)

The hydrodynamic stimulus was produced by the vertical movement of a 3 mm-diam sphere positioned with its center 3.5 to 5 mm in front of the specimen. The stimulating sphere was aligned horizontally with the lower tip of the first antenna (in most experiments) or with the rostrum. No differences were noted in the results obtained at these two positions. The vertical movement of the sphere was produced by a piezoelectric transducer (Burleigh PZL-015) under computer control. Movement closely followed imposed voltages in the frequency range used (200 to 1500 Hz), except for a resonance near 450 Hz, which was avoided (see Gassie et al. 1993 for details). Sphere displacements were determined from the manufacturer's specifications, confirmed in previous work by direct measurement (Gassie et al. 1993). As in other studies of sensitivity of aquatic organisms to hydrodynamic perturbations (e.g. Harris and van Bergeijk 1962; Tautz et al. 1981; Kalmijn 1988; Coombs et al. 1989; Janssen and Corcoran 1993; Wubbels et al. 1993; Coombs 1994), the resulting near-field water disturbances were calculated using dipole equations, as reported previously (Gassie et al. 1993). Because copepods are insensitive to propagated sound (Hawkins and Myrberg 1983; Lenz and Yen 1993), pressure waves generated by the stimulus were not considered. The computed radial (d_r) and tangential (d_θ) displacements of water in the absence of obstructions, at the distance (r) from the center of the moving sphere are given by:

$$d_r = Da^3 \cos\theta \cdot r^{-3} \tag{1a}$$

and

$$d_\theta = {}^1/_2\, Da^3 \sin\theta \cdot r^{-3} \ , \tag{1b}$$

where D = sphere displacement, a = radius of the sphere, and θ = angle from the axis of sphere movement (van Bergeijk 1967). Along a horizontal line through the center of the sphere ($\theta = 90°$), computed flow in the dipole field is tangential (opposite to sphere movement) and given by:

$$d = -{}^1/_2\, Da^3 \cdot r^{-3} \ . \tag{2}$$

Fluid movements in this paper are given in terms of this number computed at A1. One potential error is that this equation applies to laminar, low Reynolds-numbers situations. In our experiments, peak sphere velocities at threshold (typically ~2 mm s^{-1}) give a Reynolds number of ~6, a range in which actual displacements drop somewhat below those predicted by Eq. (2). In studies using similar stimulation methods on fish lateral line, such errors have been found to be minimal (Coombs et al. 1989), and in any event they would underestimate the sensitivity of the copepod detection-system. A second potential source of error is the presence of obstructions in the flowfield, including the copepod, the tether, the water surface and the walls of the aquarium. As the A1 (the reference point for measurements) is the body part closest to the sphere, and given the rapid r^{-3} drop-off of the flow field, we did not correct for more distant obstructions which were of negligible consequence. We also did not correct for boundary layers around the sphere which, at the stimulus frequencies used (> 100 Hz), were small (e.g. Tautz 1979; Kalmijn 1988). Potential sources of artifact in sensory stimulation involving water movements of minute size have been dealt with in more detail by Gassie et al. (1993) and Lenz and Yen (1993). Controls for such artifacts include changing the distance from the sphere to A1 (threshold sphere displacement increases as expected of a r^{-3} relation: Lenz and Yen 1993) and removing the sphere from the bath (behavioral responsiveness disappears). Of greater consequence is the fact that the precise location of the sensor or sensors responsible for eliciting a rapid swim in these copepods is not known (albeit setae on the first antennae are presumably preeminent; Gill 1985). Setal sensors on A1 are distributed over distances of up to several millimeters, representing as much as an order of magnitude in additional attenuation to the most distant antennal locations, so a more precise determination of water movement is of limited value.

The "suddenness" of a stimulus contributes to the generation of many escape responses. We utilized three types of controlled "sudden" sphere movements: in the trapezoidal stimulus, the sphere was moved rapidly from the starting position, maintained at the new position for a pre-determined interval, and then returned to the staring point. The other two types of stimuli were trapezoidally-modulated sinusoids (0.4-cycle turn-on and turn-off: see Gassie et al. 1993 for details), one short (1.5 cycles at frequencies ranging from 100 to 1500 Hz), and one long (7 cycles at 700 Hz). The stimuli differed in the abruptness of achieving a peak velocity (microseconds for the trapezoid; hundreds of microseconds for the sinusoids) and the fact that the trapezoids had velocity peaks with larger temporal separations (10 to 100 ms) than the sinusoids (0.7 ms) at 700 Hz. Following stimulus presentation, a period of 5 to 30 min was allowed for recovery. Decline in responsiveness was seen for presentations separated by < 30 s.

During a rapid swim, the copepod exerted a force on the tether causing a small (< 10 μm) displacement. The component of this force along a horizontal axis, roughly parallel to the copepod's body axis, was measured with a fiberoptic displacement sensor (Philtec 88N) positioned opposite to a small reflective disk mounted near the base of the tether (Fig. 1). The force represented by the displacement was calibrated by pushing against the tether with a wire, deflection of which had been calibrated using weights. Off-axis forces, such as turning movements, were not measured. Force-transducer responses were monitored with an oscilloscope and stored on computer. Signals were digitized at 42 kHz per channel. The transducer was underdamped, with an overshoot of $\sim 20\%$ to abruptly-applied (0.5 ms rise) forces, and had a damping time-constant of 4 ms. The natural resonance of the force-monitoring system (1.5 to 2 kHz) was kept as higher possible while maintaining sensitivity adequate for making measurements. Force signals were filtered at 2 kHz with an eight-pole Bessel filter, but still showed some effects of resonance, as seen in some of the records presented (filtering is a standard method of electronic signal conditioning used to reduce high-frequency noise). Preparations with strong resonance were not used for quantitative force measurements; they were analyzed for timing and amplitude of behavioral events. The timing of events was measured to the nearest 25 μs. Resolution on the displacement sensor was to the nearest 2 dynes. Computer software for stimulus production, data acquisition, and data analysis have been described previously (Gassie et al. 1993).

Results

In the absence of hydrodynamic stimuli, the tethered *Undinula vulgaris* assumed a pattern of periods of beating their cephalic appendages alternating with periods of quiescence. In some cases, occasional power strokes, or what appeared to be A1 wiping was observed. Several forms of response were observed to small brief stimuli. Not all registered clearly on the force-transducer. Stimuli too weak (typically by a factor of two) to elicit a full rapid swim often elicited a bout of beating of the feeding appendages. Sometimes A1 flexion and more exaggerated appendage movements were observed. Since these behaviors did not register on the sensor, they were noted for future reference but not examined in detail.

Undinula vulgaris generated a rapid swim (or "jump") in response to a sufficient stimulus. Threshold water velocities at A1 that elicited a rapid swim ranged from 36 to 86 μm s^{-1} (Fig. 2). Thresholds for short and long 700 Hz sinusoidal stimuli were comparable. Those for trapezoidal stimuli were higher, perhaps relating to the differences in temporal separation of the velocity peaks

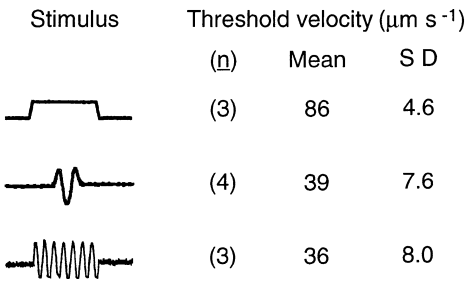


Fig. 2 *Undinula vulgaris giesbrechti*. Minimum water velocities at first antenna eliciting a rapid swim for different stimulus time-courses (*n* number of specimens)

for the two types of stimulus. Varying the frequency of a 1.5-cycle sine wave stimulus, we found a similar range of threshold velocities (Fig. 3A). Calculated minimum water velocities that produced a rapid swim typically ranged between 30 and 100 μm s^{-1} for stimuli between 200 and 1000 Hz (velocity peaks separated by 0.5 to 2.5 ms). Sensitivity appeared to decrease somewhat with wider peak separation. One particularly sensitive individual responded with a rapid swim to water velocities of < 30 μm s^{-1}. Loss of sensitivity occurred at frequencies of > 1000 Hz. Comparing the same threshold data plotted as peak water-displacement, velocity or acceleration (Fig. 3B, A, C, respectively), it appeared that velocity threshold was the most independent of frequency below 1000 Hz. This result was similar to that found physiologically for sensory neuron thresholds in A1 mechanoreceptors, and supports the conclusion that the mechanosensory rapid-swim system is "velocity sensitive" (Yen et al. 1992; Hartline et al. 1996).

Once threshold was reached, a rapid swim followed immediately. Fig. 4 shows a rapid swim monitored by video, as well as the accompanying force-transducer output. The first frame shows the copepod at rest. In the second frame, the copepod is generating a rapid swim with first antennae and anterior appendages retracted. By the third frame, the first antennae are extended again, and by the fourth frame the copepod is in its original position (Fig. 4A). The pattern registered by the transducer shows a rapid and brief impulsive force that takes < 10 ms to complete (Fig. 4B). The distinctive characteristics of a typical force-transient, which we term a "kick", are shown in Fig. 5. The first force detected (a "preparatory" movement, Pr) is directed against the tether in a posterior direction. This corresponds to a backward movement of the body. At the present resolution, we cannot assign this component to an identifiable appendage movement. The preparatory movement is followed by a force in the opposite direction, and the forward-propulsion latency (L) is measured from the onset of the stimulus to this point. This leads to a rapidly rising forward thrust (R), which leads to a prolonged forward propulsion. In some preparations, we were able to distinguish individual peaks in force (arrowed in Fig. 5). Svetlichnyy and Svetlichnyy (1986) observed

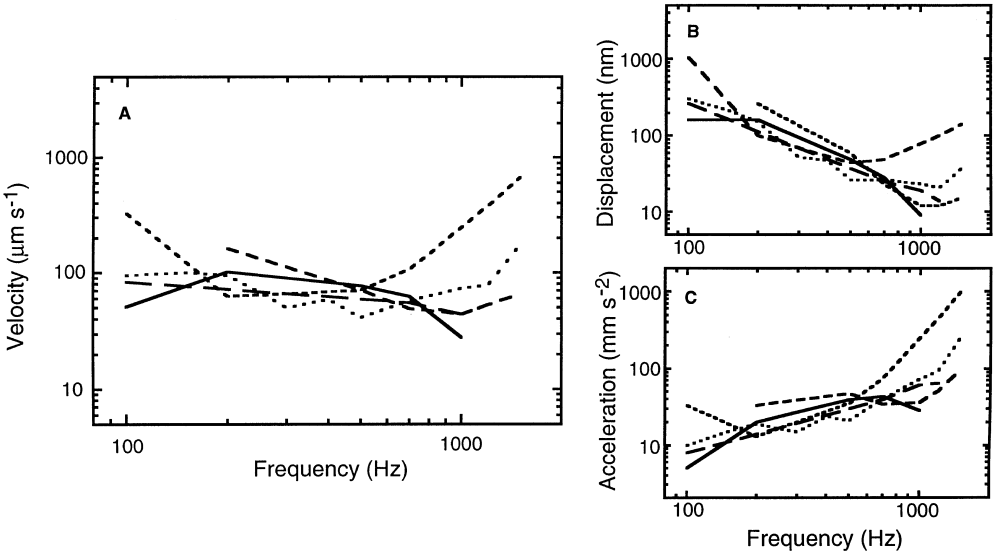


Fig. 3 *Undinula vulgaris giesbrechti* (Experiments UN96-8, UN96-9, UN96-10, UN97-3, UN97-5). **A** Minimum water velocities computed at first antenna (Eq. 2) that elicited a rapid swim, as a function of frequency for sinusoidal stimuli of 1.5 cycle length; data from five adult females; **B**, **C** data in **A** replotted to show threshold water displacements (**B**) and accelerations (**C**) at first antenna

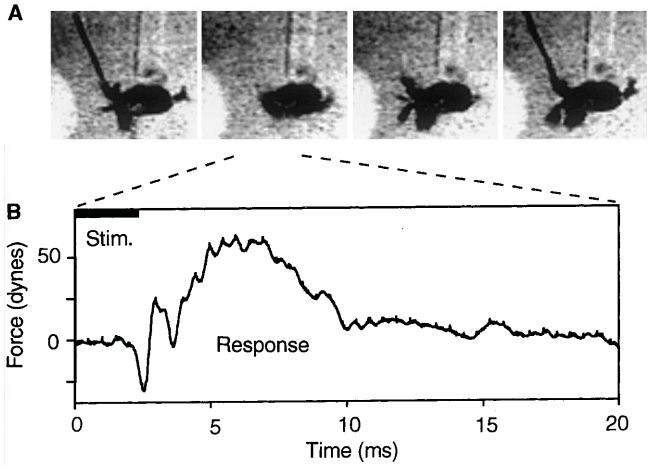


Fig. 4 *Undinula vulgaris typica* (Experiment UN97-1). Escape reaction monitored by conventional video (**A**) and by force-transducer (**B**). **A** Four consecutive video images taken with conventional video (30 frames per second) showing copepod on a stiff tether, anterior towards sphere, part of which is visible in left lower corner of each frame; brief mechanical stimulus (1.5-cycle sinusoid at 700 Hz) is delivered between first and second frame; time period covered by the four frames spans 100 ms. **B** plot of force developed by copepod during escape (*bar in upper left corner* time period that stimulus was on; *dashed lines* indicate that temporal sequence in **B** occurred between first and third video frame; the doubling of downward deflections (backward thrusts) was unusual for this study

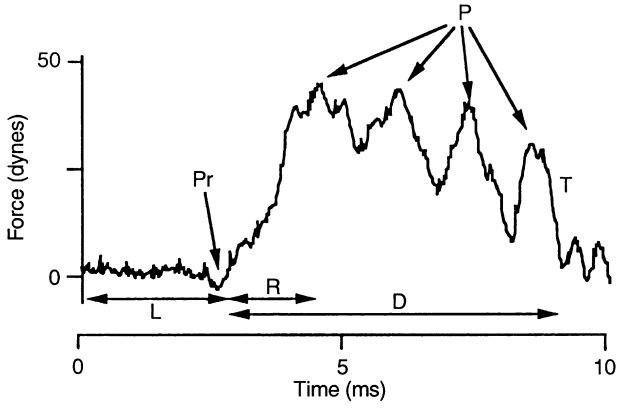


Fig. 5 *Undinula vulgaris giesbrechti* (Experiment UN96-10). Response to sinusoidal stimulus of 1.5 cycle. Water velocity at first antenna = 44 μm s^{-1}. Force-transducer trace of escape indicating identified phases (*L* latency to forward propulsion; *R* rise; *D* kick duration; *Pr* preparation; *P* force peaks; *T* termination). Note that small rapid peaks and notches (especially visible at end of record) are mostly ascribable to high-frequency resonance in force-transducer in this and subsequent figures

similar peaks in force, and correlated these with the beating of the metachronal power strokes of the individual pairs of swimming legs of *Calanus helgolandicus*. Thus, in Fig. 5, the first force-peak would have been generated by the fourth pereiopod pair, the second by the third pair, etc. The maximum force-point of a kick usually occurred at the first or second peak after the rise, with a pattern of decreasing force thereafter and often with abrupt termination (T). Changes in force, during and at the end of a kick were sometimes so abrupt as to be poorly monitored with a 2 kHz filter, and could produce enough resonance in the transducer to obscure details of the force records. Nevertheless, the characteristics described above were present and reproducible in most healthy specimens. The stereotypical response was stimulus-independent. The response pattern was similar for both long and short sinusoidal and for trapezoidal hydrodynamic stimuli.

The reaction of adult *Undinula vulgaris* of both varieties to a hydrodynamic stimulus was rapid. At threshold, forward-propulsion latencies from the onset of the stimulus were ≃2.5 ms (Table 1). Response times shortened by 5 to 30% for stimuli that were three to five times greater in amplitude than threshold (Table 2). The shortest recorded reaction time (1.5 ms) was in response to a very abrupt trapezoidal stimulus. The initial pre-

Table 1 *Undinula vulgaris giesbrechti*. Characteristics of escape behavior under just-threshold conditions [(*n*) no. of responses measured; *values in parentheses* indicate sample size when different from *n*; *Max force* mean peak force ± SD developed during first kick (as shown in Fig. 5) measured from responses early in experiments; *Latency* time interval ± SD from beginning of stimulus to start of forward propulsion (Fig. 5); *Rise* time interval ± SD from start of forward propulsion to first peak in force (Fig. 5); *Duration* time interval ± SD from start of forward propulsion to termination of kick (Fig. 5); K_1-K_2 interkick interval ± SD, i.e. time between termination of first kick (Fig. 5) and beginning of second kick; K_2-K_3 interkick interval ± SD between second and third kicks; – no data]

Experiment No.	Sex	(*n*)	Max. force (dynes)	Latency (ms)	Rise (ms)	Duration (ms)	K_1-K_2 (ms)	K_2-K_3 (ms)
UN96-8	female	(2)		2.36 ± 0.02	1.15 ± 0	5.20 ± 0.02	4.46 ± 0.62	5.66 ± 0.62
UN96-9	female	(3)	124 ± 21 (2)	3.14 ± 0.38	1.88 ± 0.45	3.92 ± 0.31	8.09 ± 0.69 (2)	–
UN96-10	female	(3)	41 ± 1	2.35 ± 0.38	1.61 ± 0.07	6.27 ± 0.06	3.60 (1)	3.96 (1)
UN96-11	female	(2)	61 ± 2	2.40 ± 0.07	2.08 ± 0.02	7.06 ± 0.44	4.55 ± 0.57	6.84 (1)
UN97-2	male[a]	(4)	102 ± 7	2.12 ± 0.23	1.76 ± 0.19	7.34 ± 0.44	–	–
UN97-5	female	(3)	55 ± 0	2.23 ± 0.20	1.14 ± 0.17	5.68 ± 0.58	–	–

[a] Subspecies not known

Table 2 *Undinula vulgaris giesbrechti*. Characteristics of escape behavior under suprathreshold conditions. Further details as in legend to Table 1

Experiment No.	Sex	(*n*)	Max force (dynes)	Latency (ms)	Rise (ms)	Duration (ms)	K_1-K_2 (ms)	K_2-K_3 (ms)
UN96-08	female	(4)		2.25 ± 0.05	1.11 ± 0.02	5.59 ± 0.22	3.79 ± 0.10	4.98 ± 0.35
UN96-09	female	(2)	125 ± 6	2.70 ± 0.33	2.36 ± 0.06	3.99 ± 0.33	8.60 ± 1.07	8.79 ± 1.94
UN96-10	female	(2)	46 ± 0	2.30 ± 0.07	1.60 ± 0.01	6.04 ± 0.16	3.67 ± 0.51	3.96 (1)
UN96-11	female	(2)	71 ± 0	1.70 ± 0	1.72 ± 0.28	7.28 ± 0.17	3.48 ± 0.06	4.57 ± 1.17
UN97-05	female	(2)		1.48 ± 0.05	1.26 ± 0.01	5.62 ± 0.23	–	–

paratory backward movement was observed in most, but not all specimens. Its magnitude varied greatly from near zero to 10 dynes (dyn). This phase was usually completed within 0.2 to 0.4 ms, and was followed by the rising phase of the forward propulsion. A force of 40 to 120 dyn developed within 2 ms during this phase (Table 1 and 2). Although thresholds and the temporal sequences were maintained throughout the experiments, peak forces declined over time. The maximum forces in Tables 1 and 2 were measured from responses early in the experiments. Peak forces were sustained for 3 to 5 ms. Multiple peaks, when they occurred, were typically 1 ms long (Fig. 5B). Up to four major peaks have been observed. The abrupt termination, and return to zero force occurred within 1 ms in most preparations. The duration of the kick varied among specimens, ranging from 4 to >7 ms. The total force-impulse developed during this brief behavior (integral of force over time) was typically 0.2 to 0.3 dyne-s.

Frequently, a specimen responded to a single stimulus with multiple kicks in quick succession (Figs. 6, 7, 8). A single rapid swim consisted to 1 to 9 kicks, with 2 (44%) and 3 (30%) being most frequent in our experiments. The timing and pattern of the kicks showed little variation in any one individual (e.g. Fig. 6), even over the course of long experiments. Fig. 6 shows responses from a specimen near the beginning of the experiment, then after 5 and 9 h. Throughout the experiment the specimen was stimulated at 5 to 30 min intervals. Among different individuals, the timing and pattern of the kicks was quite similar, albeit showing greater variation

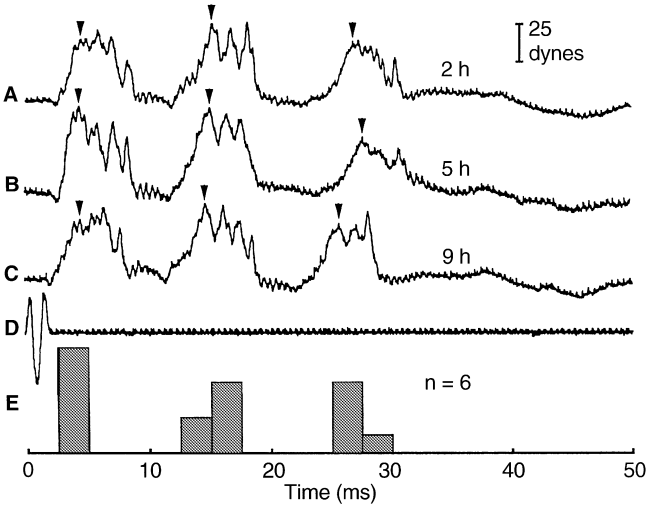


Fig. 6 *Undinula vulgaris giesbrechti* (Experiment UN96-10). Multiple-kick responses in one individual over course of an experiment [*A*, *B*, *C* Responses to water-velocity stimuli of 56, 44 and 145 μm s^{-1} at 2, 5 and 9 h after mounting of specimen, respectively; *D* stimulus trace; *E* histogram of timing of kicks for same experiment (total of six stimuli, including those shown in *A*, *B*, *C*); *arrowheads* peak timing used for histogram]

(Fig. 7). In such a train, successive kicks were of decreasing strength (Figs. 7, 8B).

Comparing responses to stimuli that were well above threshold to those just at threshold, we observed a shortened latency, an increase in the peak force, and an increase in the number of kicks per response (Tables 1 and 2, Fig. 8B, C). Fig. 8A shows the cumulative force-

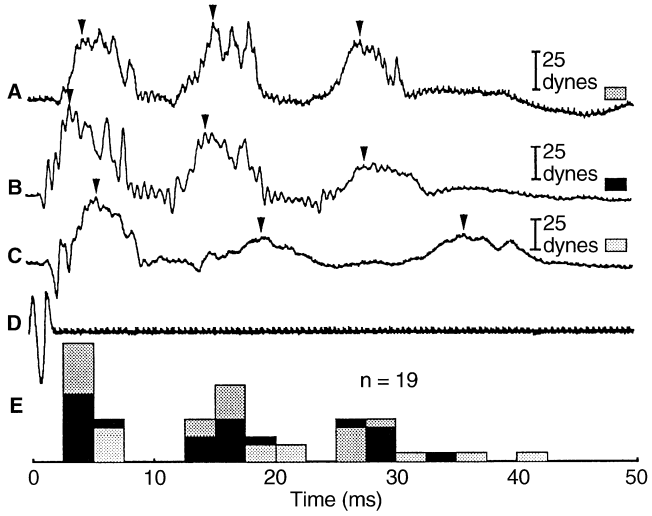


Fig. 7 *Undinula vulgaris giesbrechti* (*A*, *B* Experiments UN96-10, UN96-11) and *U. vulgaris typica* (*C* Experiment UN97-1). Multiple-kick responses for three adult females (*A*, *B*, *C* responses to peak water-velocity stimuli of 56, 114 and 980 μm s^{-1}, respectively; *D* stimulus trace; *E* histogram of timing of initial peak force from 19 responses for the three specimens; *arrowheads* peak timing used for histogram)

impulse integrated over time for the responses shown in Fig. 8B, C (arrowed), as well as additional responses to threshold and suprathreshold stimuli recorded for this preparation. The changes in the strength and timing of responses to a strong stimulus are evident. The differences in the magnitude of the response become more dramatic with time; and by 70 ms post-stimulus, the total force-impulse is more than double that at threshold (1 vs 0.4 dyne-s). Cumulative impulse is related to the distance the copepod would be expected to travel if free-swimming. These latency and force results suggest that the copepod can respond with a faster escape to a stronger threat stimulus.

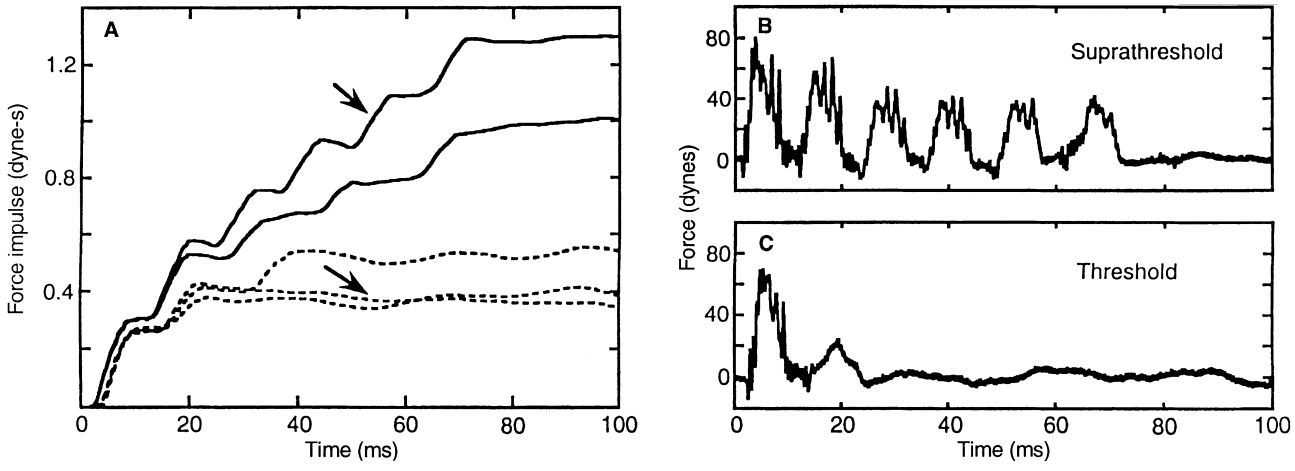
Fig. 8 *Unidula vulgaris giesbrechti* (Experiment UN96-11). Escape forces generated in response to two different intensities of hydrodynamic stimulus. **A** Integral of force over time for responses to two well-suprathreshold stimuli (magnitude = 205 μm s^{-1}; *continuous traces*) and three just-threshold stimuli (magnitude = 64 μm s^{-1}; *dashed traces*); **B**, **C** raw force-records for, respectively, suprathreshold and threshold responses marked with arrows in **A**

Discussion

The quantitative parameters of mechanically-triggered rapid swim in *Undinula vulgaris* appear to reach, or even exceed, the limits of known physiological processes, in the sensory detection of minute hydrodynamic disturbances, in the rapid triggering of responses, and in the kinetics of the response itself.

Escape behavior

Escape probabilities for copepods have been estimated to be 50% higher than for non-evasive prey under experimental conditions (Drenner et al. 1978). The escape response of adults of *Undinula vulgaris* is characterized by a rapid response, the development of a large propulsive force within a few milliseconds, and the ability to generate multiple kicks in quick succession. The force records of the rapid swim can be compared to work done with cinematographic techniques (Storch 1929; Strickler 1975; Kerfoot et al. 1980; Svetlichnyy and Svetlichnyy 1986; Svetlichnyy 1987; Alcaraz and Strickler 1988). For free-swimming cyclopoid copepods, the power strokes of the pereiopods last ~20 ms (Strickler 1975), while for the calanoid *Calanus helgolandicus* they last ~5 ms (Svetlichnyy 1987). In tethered *U. vulgaris*, escape power strokes registered on the force-transducer as a single force impulse lasting ~6 ms. Based on a cinematographic comparison between tethered and free-swimming copepods, Svetlichnyy and Svetlichnyy (1986) estimated that tethered copepods are slowed by 50%. Thus, individual kicks in free-swimming specimens of *U. vulgaris* may be completed within 2 to 3.5 ms instead of the 4 to 7 ms measured on the tethered specimens. A single rapid swim comprised of multiple kicks was usually completed within 30 to 70 ms. Cala-



noids will also respond with multiple rapid-swim sequences. Trager et al. (1994) reported up to three rapid swims within 120 ms during an escape, apparently in response to additional stimulation.

Detection

Detection capabilities of the calanoid A1 mechanosensory system are remarkable. Peak mechanoreceptor sensitivities of ≤20 μm s^{-1} at the first antenna have been measured physiologically for *Labidocera madurae* (Yen et al. 1992; Hartline et al. 1996), *Gaussia princeps* (Lenz 1993), *Euchaeta rimana* (Lenz and Yen 1993) and *Pleuromamma xiphias* (Lenz and Yen 1993). In *L. madurae*, behavioral responses paralleled physiological sensitivities (Hartline et al. 1996). *Undinula vulgaris* responded to water velocities as low as 30 to 40 μm s^{-1}. In both *L. madurae* and *U. vulgaris*, sensitivities were maintained up to 900 Hz. Free-swimming copepods are carried with the flow of surrounding water, which they thus cannot sense directly. Instead, the sensory setae respond to water deformation (Haury et al. 1980). The prominent first antennae of calanoids have long been recognized as important in mediating escape behavior, and they are well suited for detecting water deformation. Water velocities corresponding to thresholds of 30 to 100 μm s^{-1} would result from deformation rates of 0.015 to 0.05 s^{-1} along 2 mm of antenna. While such deformation rates occur commonly in the ocean, they usually rise slowly. For more slowly rising deformation rates, escape thresholds reported for calanoids are higher (0.4 to 1.2 s^{-1} for *Calanus finmarchicus*: Haury et al. 1980; 15 s^{-1} for *P. xiphias*: Fields and Yen 1996). In copepods, over-responsiveness to deformation rates is probably prevented by a combination of a requirement for a rapid rise and adaptation to ambient noise levels typical of sensory systems.

Triggering

Short reaction times are critical for escape as well as for some forms of predatory behavior. Physiologically, there are several time-consuming steps that contribute to the initial delay following stimulus (e.g. Bennett 1982), including: (1) sensory transduction latency in triggering nerve impulses; (2) propagation delays in sensory, interneuronal and motor axons; (3) synaptic delays at the sensory–interneuron, interneuron–motorneuron and neuromuscular junctions; (4) activation delay for muscle tension. Rapid motor responses in the animal kingdom include latencies of 5 ms for springing the trap-jaw mechanism of dacetine ants (Gronenberg 1996b), 10 ms for crayfish escaping from a tactile stimulus (Wine and Krasne 1982), 14 ms for cockroaches escaping air puffs to the caudal cerci (Camhi and Tom 1978), and 14 ms for goldfish responding to hydrodynamic stimuli (Eaton et al. 1988). By comparison, reaction times in *Undinula vulgaris* were extremely short, averaging 1.5 to 3 ms under suprathreshold conditions (Table 2). In the most rapid responses, we observed latencies of <1 ms for initial movement and <1.5 ms for onset of the power stroke of the posterior pereiopods. The shortest transduction latencies to sensory nerve impulses recorded in response to hydrodynamic disturbances are 0.5 ms (Yen et al. 1992). The thoracic nervous system of *Epilabidocera amphitrites* has a giant interneuron-mediated pathway, suggesting a trisynaptic reflex for thoracic appendage activation (Park 1966). In such circuits, the shortest electrical synaptic delays reported are 0.2 ms for crustacean segmental giant-interneurons (Roberts et al. 1982). Synaptic delays as short as 0.4 ms have been measured (Katz and Miledi 1964) at neuromuscular junctions. In crustacean muscle, the shortest delays reported from junctional potential to onset of tension are 2 to 3 ms in the fastest reported crustacean muscle (lobster antennular remotor: Mendelson 1969). The summation of these delays (2.7 to 3.7 ms) exceeds the observed reaction times in *U. vulgaris*, even without considering nerve impulse-propagation delays.

Motor performance

The maximum forces produced during the power strokes varied among individuals, with the largest forces measured in *Undinula vulgaris* reaching 100 dyn. This is substantially greater than the forces of 15 to 20 dyn calculated for *Pleuromamma xiphias* using a swimming model (Morris et al. 1985), or the force of up to 48 dyn for electrically-triggered kicks measured with a force-transducer in tethered *Calanus helgolandicus* (Svetlichnyy 1987). The performance of the motor system of an escaping copepod approaches that of the better-performing terrestrial insects.

Kick kinetics

Lower limits on contraction times reported for single twitches in fast muscle (measured from onset to half-peak of tension decline) are ~6 ms for cicada tymbal muscle (Josephson and Young 1985), and 10 ms for fast division of lobster antennular remotor (Mendelson 1969). With as little as 4 ms duration for the complete power stroke, the kinetics of tension build-up and release in *Undinula vulgaris* are rapid in comparison to fast-muscle twitch capabilities. Further, during the power stroke of individual pereiopods, the cycle may be as short as 1 ms in *U. vulgaris* (Fig. 5), as well as in *Calanus helgolandicus* (Svetlichnyy 1987). To provide such rapid kinetics, other mechanisms such as energy storage need to be considered.

Kick energetics

One measure of performance is the rate of energy development required of the remotor muscles producing

the power stroke in the kick. Svetlichnyy (1987) computed a work output of 8 erg for the power stroke (''working'' phase) of *Calanus helgolandicus*. We estimate a similar value for *Undinula vulgaris*, a stronger peak force being compensated by a shorter stroke duration. If in a 1 mg copepod the power stroke muscles are assumed to represent as much as 20% of the mass (see Bennett-Clark and Lucey 1967), with a maximum mass-specific rate of mechanical power-output of a high-performance insect muscle (266 mW g^{-1}: Josephson 1985), maximum muscular work-production rates for the copepod would amount to 532 erg s^{-1} (1 mW = 10^4 erg s^{-1}). To produce the estimated 8 ergs of total work for the power stroke at this output rate would require 15 ms, which is beyond the available time (4 to 10 ms).

Numerous animal forms with extremely rapid motor behaviors employ energy-storage mechanisms (reviewed by Gronenberg 1996a). Those with single-event motor acts often use a ''catapult'' mechanism, in which a powerful but slow muscle stores up energy before its explosive release in rapid movement: flea jump (1 ms: Bennett-Clark and Lucey 1967), mantis shrimp strike (8 ms: Burrows 1969), click beetle (0.5 ms: Evans 1973), pomerine ant trap-jaw action (0.33 to 1.0 ms: Gronenberg et al. 1993). These require a significant period of time to store the energy after the decision is made to prepare for the rapid action. This typically delays the response by several tens of milliseconds; such delays are not observed in *Undinula vulgaris* reactions.

An energy-storing mechanism has been proposed by Alcaraz and Strickler (1988) based on their histological identification of an elastic protein, resilin, in association with the swimming appendages of *Cyclops scutifer*. It is also supported by our observations that the pereiopods of weak or recently dead individuals of *Undinula vulgaris* appear to have two stable positions, one directed anteriorly (promoted) and one directed posteriorly (remoted). The appendages move abruptly to the opposite position if manipulated past the point approximately perpendicular to the body axis (DKH and PHL personal observations). Displacing the posterior pereiopod pair from its promoted position initiates a cascade of transitions to the remoted position in successively more anterior pereiopods, suggesting that a single muscular contraction could trigger the metachronal sequence. Such a ''click mechanism'' between relatively stable positions is another often-employed approach to energy storage (Gronenberg 1996a).

Multiple-kick kinetics

The overall cycle rate of multiple kicks in *Undinula vulgaris* (100 Hz) is high compared to that usually measured for normal neurogenic muscle (~20 to 40 Hz in insect flight, but up to 100 Hz: Gronenberg 1996a). The fastest crustacean muscle on record, the antennular remotor muscle of lobster (*Homarus americanus*) can operate at a rate of 100 Hz (Mendelson 1969). Myogenic muscles, on the other hand, are capable of sustaining much higher rates. In the midge, a maximum wing-beat frequency of 1 kHz has been reported for intact wings (Prosser 1991); however, usually wing-beat frequencies are at ≤200 Hz, as during flight in larger dipterans. Such muscles tend to require warm-up mechanisms to bring them into the physiological range. Building up the energy-storing resonance often held to be needed to optimize power output is also typically slow (e.g. 3 ms from the initial muscle spike to the first movement in dipterans: Nachtigall and Wilson 1967). Were the copepod system preloaded at rest (a distinct possibility given the rest posture of the pereiopods), a resonance might be more rapidly activated than in the case of insects. Preloading as a means of reducing reaction times in escape behavior has been suggested for springtails (Manton 1972), although the idea has been disputed (Brackenbury and Hunt 1993). Either myogenic or fast neurogenic mechanisms, especially with a kick-start and efficient energy-storage provisions, seem to be possibilities for *U. vulgaris* power strokes.

Multiple-kick energetics

The energy output of *Undinula vulgaris* during multiple kicks is very high. Eight erg generated repeatedly on a 10 ms cycle represents a rate of 800 erg s^{-1} of mechanical energy, or (for 0.2 mg of muscle) a mass-specific rate of 400 mW g^{-1}. This estimate is above values measured for high-output muscles of several other species. For example, Evans (1973) calculated 130 mW g^{-1} for the energy-storage rate in a click beetle, Wakeling and Johnston (1998) obtained 143 mW g^{-1} for fast myotomal fibers in a fish, and Josephson (1985) reported rates of 266 mW g^{-1} for the metathoracic wing muscle of the tettigoniid fly *Neoconocephalus triops*. In addition to the high-power output, the total energy expenditure in a copepod's rapid swim is considerable. Svetlichnyy (1987) calculated 260 erg for a prolonged electrically-evoked jump in *Calanus helgolandicus*. The hydrodynamically-triggered sequence in Fig. 8B generated an estimated 25 erg in 70 ms (~350 erg s^{-1}), or at 20% efficiency, an energy expenditure of 125 erg. Although estimates for *U. vulgaris* need to be refined by more careful measurements, our results, in agreement with those of Svetlichnyy, suggest that copepod power stroke muscles are among the higher-performers of the animal kingdom.

Predator–prey interactions

An escape system with high sensitivity to rapidly-rising deformation rates seems well adapted to evading high-speed pounces of limited spatial extent. A short-latency high-speed escape has little selective advantage in defense against slow predatory strategies.

Lunging attacks by small invertebrates such as predatory copepods and chaetognaths would seem more likely to activate the escape system we have described than attacks from such predators as whales, jellyfish and fishes. Short attack distances have been reported for several invertebrate predators: 3 mm for a pelagic chaetognath attacking a vibrating probe (*Sagitta hispida*: Feigenbaum and Reeve 1977); 3.1 mm for fourth instar *Chaoborus trivitattus* attacking a cladoceran (Kirk 1985); 3.7 mm for a predatory cladoceran (*Leptodora kindti*) attacking copepods (Browman et al. 1989). In spite of the short attack distance, Browman et al. reported that the copepods consistently escaped from the cladoceran predator. The difficulty of catching a copepod was demonstrated experimentally by Chen et al. (1996): juvenile squid have to acquire, through experience, the skill to capture these evasive prey.

A sensitive detection system, a rapid response, and powerful muscle output during the escape contribute to the success of calanoids and cyclopoids in planktonic communities. *Undinula vulgaris* matches or exceeds the physiological performance reported for other crustaceans and arthropods. Mortality by predation is thought to be a limiting factor in many planktonic populations, although data to support this hypothesis are difficult to obtain (e.g. Ohman and Wood 1996). The behavioral data suggest that predation risk is sufficiently important to warrant the evolution of an escape system that approaches the physiological limits. How these copepods achieve this performance is still unknown. Morphological studies of the A1 mechanoreceptors have shown many unique structural features in calanoids that are not present in other crustaceans (Weatherby et al. 1994). These structures probably contribute to the high mechanosensitivities. Further studies are needed to understand how the neuromotor performance is achieved.

Acknowledgements We thank S. Lum for technical assistance, including participation in some of the experiments, E. Buskey for the loan of video equipment, A. Davis for assistance in the collection, maintenance and identification of *Undinula vulgaris*, C. Unabia for helping us set-up the algal cultures, B. Jones for making the data acquisition and analysis programs available to us, and four anonymous reviewers for their thoughtful comments. H. Akaka, B. Kodama, T. Murphy and R. Sanborn provided invaluable technical assistance. The Hawaii Institute of Marine Biology kindly allowed us to use their facilities and boats for copepod collections. The experiments comply with the current laws of the country in which they were performed. The research was supported by NSF OCE 95-21375.

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