A KINEMATIC ANALYSIS OF TENTACLE EXTENSION IN THE SQUID *LOLIGO PEALEI*

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Summary

High-speed ciné recordings of prey capture by the squid *Loligo pealei* were used to analyze the kinematics of the rapid tentacular strike. The proximal portion of the tentacle, the stalk, elongates during the strike. The non-extensible distal portion of the tentacle, the club, contacts the prey and attaches using suckers. Seven sequences of prey capture filmed at $750\,\mathrm{frames\,s^{-1}}$ were analyzed frame by frame. The positions of the head, the tentacles and the prey were digitized, and the data were smoothed using quintic natural B-splines and the generalized cross-validation (GCV) criterion. During the strike, the animal swims forward at velocities ranging from $0.7–1.2\,\mathrm{m\,s^{-1}}$, and as the eight arms are flared, the tentacular stalks elongate. Tentacular extension occurred in approximately $20–40\,\mathrm{ms}$ with peak strains in the tentacular stalk ranging from $0.43–0.8$. Peak longitudinal strain rates varied from $23–45\,\mathrm{s^{-1}}$. Maximum extension velocities of the stalk were calculated to be over $2\,\mathrm{m\,s^{-1}}$ with peak accelerations of approximately $250\,\mathrm{m\,s^{-2}}$. Once the tentacular clubs have contacted the prey, the tentacular stalks are frequently observed to buckle.

Key words: cephalopod, kinematics, prey capture, squid, tentacle, *Loligo pealei*.

Introduction

This study describes the kinematics of the tentacular strike in the squid *Loligo pealei* based on high-speed ciné recordings of prey capture. Previous studies of decapod cephalopods including the cuttlefish *Sepia officinalis* (Holmes, 1940; Messenger, 1968, 1977; Sanders and Young, 1940; Wells, 1958; Wilson, 1946), young sepioids (Boletzky, 1987) and loliginid squid (Chen *et al.* 1996; Fields, 1965; Hurley, 1976; Kier, 1982; LaRoe, 1971; Lee *et al.* 1994; Neill and Cullen, 1974; Nicol and O'Dor, 1985) have provided descriptions of the sequence of prey-capture behaviour and the tentacle strike. A detailed kinematic analysis of the remarkable tentacular strike of decapods has not, however, been performed. In addition to providing the first precise, quantitative description of the tentacular strike in decapod cephalopods, the kinematic results from the present study have been used in a separate study to test portions of a forward-dynamics model. In the forward-dynamics method, movements of body parts are calculated from a prescribed mechanical stress distribution, or a prescribed distribution of muscle activation. The model was used to predict the changing geometry, the pressure and stress distribution, and the velocity and kinetic energy distribution of the tentacle (van Leeuwen and Kier, 1997). The tentacular strike is of particular interest because support and movement

in these appendages is provided by a complex three-dimensional array of musculature, termed a "muscular hydrostat" (Kier and Smith, 1985; Smith and Kier, 1989), rather than by the more commonly studied musculoskeletal systems. In addition, the muscular morphology (Kier, 1982), muscle fibre ultrastructure (Kier, 1985), muscle fibre biochemistry (Kier and Schachat, 1992; Kier, 1991) and muscle fibre development (Kier, 1996) of the tentacles have been documented previously, and we are thus in a unique position to integrate these multiple levels of analysis in understanding the production of this specialized behaviour.

Overview of prey-capture behaviour in loliginid squids

Although the primary focus of the present study is the tentacular strike, it is useful to place the strike in the context of the typical sequence of prey-capture behaviour observed. Three sequential phases of prey capture by decapod cephalopods in the laboratory have been defined: attention, positioning and strike (Messenger, 1968, 1977). The attention phase occurs when prey is introduced into the aquarium. The squid responds by rapidly turning the head so that the arms and tentacles project towards the prey and the eyes are directed forward. While maintaining the orientation of the arms and

tentacles towards the prey, the animal then turns so that its long axis is also pointed towards the prey. Changes in colouration frequently accompany this phase, which lasts for 0.5–2 s (Kier, 1982).

During the positioning phase, the squid swims directly towards the prey with the arms and tentacles held forward. The arms are held together in a tight cone-shaped arrangement enclosing the two tentacles, with the distal tip of the tentacular clubs protruding just beyond the arms. If the prey is moving, the animal keeps the tips of the arms and tentacles pointed at the prey by bending the arms and tentacles in the direction of prey movement, moving the head, and altering course. The duration of the positioning phase is variable (approximately 1–4 s) and depends on the distance that the squid must swim to the prey (Kier, 1982).

The final phase of the attack, the strike, occurs as the animal continues to approach the prey. When the distal ends of the tentacles are approximately 4–6 cm from the prey (squid dorsal mantle length is 13–20 cm), the animal lunges forward, flares the arms outwards, and rapidly elongates the tentacles. The tentacles are extended in a straight trajectory and reach the prey in as little as 20–30 ms (Kier, 1982). When the tentacles strike the prey, the prey is frequently pushed away from the squid, and the compressive force on the tentacular stalk causes it to buckle or become folded. The buckling disappears as the tentacles shorten, bringing the prey within reach of the arms. In addition to elongation, the tentacular stalks are frequently observed to twist around their long axes during the strike. This twisting or torsion is observed to occur in either a clockwise or anticlockwise direction. Torsion of the tentacular stalk may be important in orienting the club so that the suckered surface strikes the prey (Kier, 1982). The arms subdue and manipulate the prey into an appropriate position to be eaten. The tentacular clubs are released from the prey once it is enclosed in the arms, and the tentacles are not involved further in prey manipulation.

In the present study, the position of the animal and the dimensional changes of the tentacles are analyzed in order to measure the body and tentacular velocities and accelerations, and the tentacular strain and strain rates.

Materials and methods
Experimental animals

Specimens of the squid *Loligo pealei* Lesueur, 1821 were collected and maintained in the laboratory by the staff of the Marine Biomedical Institute, University of Texas Medical Branch at Galveston, TX, USA. The squid were captured offshore from a research vessel by attracting them to the surface using bright lights at night and lifting them onboard using dip nets. Special attention was given to minimizing handling during capture, transport to shore and transfer to closed seawater systems in the laboratory (temperature 19 °C, salinity 35 ‰). Detailed descriptions of the capture and transport methods, and the closed seawater systems can be found in Hanlon *et al.* (1978, 1983).

High-speed photography

A Redlake Industries HYCAM 16 mm high-speed ciné camera equipped with 1000 Hz dual LED timing lights was mounted above a large raceway tank (9.1 m long, 1.8 m wide, 0.24 m deep) containing the squid. Lighting was provided by eight 300 W dichroic mirror bulbs mounted in two fan-cooled pallets. Penaeid shrimp were used as prey and were sutured to the end of a fine wire so that they could be tethered on the bottom of the raceway in the centre of the camera field. A grid (0.02 m spacing) large enough to fill the entire camera field was placed on the floor of the tank. For several days prior to filming, the lights were turned on, and the prey offered only in the centre of the camera field. After 2 days of this conditioning routine, most squid in the tank would immediately gather around the camera field when the lights were turned on. After watching the feeding for several days, it was possible to anticipate strikes on the prey by the squid so that the camera could be turned on and allowed to accelerate up to speed prior to the strike, yet not waste film. Approximately 40 sequences of prey capture were filmed at 750 frames s^{-1} on Kodak Tri-X reversal film. Although filming in a tank containing several animals was helpful in obtaining a large sample of prey-capture sequences, it precluded weighing and measuring the individual animals filmed.

Frame-by-frame analysis and digitizing

Seven prey-capture sequences were analyzed in detail for the present study. These sequences were chosen because they included, in the camera field, a view of the head of the squid at the initiation of the strike. A view of the head was necessary in order to determine the location of the base of the tentacular stalks. An NAC DF16C 16 mm analysis projector was used to project images of single ciné frames onto a vertically oriented Numonics 2210 digitizing tablet interfaced with a microcomputer. The distance to the prey and the length of the tentacles were digitized using Sigma-Scan software (Jandel Scientific, Corte Madera, CA, USA). Since the tentacle base is enclosed in the arm array, it was necessary to use an external landmark for the position of the tentacle base. Based on dissection of preserved specimens, the anterior margin of the lens of the eye was determined to be at the same location along the longitudinal axis as the tentacle base and was easily observed (the bulge of the lens is obvious from above) in the prey-capture sequences. For each sequence, the club length was measured on those frames that showed the border between the club and stalk clearly, and this value was subtracted from the total length of the tentacle to calculate tentacular stalk length. We assume that the club length does not change during the strike. Since we were unable to weigh or measure individual animals at the time of the filming, animal size was measured as the width of the head at the position of the eyes for each film sequence. The grid background was used for calibration. The timing-light marks on the film edge were used to determine the actual frame rate and to compensate for any changes in frame rate as the film was accelerated up to speed

at the beginning of a sequence. The elapsed time in 10 ms intervals from the first frame of the sequence was noted on the appropriate frames of the sequence.

The data were smoothed using quintic natural B-splines and the generalized cross-validation (GCV) criterion (Woltring, 1986). Uncorrelated, additive noise in the data and essentially smooth underlying functions are assumed in this procedure. The noise may be non-stationary. For four out of seven sequences analyzed, this method was applied successfully. In three cases, the GCV criterion resulted in too low a smoothing parameter, probably caused by correlated errors in subsequently digitized frames. For these cases, we applied a value of 250 for the smoothing parameter (see Table 1). This value was in the range of values found with the GCV method for the other sequences. Velocities and accelerations were obtained by single and double differentiation of the smoothed curves.

Results

Kinematics of the tentacular strike

The sequence with the highest measured tentacular strain rate (sequence 3) will be described in detail (head width at the eyes of this animal was 27 mm). Fig. 1 shows individual frames from the high-speed ciné sequence, and Fig. 2 is a plot of the data obtained by digitizing individual frames from this sequence. Fig. 2A is a plot of the distance from the base of the tentacles to the prey and includes both the raw data and a plot of the data after smoothing with the GCV criterion. The prey was essentially stationary during this period so this plot provides a reasonable measure of body displacement. Fig. 2C is a plot of the velocity derived from the smoothed distance-to-prey data and Fig. 2E is a plot of the acceleration. The beginning of the sequence is approximately 65 ms before the initiation of the tentacular strike. During this period, the animal accelerated as it approached the prey from a velocity of approximately $0.5\,\mathrm{m\,s^{-1}}$ to a maximum of $0.9\,\mathrm{m\,s^{-1}}$. The highest acceleration during the approach (approximately $30\,\mathrm{m\,s^{-2}}$) occurred immediately before the initiation of rapid tentacular extension. The velocity decreases rapidly (Fig. 2C and negative acceleration peak in Fig. 2E) when the tentacles strike the prey.

Both the raw and the smoothed tentacle-length data are plotted in Fig. 2B, and the tentacle strain [strain, $\varepsilon = (l-l_0)/l_0$, where l=instantaneous tentacle length and l_0=initial tentacle length] and strain rate are plotted in Fig. 2D and Fig. 2F, respectively. During the approach to the prey prior to the strike, the tentacles first elongate slowly (strain of 0.08 in 40 ms) and then shorten slightly. The tentacular strike is then initiated and involves an explosive and extremely rapid elongation of the tentacles in approximately 30 ms. The peak average longitudinal strain in the tentacular stalk during the strike was estimated to be 0.69. The peak strain rate of the stalk was estimated to be $45\,\mathrm{s^{-1}}$ with a peak velocity of $2.3\,\mathrm{m\,s^{-1}}$ (Fig. 2C) and a peak acceleration of $250\,\mathrm{m\,s^{-2}}$ (Fig. 2E).

The other prey-capture sequences analyzed were, in general, similar to sequence 3 described above. For comparison, a sequence of individual frames for sequence 4 (Fig. 3) and sequence 20 (Fig. 4) are provided together with plots of the digitized data and analyses for these sequences (Figs 5 and 6, respectively). Table 1 summarizes the results for the sequences analyzed. The maximum velocity of the animals as they approached the prey ranged from 0.77 to $1.19\,\mathrm{m\,s^{-1}}$. The amount of time elapsed between the initiation of tentacular extension and prey contact ranged from approximately 20 to 40 ms. The range of maximum strains measured in the tentacular stalk was 0.43–0.80 with strain rates from 22.8 to $45.4\,\mathrm{s^{-1}}$. Maximum extension velocities of the tentacles were calculated to range from approximately 1.75 to $2.5\,\mathrm{m\,s^{-1}}$ with accelerations of the club with respect to the tentacular base of 150–$250\,\mathrm{m\,s^{-2}}$.

Additional observations concerning tentacular strike behaviour

We observed several additional aspects of the tentacular strike that have not been described previously. As described above, the

Table 1. *Morphological and kinematic data from prey-capture sequences by* Loligo pealei

Sequence	Head width* ± S.D. (mm)	l_{tent} (mm)	l_{club} (mm)	Smoothing	p_s	ε_{max}	$\dot{\varepsilon}_{max}$ (s⁻¹)	v_{bpmax} (ms⁻¹)
3	27.1±0.6	93.0	40.8	GCV	173	0.69	45.4	0.93
4	31.0±0.5	130.0	48.5	Hand	250	0.58	27.4	0.97
5	31.4±0.4	121.0	51.6	Hand	250	0.49	30.3	0.77
6	31.3±0.5	121.0	50.1	GCV	370	0.62	22.8	0.80
15	32.6±0.4	122.0	50.0	GCV	240	0.77	32.2	1.19
20	31.6±0.3	123.0	48.0	GCV	327	0.43	23.9	0.90
25	31.7±0.5	130.5	46.9	Hand	250	0.80	29.0	1.19

Smoothing was carried out either by application of the generalized cross-validation criterion (GCV) or by prescribing the smoothing parameter ('hand', see Materials and methods).

*Head width values are the mean of measurements made on 20 frames from each high-speed ciné sequence.

Abbreviations: l_{club} = club length used in film analysis; l_{tent} = retracted tentacle length used in film analysis; p_s = smoothing parameter; v_{bpmax} = maximum velocity of squid relative to prey; ε_{max} = maximum strain of tentacular stalk; $\dot{\varepsilon}_{max}$ = maximum strain rate in longitudinal direction of tentacular stalk.
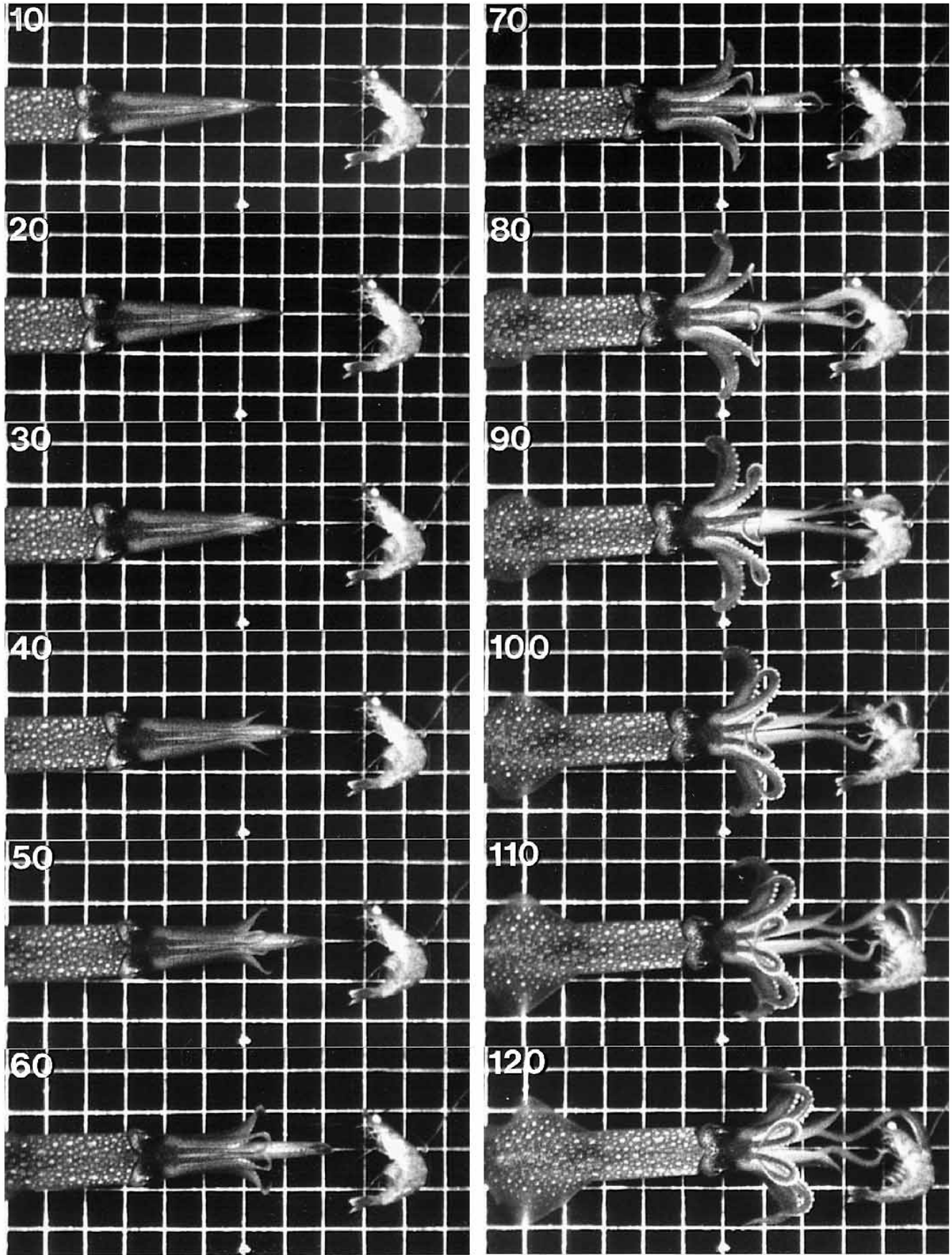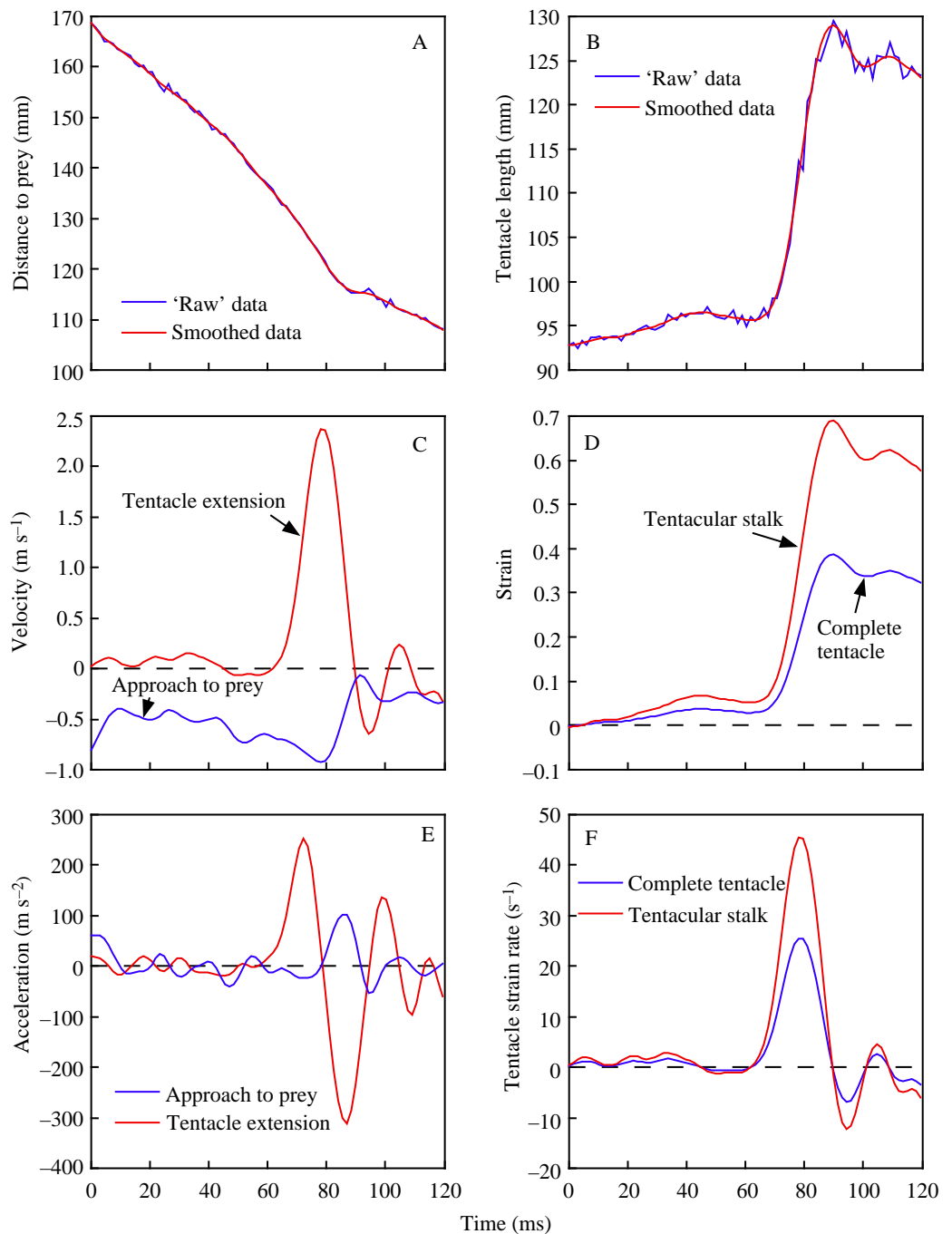
Fig. 1

Fig. 1. Photographs of selected frames from a high-speed ciné sequence (sequence 3) of the capture of prey (a penaeid shrimp) with the tentacles by *Loligo pealei*. The elapsed time (ms) from the start of the sequence is indicated in the upper left-hand corner of each frame and corresponds to the time indicated by the abscissa of the plots in Fig. 2. The grid spacing in the background is 0.02 m.

arms are flared just prior to the initiation of the strike. The arm flare involves a bending of the arms away from the tight cone-shaped arrangement in which they are held during the attention and positioning phases of prey capture. The bend is initiated at the terminal portions of the arms and proceeds proximally so

that the arms 'peel away' from the cone. The ciné films show that arm-pairs I, II and III are flared prior to the strike, but arm-pair IV remains straight, aligned with the tentacular stalks during the entire elongation phase of the strike (Figs 1, 3, 4). In several sequences, the tentacles were deflected upon striking the prey. In these sequences, the tentacular stalks remained straight and were aligned along the length of arm-pair IV, and bending of the stalks was localized at the point that they extended beyond the arm pair (Fig. 7), suggesting that the arms provide stability and alignment to the tentacular stalks during the extension. Flaring of arm-pair IV occurs after elongation of the tentacles in a similar manner to that described above for the other arms.

Fig. 2. Plots of data obtained by digitizing each frame of the prey-capture sequence (sequence 3) shown in Fig. 1. (A) The distance from an arbitrary point on the prey to a point on the head of the squid, data are presented both in 'raw' form (blue) and after smoothing (red). (B) The length of the entire tentacle. 'Raw' data are in blue, smoothed data are in red. (C) The smoothed data from A and B were used to plot the velocity of the animal (blue) and the velocity of the tentacle tip relative to the tentacle base (red). Note that the velocity of the squid relative to the prey is obtained by differentiation of the squid-to-prey distance. Therefore, the velocity is negative on the plot if the animal is approaching the prey. (D) The strain of the entire tentacle (blue), and the strain of the tentacular stalk (red) obtained by subtracting the length of the club (assumed to be constant in length) from the measurements of tentacle length. (E) The accelerations of the animal (blue) and the tentacle (red). (F) The strain rates of the tentacle (blue) and the tentacular stalk (red).
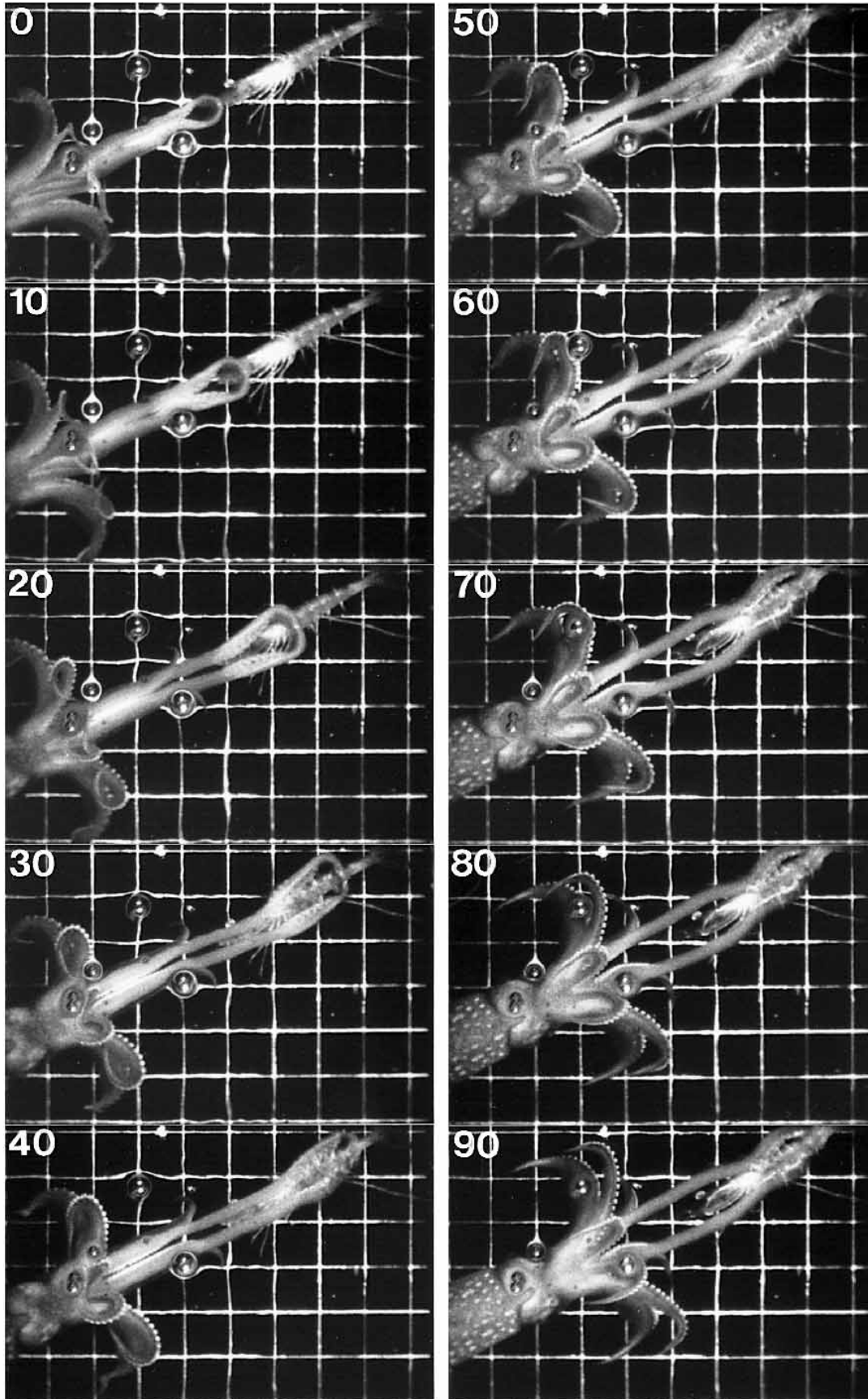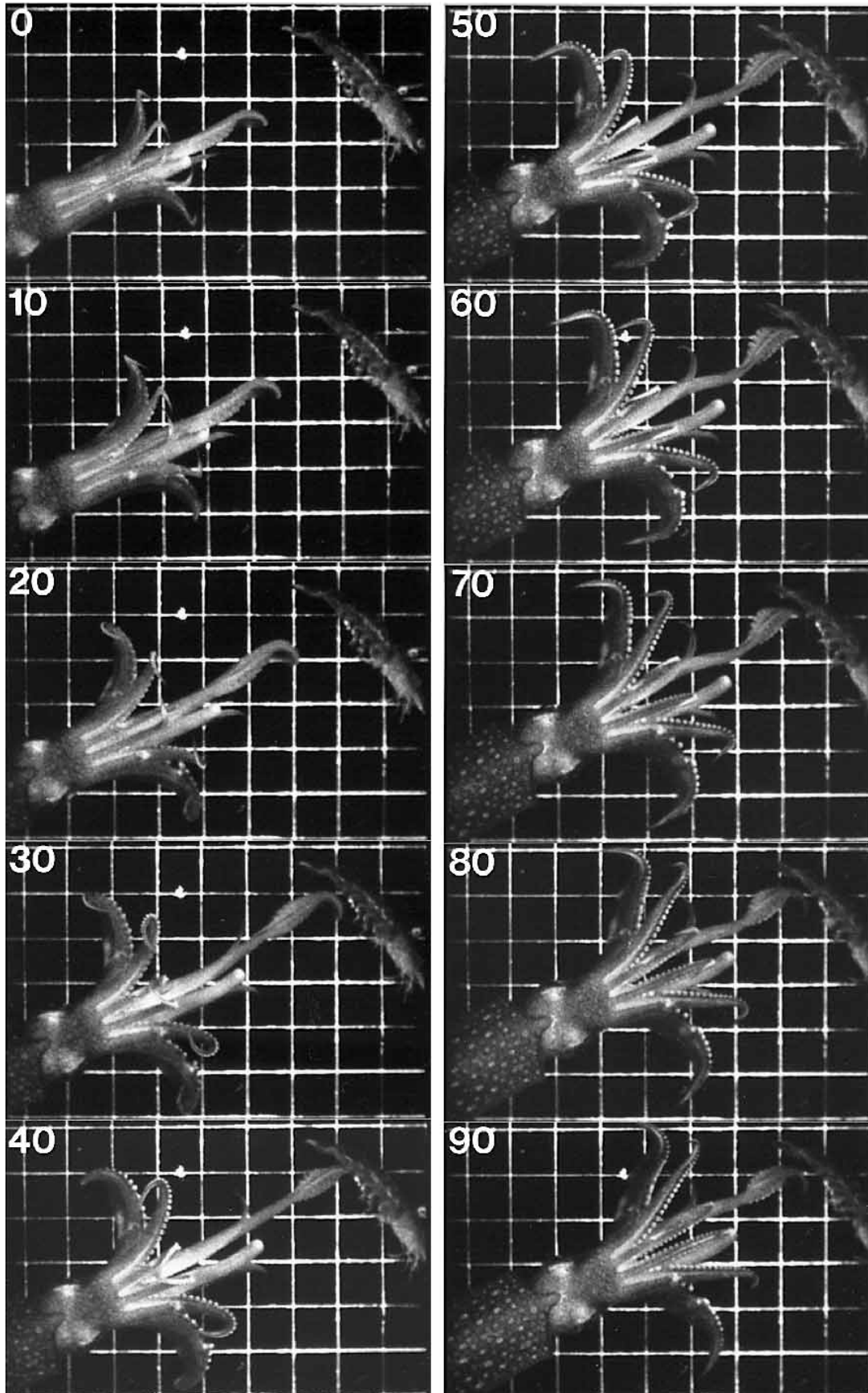
Fig. 3. For legend see p. 48.

Fig. 4. For legend see p. 48.

Fig. 3. Photographs of selected frames from a high-speed ciné sequence (sequence 4) of the capture of prey (a penaeid shrimp) with the tentacles by *Loligo pealei*. The elapsed time (ms) from the start of the sequence is indicated in the upper left-hand corner of each frame and corresponds to the time indicated by the abscissa of the plots in Fig. 5. The grid spacing in the background is 0.02 m. Note that in the first three frames shown, the tip of the tentacular clubs remain attached to one another. The circular objects are bubbles on the water surface.

Fig. 4. Photographs of selected frames from a high-speed ciné sequence (sequence 20) of the capture of prey (a penaeid shrimp) with a single tentacle by *Loligo pealei*. The animal in this sequence is missing the right tentacular club. The elapsed time (ms) from the start of the sequence is indicated in the upper left-hand corner of each frame and corresponds to the time indicated by the abscissa of the plots in Fig. 6. The grid spacing in the background is 0.02 m.

Several additional movements of the tentacles are also worth noting here. During the entire elongation phase of the strike, the terminal tips of the two tentacular clubs were observed to remain closely opposed. As the tentacles extend, the clubs often separate from one another, yet the tips of the clubs appear to remain attached to each other forming an 'arch' between the two clubs (Fig. 3). This attachment also appears to be maintained during torsion or twisting around the long axis. Torsion appears to be used to orient the clubs in such a way that the suckered surface strikes the prey. Torsion in both clockwise and anticlockwise directions was observed. In the retracted tentacles, the suckered surfaces of the two clubs are opposed. As the tentacles elongate, they twist so that the suckers face outward and the tips of the clubs remain attached.

Although the majority of the strikes involved extension of the tentacles in a straight trajectory, in several sequences the tentacles followed a curved path. In these sequences, the tentacles appeared to be aimed too high, and although the initial elongation occurred in a straight path, as the clubs passed over the prey they looped down around it. It did not appear to be the case that contact with the prey caused this curved trajectory. As noted previously, when the clubs actually strike the prey, the tentacular stalks often buckle so that the stalks are thrown into series of waves or folds and the prey is frequently pushed away from the squid. In the instances when the tentacles followed a curved path, the proximal portion of the stalk remained straight and only the distal portion of the stalk and the club bent to curve around the prey, which remained stationary.

Finally, in several sequences, the animals followed the typical sequence of attention and positioning, but did not extend the tentacles. In these instances, all eight arms and the tentacles were flared and the animals jetted forward to enclose the prey in the arms. This mode of prey capture was used with more slowly moving or moribund prey.

Discussion

Sources of error in the kinematic analysis

There are several sources of error in the measurement of the length of the tentacles during the strike. As described above, the tentacular stalks frequently buckle upon striking the prey. Since the buckling of the tentacles may occur in and out of the plane of focus of the camera, measurements from a single camera view will tend to underestimate the true length of the stalks. Although this should not affect the measurements of tentacular extension during the initial portion of the strike, the maximum tentacular stalk strain is likely to be larger than the values reported here. A similar potential problem exists if the animal was not horizontal during the sequence so that the tentacles were oriented obliquely to the plane of focus. In order to minimize this potential source of error, the depth of the water was kept relatively shallow, but slight oblique orientation by the squid during feeding was still possible. Finally, although the base of the tentacles could be accurately identified using the eyes as landmarks, and the tips of the tentacles were generally clearly visible, estimating the tentacular club length was more difficult. The transition between the proximal stalk and terminal club was visible at some point in all of the sequences analyzed (it is hidden by the arms during the initial portion of the strike), but there is some uncertainty in localizing the precise border between the two portions of the tentacle. This is a potential source of error because the club length was subtracted from the total length to obtain an estimate of the stalk length. For example, if the club length was overestimated, then the maximum strain and strain rate of the tentacular stalk would also be overestimated.

Stereotypy and variability in strike behaviour

Although the general form of the strike and the prey-capture behaviour of *Loligo pealei* appears to be quite stereotyped, we observed variability in the kinematic parameters, in particular with respect to maximum strain and strain rate. At this point, however, it is difficult to assess the extent to which factors such as contact with the prey, buckling of the stalks and errors in estimating club length are responsible for the variation observed. We were interested to note, however, that by far the highest strain rate and acceleration was observed in the smallest animal filmed (sequence 3). Although a larger sample size with greater size variation is required to confirm this trend, a forward-dynamic model of the tentacle strike (van Leeuwen and Kier, 1997) predicts that there should be a decrease in the acceleration capabilities of the tentacles with isometric growth if sarcomere properties remain constant. This is due to the fact that the extension force of the tentacles is proportional to l^2 (where l is any length measure) but the mass to be pushed forward is proportional to l^3. Thus, the high acceleration and strain rate in the smallest animal may be an effect of scale.

In all sequences analyzed, high-amplitude oscillations are observed in the acceleration curves of the tentacles (e.g. Fig. 2E). The first strong positive peak is most likely to be due to extensor muscle activity. The strong negative peak that follows is probably a complex combination of impact with the prey, elastic counter-forces of connective tissue, and varying tensile stresses in the extensor muscles, as well as the
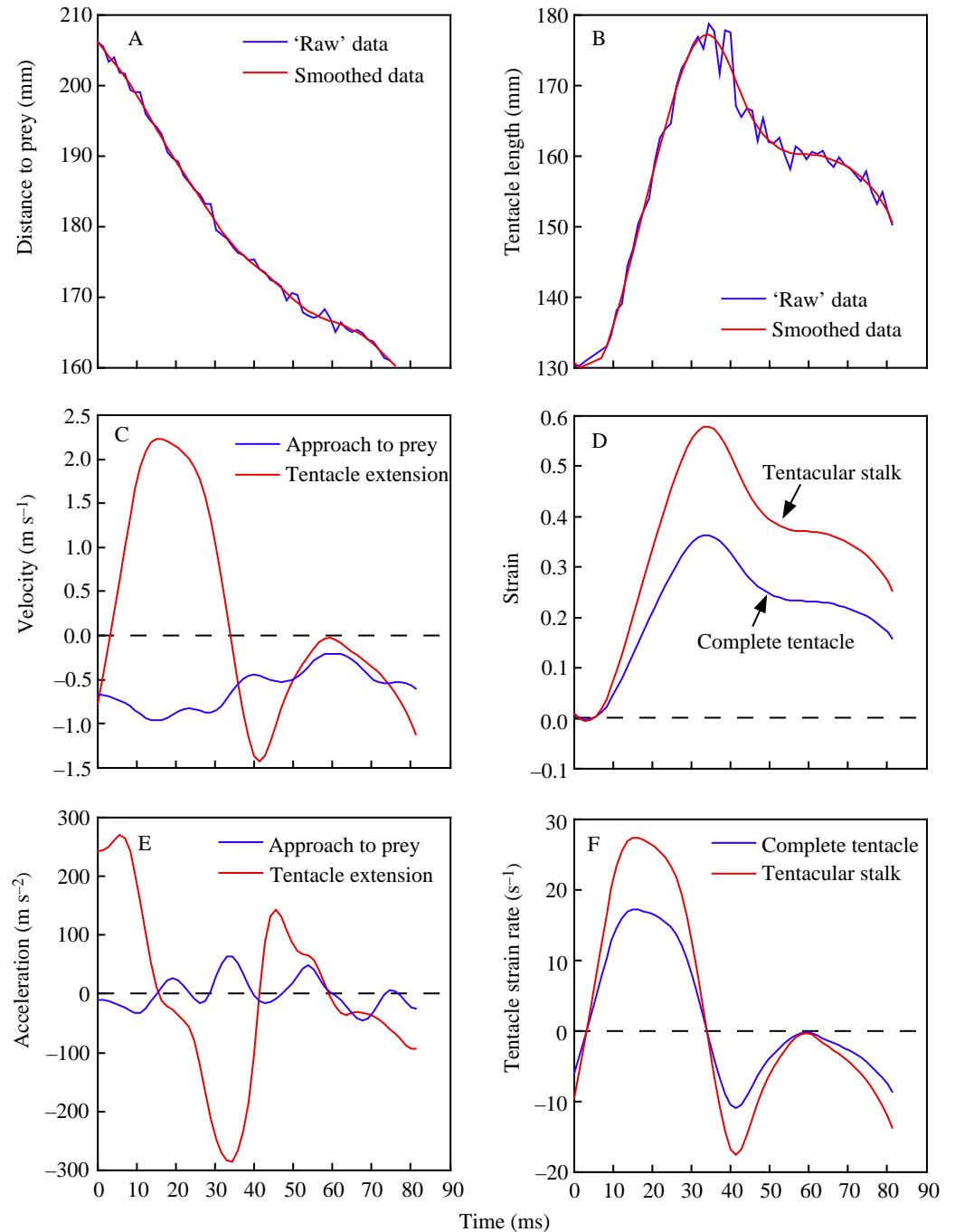
Fig. 5. Plots of data obtained by digitizing each frame of the prey-capture sequence (sequence 4) shown in Fig. 3. See Fig. 2 for further details.

properties of longitudinal and helical muscle fibres. These peaks are fairly accurately reproduced by our forward-dynamics model (van Leeuwen and Kier, 1997).

Messenger (1977) suggests that in the cuttlefish *Sepia officinalis*, which has a similar tentacular strike, the high speed of the strike does not allow control by visual feedback, and it is therefore likely to be under 'open-loop' control. The same is likely to be true for the tentacular strike of *Loligo pealei*. Our observations suggest that some modulation of the strike behaviour can occur. The torsional movements of the stalks are of particular interest in this regard since the direction and the extent of torsion during the strike were variable and, as

described above, appear to depend on prey orientation. Torsional movements are created by the helically arranged muscle fibres that wrap the tentacular stalk (Kier, 1982; Kier and Smith, 1985). Contractile activity in one of the helical muscle layers during the strike would create torsion (the direction depends on the handedness of the helical muscle layer contracting) and the decision could be made prior to the strike to contract a given helical muscle layer simultaneously with the musculature responsible for extension.

Specializations of the tentacles for rapid elongation

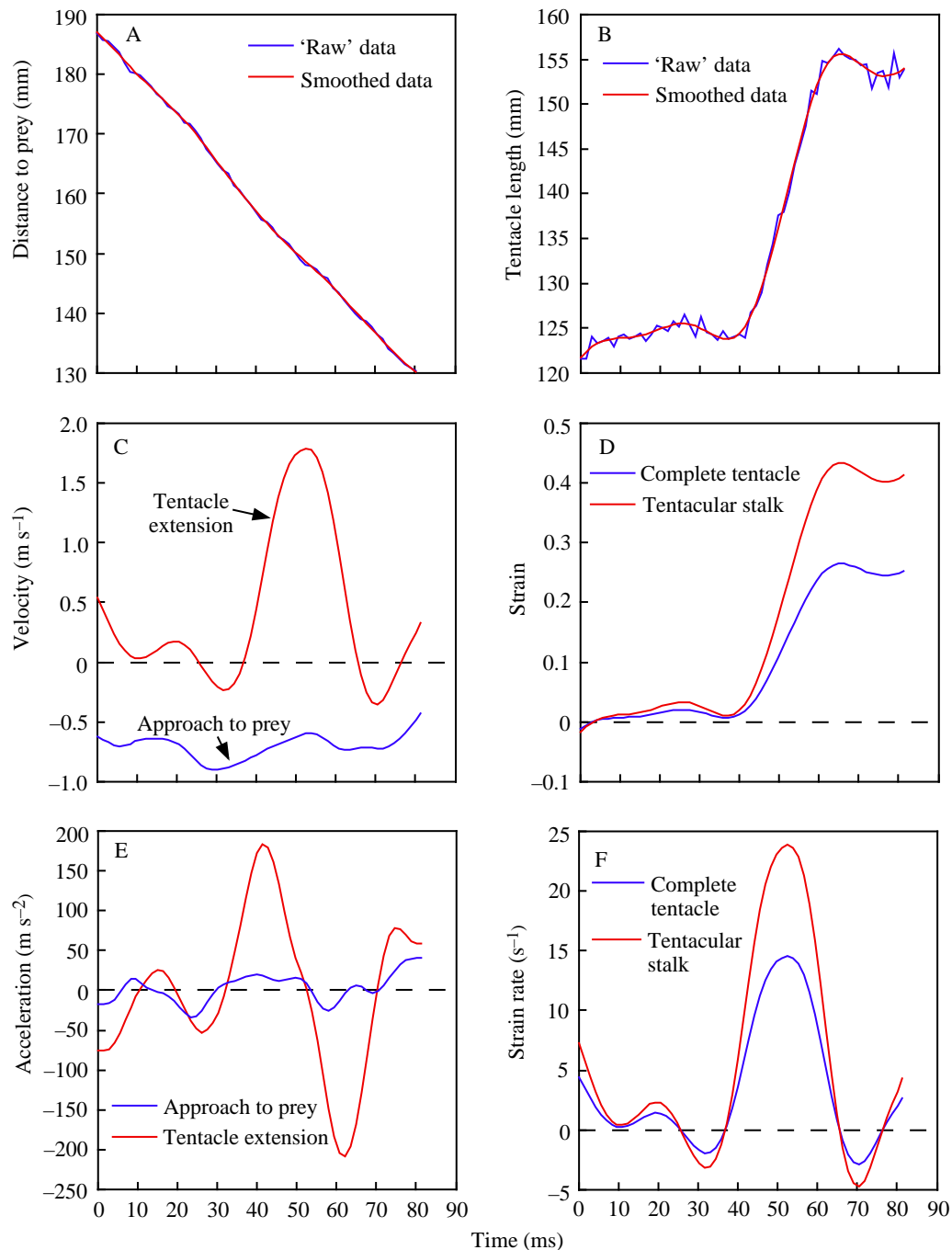The high-speed ciné films reveal the tentacular strike of

Fig. 6. Plots of data obtained by digitizing each frame of the prey-capture sequence (sequence 20) shown in Fig. 4. See Fig. 2 for further details.

Loligo pealei to be remarkable in terms of acceleration (as high as 250 m s^{-2}) and brevity (as little as 20 ms) implying specializations of the tentacle for rapid elongation. What aspects of the structure of the tentacles have been specialized for the rapid strike? To address this question it is useful first to describe the likely evolutionary history of the tentacles. Based on comparative and developmental evidence, the ancestral coleoid [coleoids include the vampyromorphs (vampire squids), octopods (octopuses), sepioids (cuttlefish and sepiolids) and teuthoids (squids)] is thought to have possessed 10 arm-like appendages (Naef, 1921/1923; Boletzky, 1993, 1996). In the octopods, one arm pair was lost

(probably arm-pair II), and in the decapods (sepioids and teuthoids) arm-pair IV was modified and elaborated to form the tentacles (Boletzky, 1993). Thus, by comparing the structure of the tentacles with the arms, we gain insight into the specializations that may have occurred during the evolution of the tentacles.

The general muscle arrangement and architecture of the arms and tentacles are similar (Kier, 1982). Both appendage types are characterized by a large central mass of transverse muscle, i.e. muscle fibres arranged in planes perpendicular to the long axis of the appendage, with bundles of longitudinal muscle situated around the periphery. The relative cross-
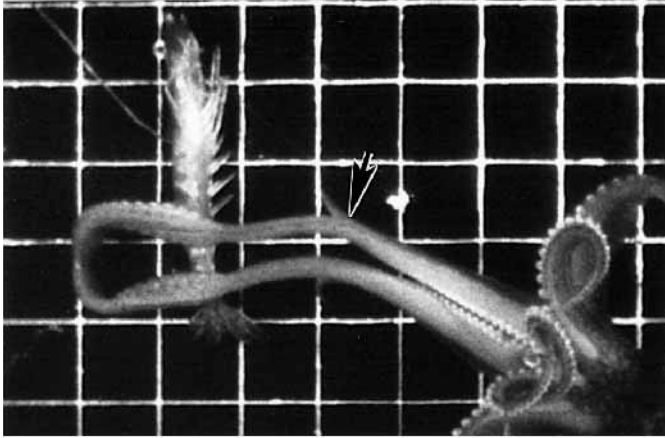
Fig. 7. Photograph of an individual frame from a high-speed ciné sequence (sequence 15) of the capture of prey (a penaeid shrimp) with the tentacles by *Loligo pealei*. The tentacles were deflected upon striking the prey. The tentacular stalks appear to be stabilized by arm-pair IV. The proximal portions of the stalks remain aligned with the two arms which, unlike the other arms, are not flared during the strike. The distal portions of the stalks bend (arrow) as they extend beyond the tips of the arms. The grid spacing in the background is 0.02 m.

sectional area of the transverse muscle mass is larger in the tentacular stalk compared with the arm (approximately 60 % *versus* 45 %, respectively), while the cross-sectional area of longitudinal muscle is smaller in the tentacular stalk (Kier, 1996). Associated with the transverse muscle mass of the tentacles is a very thin layer of circumferential muscle that is not present in the arms. Previous biomechanical analyses suggest that the transverse muscle mass and associated circular muscle layer of the tentacles are responsible for rapid elongation during the strike. The similarly arranged transverse muscle mass in the arms provides the support that is required for the slower arm-bending movements (Kier, 1982). The longitudinal muscle shortens the tentacles after the strike, while in the arms the longitudinal muscle generates bending moments.

Examination of the ultrastructure of the transverse and associated circular muscle of the tentacles reveals the most significant specializations for rapid elongation. Although virtually all other muscle fibres in cephalopods are obliquely striated cells, the muscle cells of the transverse muscle mass (and thin circumferential muscle layer) are cross-striated cells that show ultrastructural characteristics of high shortening velocity and rapid excitation–contraction coupling (Kier, 1985, 1991, 1996). In particular, the thick-filament lengths of these fibres are unusually short, ranging from approximately 0.5 to 1.2 μm compared with a thick-filament length of approximately 6.4 μm in the obliquely striated cells (Kier, 1985, 1996). An approximate inverse correlation has been observed between the thick-filament length and the unloaded shortening velocity of muscle cells (Millman, 1967; Josephson, 1975). Shortening velocity is increased as thick-filament length decreases because muscles with short thick filaments and short sarcomeres have a greater number of elements in series, per unit length of

muscle. Because the shortening velocity of elements in series is additive, muscles with shorter sarcomeres contract at a higher maximum velocity, assuming that other factors are held constant (Huxley and Simmons, 1972; Josephson, 1975; van Leeuwen, 1991, 1992). In addition to the specializations of the myofilament lattice, the tentacle cells also show reduced cell diameter and elaboration of the sarcoplasmic reticulum relative to the obliquely striated cells of the arm. The smaller cell diameter may be important in reducing the diffusion distance for Ca^{2+} and this, in combination with extensive sarcoplasmic reticulum, suggests specialization for rapid excitation–contraction coupling (Kier, 1985, 1991).

Although the ultrastructure of the fibres of the transverse muscle of the tentacles shows significant specialization, the protein composition of the myofilaments is remarkably similar to that of the fibres from the transverse muscle of the arms. Comparison of the two fibre types was made using sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS–PAGE) and peptide mapping of the myosin heavy chains (Kier and Schachat, 1992). These techniques have been used in studies of vertebrate skeletal muscle and nematode muscle to resolve differences in myosin light and heavy chains, troponins and tropomyosins, and these differences have been correlated with differences in physiological performance (see, for example, Bárány, 1967; Schiaffino *et al.* 1988; Sweeney *et al.* 1988). These techniques reveal no significant differences in protein composition between the cross-striated tentacle cells and obliquely striated arm cells (Kier and Schachat, 1992).

In summary, dramatic specialization of the ultrastructure of the muscle fibres of the transverse and associated circular muscle of the tentacles has been observed. The ultrastructural characteristics suggest specialization for increased shortening velocity and rapid excitation–contraction coupling. In addition, the relative cross-sectional area of the transverse muscle mass of the tentacles increased and that of the longitudinal muscle decreased, compared with the arms, reflecting specialization for elongation rather than bending. In contrast, little specialization has been observed in the protein composition of the myofilaments of the muscle fibres of the transverse and circular muscle of the tentacles, or in the gross arrangement of the musculature.

Implications of the mechanics of the tentacular stalk for rapid elongation

In addition to the specialization of the muscle fibres of the tentacles for high shortening velocity and rapid excitation–contraction coupling, the mechanics of elongation of the tentacles by these cells also contribute to rapid elongation of the tentacles. Upon contraction, the transverse muscle cells of the tentacles decrease the cross-sectional area of the stalk and since the stalk is constant in volume, its length increases. Because a decrease in area generates an increase in length, the longitudinal strain and strain rate are an amplification of the strain and strain rate of the transverse muscle fibres. For example, the maximum strain in the tentacular stalk was measured to be 0.80 (sequence 25). Based on the assumption of constant volume in the tentacular stalk, the

strain in the radial direction required to produce this elongation is only −0.25 (Kier, 1982; Kier and Smith, 1985; van Leeuwen and Kier, 1997). Thus, the displacement and the velocity (in terms of elongation of the tentacles) created by the transverse muscle fibres of the stalk are amplified in a manner analogous to a lever system (Kier and Smith, 1985).

Conclusions and future directions

The tentacular strike of *Loligo pealei* during prey capture is remarkable for its brevity (as little as 20 ms), the total strain developed in the tentacular stalk (as much as 0.8) and the acceleration of the tentacular club relative to the tentacle base (maximum observed acceleration $250\,\mathrm{m\,s^{-2}}$). The results from the present study were used to develop and test a forward-dynamics model of tentacle extension (van Leeuwen and Kier, 1997) which includes morphological and physiological properties of the tentacle tissue, and an assumed activation of the sarcomeres of the transverse and circular musculature. The model suggests that the remarkable performance observed in the present study can be achieved using typical muscle physiological properties. The physiological properties of the tentacular musculature and its neuromuscular control have not, however, been examined. Future studies are planned to address these important issues.

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