

FINE ANALYSIS OF PREDATORY AND DEFENSIVE MOTOR EVENTS IN *TORPEDO MARMORATA* (PISCES)

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Accepted 15 October 1985

SUMMARY

1. Predation and defence of *Torpedo marmorata*, elicited with biological and inanimate stimuli, were studied in experimental conditions.
2. Patterns of responses of neonates and adults are described, and chains of separate, coordinated motor acts are defined.
3. Jumping predation, creeping predation, defence of the disc and defence of the tail are distinguished. Each predatory behaviour consists of stimulus reaction chains, whereas defensive types of behaviour involve single stimulus reactions.
4. During jumping behaviour, tail strokes provoked by the initial response in the chain are displayed during the whole period of predation; these 'delayed' tail strokes provoke displacements of the prey, thus probing the substrate and furnishing biological cues.
5. Large behavioural variations are reported, including incomplete chains of responses, repetition of responses, oriented responses, stimulus intensity/response magnitude relationships and missing of certain motor acts.
6. Ontogenetic maturation of the behaviour patterns is observed in embryos and in immature neonates.
7. Sets of electric organ discharges (EODs), which accompany the defensive responses and certain predatory responses, show a stereotyped pattern, characteristic for each EOD motor act. Variations found in the EOD pattern are often related to the effects of fatigue on the EOD rate. Electric shock provokes the immobilization of the prey, or the flight of the aggressor. Effective use of the EOD by neonates as a weapon against prey is reported.
8. The possible neuronal basis of the sensorimotor organization which may account for the results is discussed.

INTRODUCTION

The phenomenon of the electric discharge of *Torpedo* has been known since antiquity. But in recent times little data have been collected on the general behaviour

Key words: *Torpedo marmorata*, electric fish, predation, defence, locomotor activity, electric organ discharge, ontogeny, motor control, neuronal fatigue.

and biological aspects of these animals' life history which would make it possible to determine the exact function of their electric activity. Humboldt & Gay-Lussac (1805) and Humboldt (1819) observed that the *Torpedo* remained immobile during electric emission, in contrast to the South American electric eel. In *Torpedo*, the discharge phenomenon was thus interpreted as a defensive weapon by Humboldt (1819) and this opinion remained the ruling hypothesis throughout the nineteenth century. However, other authors, for example Whitley (1940), observed that fish or invertebrates placed in contact with an electric ray did not seem to suffer any ill effects from the discharge. In 1953, the controversy concerning the efficacy of the electric discharge as a weapon was still unresolved (see review by Bigelow & Schroeder, 1953).

Defensive behaviour, including the involvement of electric organ discharges (EODs) as a weapon, has been described by several authors (Cox & Breder, 1943; Wilson, 1953; Fessard, 1958; Bennett, Würzel & Grundfest, 1961; Szabo, 1965; Roberts, 1969). Wilson (1953) and Fessard (1958) have found that EODs cause crabs pinching the ray and dogfish or conger eels nosing its disc to retreat.

Predatory behaviour of *Torpedo* was described briefly by Schönlein (1895). More detailed visual observations of predatory behaviour in *Torpedo nobiliana* were made by Wilson (1953) who detected the associated electric activity using a galvanometer. These observations were extended and systematized in *Torpedo marmorata* by Belbenoit (1968, 1970, 1974a) and Belbenoit & Bauer (1972), confirming the efficacy of the electric discharge as a predatory weapon. Characteristics of stimuli associated with predation and defence of *T. marmorata* were given by Belbenoit (1981). The first field observations of active nocturnal predation of *Torpedo californica* were made by Bray & Hixon (1978). A brief description of the maturation of predatory behaviour in newborn *Torpedo torpedo* was given by Michaelson, Sternberg & Fishelson (1979). Maturation of the EOD and development of the electric system of *Torpedo marmorata* have been described by Mellinger, Belbenoit, Ravaille & Szabo (1978), Fox & Richardson (1978, 1979), Belbenoit (1979), Krenz *et al.* (1980) and Richardson, Krenz, Kirk & Fox (1981), using electron microscopic, biochemical, electrophysiological or organotypic culture techniques. During embryonic development, a 10^5 -fold increase in EOD amplitude is observed, reaching a plateau of up to 50 V in the neonatal stage.

The present study gives a detailed analysis of the locomotor components and of the associated electromotor activity of these behaviour patterns.

Important information on the characteristics of a phenomenon is lost when studies discard occasional activities or when statistical analyses are made. Thus, a precise description of the whole observed behavioural activities was necessary to obtain a better understanding of the sensory control and neuronal integration of stereotyped motor acts contributing to the overall predatory and defensive behaviour. As the results show, the detailed description of the whole observed patterns has been useful in solving questions such as the endogenous or exogenous activation of each series of motor acts in a repetitive sequence, previously insufficiently understood.

METHODS

Experimental animals

Male and female *Torpedo marmorata* Risso (140–620 mm in length) were caught in the Bay of Biscay and the Arcachon basin (in the North Eastern Atlantic). Embryos (50–100 mm) with external yolk sac and neonates (120–130 mm) were obtained by Caesarean section of pregnant females (see Mellinger *et al.* 1978). All the animals were placed in circulating seawater tanks; embryos were placed in separate cups held inside the tank. During the summer and autumn, individuals were maintained over normal ranges of temperature (19–26°C), without rapid changes, under natural light conditions. The experiments were performed in glass tanks (40×100×35 cm for adults and 24×29×9 cm for neonates and embryos), during day or night, under artificial light (intensity 400 lx). As a precondition the animals had to lie at rest on the bottom of the tank.

Recording techniques

The activity of both prey and electric rays was observed directly or recorded on a Sony video system (see also Belbenoit & Bauer, 1972). Single-frame video pictures (with a lateral view of the tank and a bottom view obtained by reflection from a 45° inclined mirror) were photographed from a video monitor with a Grass camera for a detailed three-dimensional analysis. The electric organ discharges (EODs) detected by carbon electrodes, placed on opposite walls of the tank, were differentially amplified, routinely monitored with a loudspeaker, and recorded on the audio channel of the video recorder, as well as on 0.6 mm magnetic tape. The EOD recordings were monitored with an oscilloscope (Tektronix) and filmed with a Grass camera. In experiments with neonates, video and audio recordings were synchronized by the EOD which triggered a signal on the video picture, displayed as a lateral black bar. In experiments with adults, video and audio recordings were synchronized by the onset of EOD activity which triggered the Grass camera.

Stimuli

Several kinds of stimuli were used to elicit predatory or defensive behaviour under laboratory conditions. (1) Biological stimuli: live fish (*Trachurus*, *Mugil*, *Mullus*, *Dicentrarchus*, *Spondylosoma*, *Boops*, *Labrus*, *Dascylus*, *Pomacentrus*) 20–200 mm in length, were chased close to the *Torpedo* to increase the number of attacks. Live crustaceans (*Macropodia*) were used as well as dead fish (*Trachurus*). (2) Inanimate stimuli: rods were moved in the vicinity of the ray, or displaced along the skin surface of the animal; rods, needles or forceps were used to press, pinch, prod or stretch the skin, the muscular mass, the cartilages or the caudal peduncle.

Activity analysis

Behaviour elicited by prey or rods, moved in the vicinity of the ray, was examined either directly or by analysis of video pictures. Motor acts, their consequences, and the eliciting stimuli were collected directly from this material, or reconstituted after

graphical comparison of successive video pictures. The relationship between motor behaviour and EOD activity was established using graphs in which the number of EODs per 20 ms (= duration of one video picture) was plotted against time; each EOD-set (comprising all the strong pulses emitted after a stimulation) was identified. From these data, the degree of predictability of behaviour and associated electric activity were estimated; possible causes of variation, such as temperature, ontogenetic maturation, succession of stimuli and stimulus parameters, were examined. To compare the rates of emission in certain EOD-sets, the accumulated number of EODs was plotted against time. The total range, the 'general range' (rejecting the two tails, each containing 5% of the data of the distribution), the median, or the maximal value of the number of EODs per set or of the EOD-set duration were established.

RESULTS

Predatory and defensive behaviour

The four strategies which are described in this section are adopted when *T. marmorata* is at rest on the bottom of the tank. Each predatory behaviour consists of stimulus–reaction chains, whereas the defensive behaviour patterns involve single stimulus relationships. The responses are composed of groups of stereotyped motor acts, each one triggered by adequate stimuli (Belbenoit, 1981).

Predatory behaviour

Two types of predatory behaviour can be distinguished: jumping predation and creeping predation, named according to whether these kinds of ambush attacks are launched by a jumping response or a creeping response (Belbenoit, 1981). Jumping predation occurs in certain neonates (see below and Belbenoit, 1974a) as well as in young and adult individuals (Belbenoit, 1970; Belbenoit & Bauer, 1972). Twenty-six sequences have been analysed on video recordings (10 jumping responses of three neonates plus 17 of four adults; other kinds of responses have been found by fine analysis of three attacks of neonates and four of adults), and 117 other attacks have been directly observed in 32 young or adults. Creeping predation is observed more rarely in adults (two directly observed sequences and one recorded) and never in neonates or in embryos.

Jumping predation. This behaviour comprises the following: a jumping response, an engulfing response, several head-suction and suction responses, and one or several swallowing responses. Biting responses can be displayed following engulfing, head-suction or suction responses. The sequence of engulfing-swallowing reactions occurs at the same time as delayed body movements which are part of the jumping response (see Belbenoit, 1981). The components of concomitant jumping and engulfing-swallowing responses could be distinguished by comparison between (a) successful predation and (b) unsuccessful jumping responses, in which the prey was not caught under the ray during the jump.

The jumping response (Figs 1, 2) is elicited by a potential prey (or an inanimate object) passing (or moved) in the vicinity of the anterior edge of the ray's disc. The animal simultaneously produces a *jump*, a *set of EODs* and an *immediate tail stroke* (left part of Figs 1, 2). To jump, the animal deforms its disc; grounding on the margins of the pectoral fins (which form the lateral and posterior parts of the disc), the ray raises the anterior and central parts of its disc (Fig. 2A, lateral views, 0.10–0.16 s); then the pectoral fins are lifted (Fig. 2A, lateral views, 0.16–0.50 s) and the *Torpedo* falls back onto the substrate in a forward gliding movement (Fig. 2A, lateral views, 0.30–0.50 s). Before the maximum rise of the jump, the immediate tail stroke causes the ray to turn to face the prey (Figs 1A, 2). Stunned and immobilized by the first EOD pulses, the prey is swept beneath the disc (Fig. 2A, ventral views, 0.10–0.30 s) by a water stream which has been produced by the upward movement of the disc. Thus, the jump, the EODs and the immediate tail stroke contribute to the capture of the prey beneath the disc.

Occasionally, in the case of failure to sweep the prey beneath the disc, the movements of the prey can elicit a second jumping response, while the first jump is still under way (Fig. 2B). In this case, the jump and the immediate tail stroke of the first jumping response are modified in that the disc and the tail are maintained in the same position (*'jump fixation'* and *'tail fixation'*) during 80 ms. This pause, which strongly limits the displacement of the ray, constitutes a preparatory phase for the second jumping response.

The initial jump, EODs and immediate tail strokes are displayed within less than 2 s (Fig. 1, 0.3 s). Regardless of whether the prey is captured or not, these are followed by activities occurring over a period of up to 1 min after onset of the attack which include *delayed tail strokes* (unilateral movements) (Fig. 1), and sometimes *burying movements* resulting in covering with sand or mud. Each tail stroke produces a rotation of the disc, which can provoke stimuli through contact with the prey under the disc, or through the erratic motor movements of the tetanized prey (see the engulfing and head-suction responses; see also Belbenoit, 1981). The immediate and delayed activities of the jumping response constitute one phase, termed 'phase 2', which may be distinguished from the preparatory phase, 'phase 1'.

In a single jumping response, the estimated latency of phase 2 is 120 ms (latency between a fast body bend of the prey and the following onset of attack); for the second jump, the latencies of phase 1 and phase 2 have been estimated at 40 and 120 ms, respectively (Fig. 2B, between active jerk of prey and onset of each phase of second jump).

The engulfing response (Fig. 3) which follows the jumping response is elicited by movements of the prey which is located beneath the disc in the pectoral area, far from the mouth: a small delayed tail stroke of the jumping response provoked a small displacement of the disc during which the prey jerked in contact with the pectoral area of the ray (Fig. 3, right, note tail movement of prey at 0.50–0.52 s). The engulfing response had two consecutive phases: phase 1, elicited 60 ms after the active jerk of the prey (or by an inanimate object rubbing the skin, see Belbenoit, 1981); phase 2, elicited only by prey, which occurred about 0.16 s after the onset of

phase 1 (Fig. 3, left). In several hundred cases, stimulations with inanimate objects applied on rays at rest always elicited phase 1 without phase 2; phase 1 was also often elicited without phase 2 during the jumping predation.

Phase 1 consists of a *set of EODs* and concomitant *tail fixation*, whereby the position of the tail is temporarily fixed at a certain angle (Fig. 3, ventral views, 0.58–0.72 s). Tail fixation also results in a lowering of the rate of the delayed tail strokes. This, together with the EODs which produce a temporary immobilization of the prey, thus maintains the relative position of the *Torpedo* and its prey. During phase 2, the prey is stunned and immobilized by a long *set of EODs*; simultaneously, an *immediate tail stroke* rotates the disc, bringing the mouth towards the prey (Fig. 3, left and right, 0.72–0.96 s). When this tail stroke is at its maximum, a sudden opening of the mouth produces a *suction* effect. That suction occurs is demonstrated by the sudden engulfing of a small prey, in about 20 ms. Large prey is only partly taken up into the mouth; then the contact of the prey with the jaws elicits a *biting response* in which the prey is held in the mouth. In other instances (Fig. 3, ventral view, 1.08 s), phase 2 only brings the mouth towards the prey without taking it up.

The head-suction responses are elicited by displacements of the prey beneath the head area of the disc. Fig. 4 shows a sequence of eleven head-suction responses, *t*, *a–j*: transitional with an engulfing response, the first response *t* (Fig. 4C,D) was provoked by a jerk of the prey's head during the engulfing EOD emission; other displacements in the same area elicited the responses *a–d* (Fig. 4C,D); displacements of the prey's body between the jaws of the ray elicited the remaining responses *e–j* (Fig. 4B,C,D). In these cases, the ray displays *tail fixation* followed by a small *rise of the rostrum* and/or by an *immediate tail stroke* (Fig. 4B,C). Then *suction*, involving mouth opening, occurs; note that the onset of jaw opening is concomitant with the onset of downward movement of the rostrum (Fig. 4B). Finally, after another interval, the ray emits a short *set of EODs* (Fig. 4A,B,C). Two consecutive phases, phase 1 at onset of tail fixation and phase 2 at onset of rise of rostrum and/or of immediate tail stroke, may be distinguished. In agreement with data on prey

Fig. 1. Jumping responses of *Torpedo marmorata* neonates (120 mm in length). Responses were triggered in A, by *Dascylus* (20 mm) and, in B, by a U-shaped plastic rod (diameter of 3 mm). Temperature = 23°C. (A) Left column and inset: time course of events; abscissae, time in s; vertical broken lines, onset of attack at 0 s. Left column refers to variation in height of anterior edge of the ray's disc, to time course of electric emission (ordinate: number of EODs per 20-ms bin) and to variations in ray's tail angle (α°). Dots refer to pictures in central and right columns. Inset, black bars or vertical lines indicate occurrence of events: jump, electric emission (see also Fig. 11A, 1), immediate tail stroke, delayed tail strokes, burying movements. Shaded area indicates presence of prey under the ray's disc. Right column: lateral and ventral views of *Torpedo* and prey. Sequential pictures indicated in s. Top horizontal lines and vertical lines indicate ray's position before attack. (B) As for A. Lateral and ventral views show *Torpedo* and inanimate object (rod). Note immediate activities: jump and associated EODs in A and B; immediate tail stroke to face the prey in A; attack without immediate tail stroke in B, when stimulus is given in the median line of the rostral edge of the disc. Note also delayed tail strokes, but that there is no burial in A (inset) after very brief presence of prey under the disc (delayed tail strokes also occurred in B, without prey present under the disc).

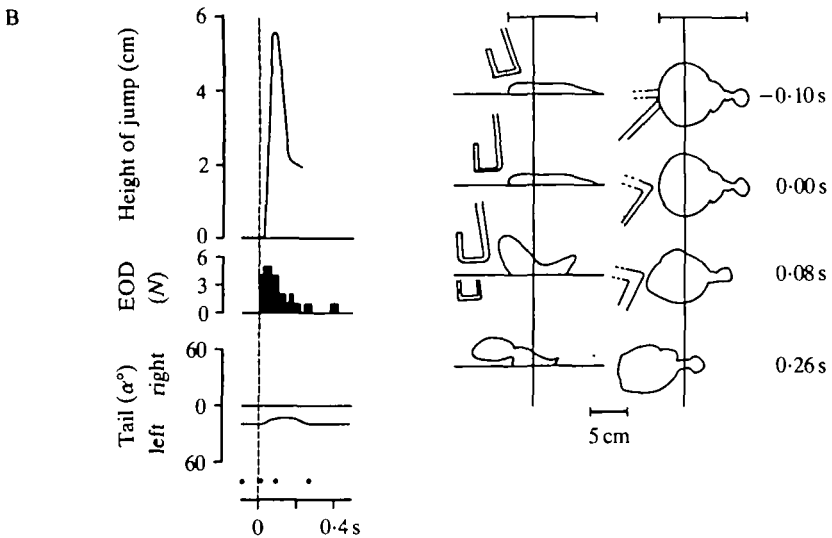
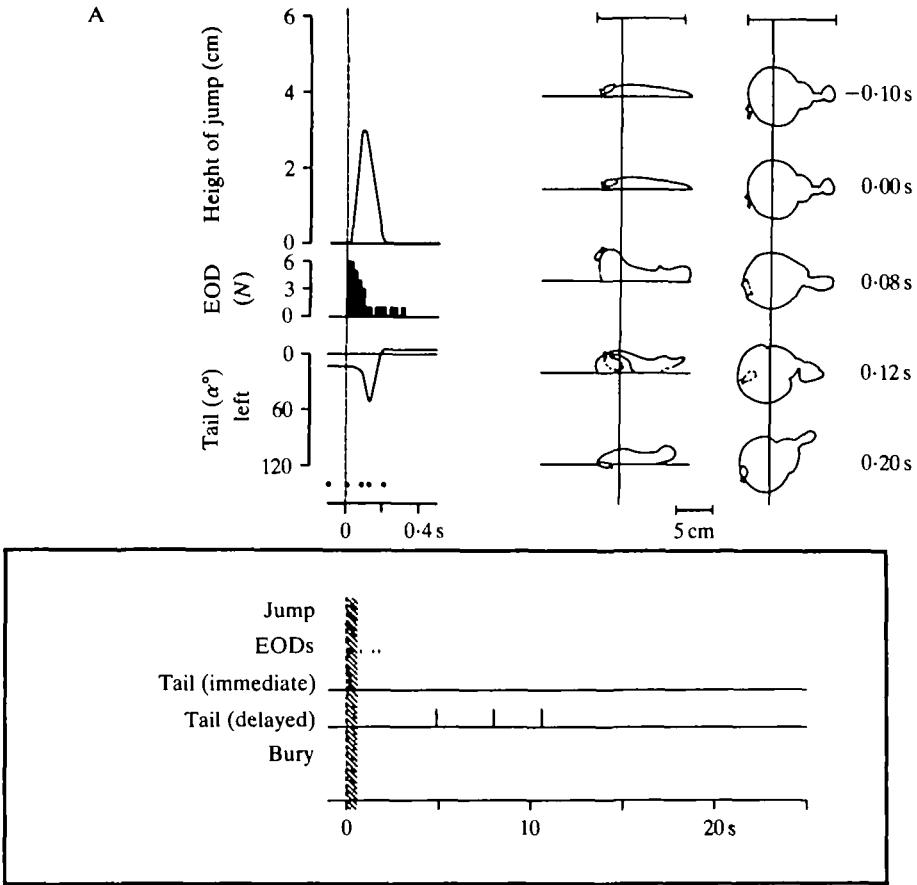
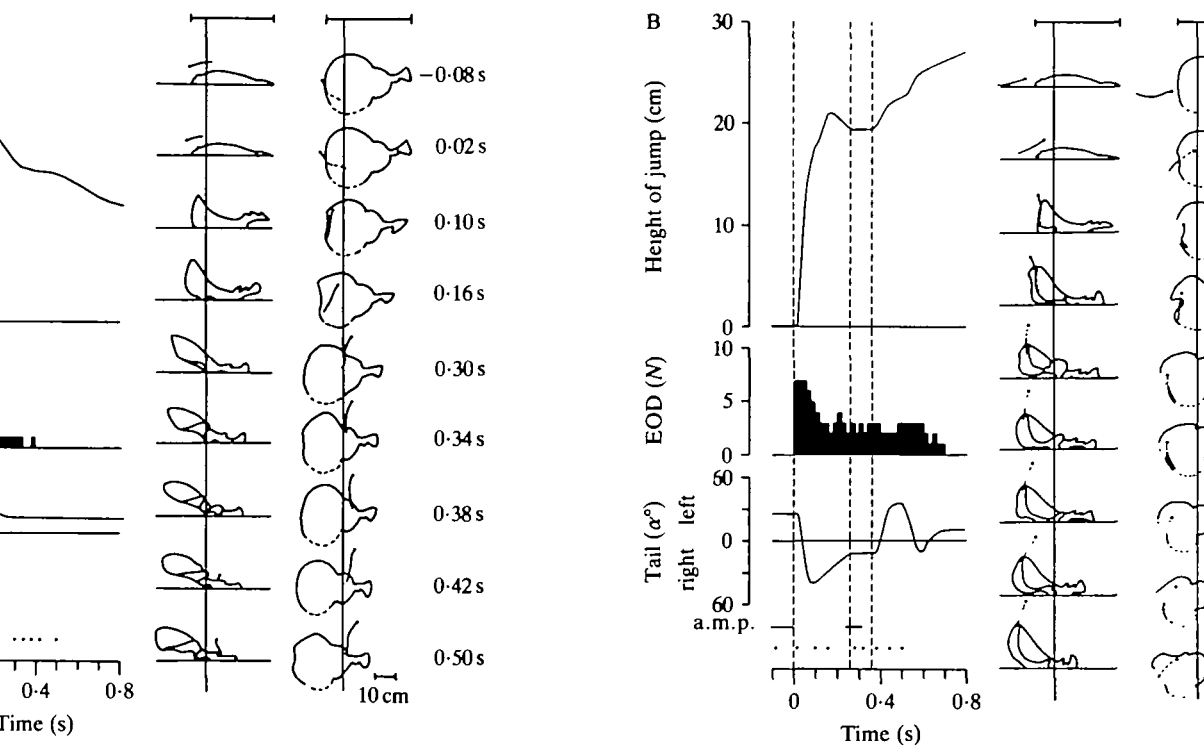


Fig. 1



Intermediate activities of jumping responses in *Torpedo marmorata* upon *Trachurus* (160 mm). (A) Typical single jumping response of a ray (adult 450 mm). (B) Double jumping response of the same ray 3 h 45 min later. The ray remained at rest between the two jumps. Temperature = 25°C. (A), (B) Left column, as for Fig. 1; note active movement of prey (a.m.p. horizontal black bars), onset of 'prey fixation' and 'tail fixation' (B, vertical broken line at 0.26 s) and onset of second jumping response (B, vertical broken line at 0.28 s), as for Fig. 1, except schematic drawing of prey (bar with a dot for prey and prey's head). (A) Note maximal height of jump (16 s; 0.02 s later the tail contacts the substrate and undulation of pectoral fin begins; water movement provokes the prey to move forward of the stunned prey successively beneath and behind the disc (0.10–0.42 s). (B) Swimming in front of ray, the prey moves forward (0.00 s) and stopped at 0.02 s when 2/5 of prey's body is above the disc; then the rostrum of the disc knocks the prey's body forward (0.02 s) and onset of pectoral undulation and of tail contact with the substrate occur at 0.16 s, i.e. at maximal height of the first jump (0.16 s). (A) A small jerk of the prey (a.m.p. at 0.24 s or shortly before) the height of the disc and the angle of the tail remain the same (0.24 s) and forward glide of the ray stops (at 0.28 s). At 0.36 s bending of vertebral column and a tail beat result in second jumping response. The rate of strong EODs is lower at the onset of the second attack than in the first.

displacements, the estimated latencies of phase 1 and phase 2 are 40 and 240 ms, respectively (Fig. 4B,C).

The tail stroke activity is highly variable: brief movements of small amplitude are preceded and followed by periods of tail immobility, during which tail fixation occasionally remains putative; stronger movements of long duration also occur, which are stopped only during the period of tail fixation (Fig. 4C). The determination of onset of rise in the sequence *f-j* has been important to the understanding of the structure of the head-suction responses (Fig. 4B). This knowledge was used in solving the sequence *t, a-e* (Fig. 4C): in cases where head-suction responses were not clearly observed, because numerous behavioural events were slight or absent, the timing of EOD activity and associated events was sufficiently stereotyped to be able to predict the onset of unidentified components of the response chain (Fig. 4C, responses *t, d, e*).

Each head-suction response produces a slight disc rotation and a weak displacement of the prey (Fig. 4D). Thus, the mouth is brought towards the prey, which is then taken up between the jaws. Contact of prey with the jaws elicits a biting response (Fig. 4B,C). During the following head-suction responses, the suction effect maintains the prey between the jaws while the ray tries to move the prey into such a position that it can catch the head of the prey first. During this realignment (Fig. 4D, responses *e-j*), the prey body is displaced stepwise.

The suction responses (Fig. 5) are elicited after the anterior part of the prey (1/5 to 1/3 of prey body) has been taken up into the mouth. During each suction response, the ray displays a small *rise of the rostrum* which comprises successive upward and downward movements; mouth opening with *suction* is associated with this downward movement; suction is followed by a biting response. A very slight *immediate tail stroke* is observed at the onset of the rise of the rostrum. Tail strokes are preceded and followed by periods of tail immobility during which tail fixation usually remains putative. Each suction response occurs without EOD emission. While the prey remained outside the mouth, or between the jaws, stimuli elicited the head-suction responses associated with EODs, as well as the following transitional suction response (Fig. 4). According to the pictures of this transitional response (Fig. 4D) and to the fact that taste buds are confined to the mouth and pharynx in elasmobranchs (Oppel, 1900), the head of the prey was sucked into the mouth during mouth opening in about 40 ms and arrived in contact with taste buds 40–60 ms before the expected EODs, which did not then occur. Several suction/biting responses complete the introduction of the entire prey into the mouth.

The swallowing response is elicited by the prey within the mouth cavity, transferring the prey from the mouth into the stomach. This can be determined indirectly in neonates in which *swallowing* is accompanied by an upward retracted position of the head.

Creeping predation. This behaviour is composed of a sequence of creeping, suction and biting, swallowing or spitting responses.

The creeping responses are elicited by a stationary prey or a prey moving slowly, close to the rostral part of a resting *Torpedo*.

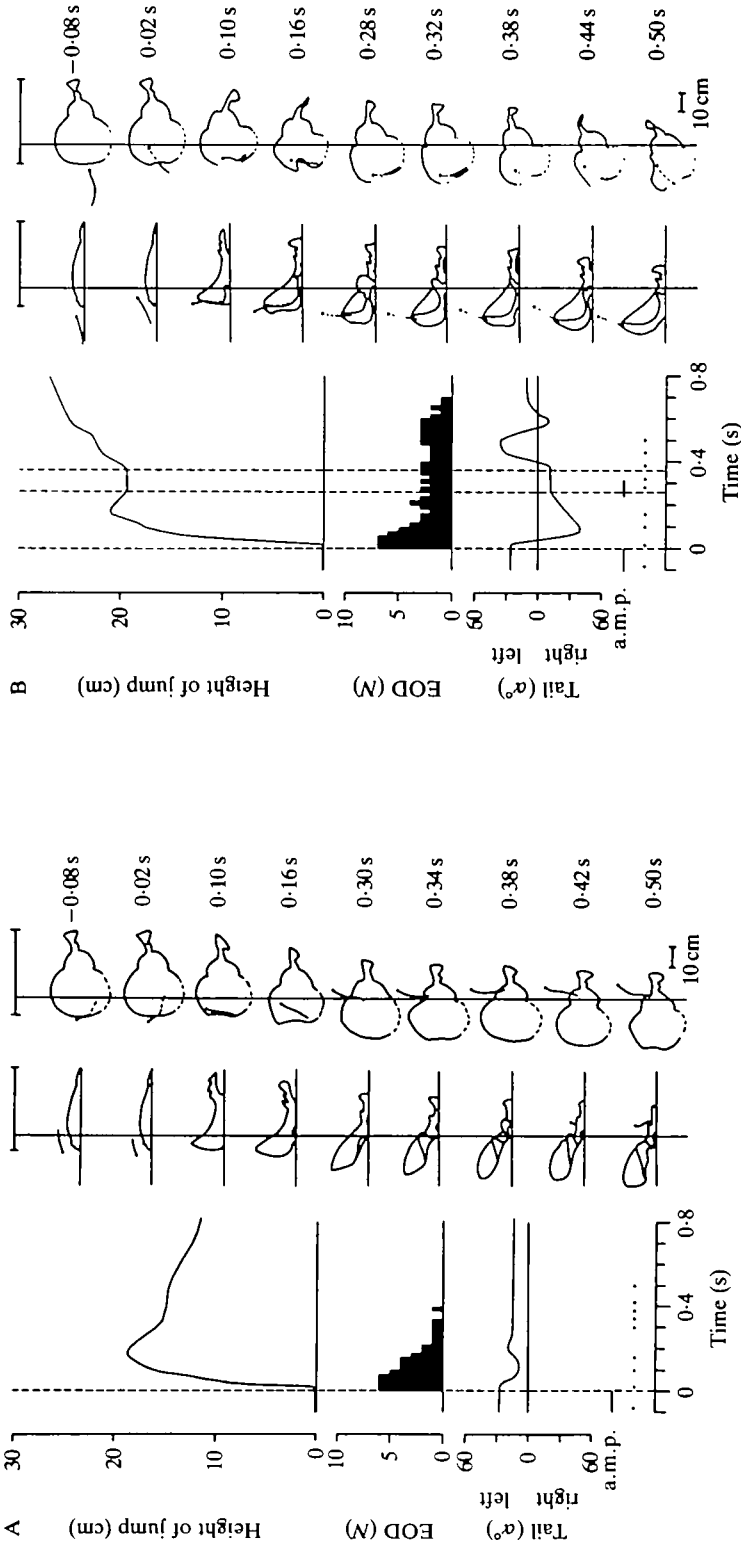


Fig. 2. Immediate activities of jumping responses in *Torpedo marmorata* upon *Trachurus* (160 mm). (A) Typical single jumping response (adult 450 mm). (B) Double jumping response of the same ray 3 h 45 min later. The ray remained at rest between the two attacks. Temperature = 25 °C. (A), (B) Left column, as for Fig. 1; note active movement of prey (a.m.p., horizontal black bars), onset of 'jump fixation' and 'tail fixation' (B, vertical broken line at 0.26 s) and onset of second jumping response (B, vertical broken line at 0.36 s). Right column, as for Fig. 1, except schematic drawing of prey (bar with a dot for prey and prey's head). (A) Note maximal height of the jump at 0.16 s; 0.02 s later the tail contacts the substrate and undulation of pectoral fin begins; water movement provokes the passive displacement of the stunned prey successively beneath and behind the disc (0.10–0.42 s). (B) Swimming in front of ray, the prey is stunned at 0.00 s and stopped at 0.02 s when 2/5 of prey's body is above the disc; then the rostrum of the disc knocks the prey's body upward. Onset of pectoral undulation and of tail contact with the substrate occur at 0.16 s, i.e. at maximal height of the first jump. After the onset of a small jerk of the prey (a.m.p. at 0.24 s or shortly before) the height of the disc and the angle of the tail remain the same (0.26–0.36 s) and forward glide of the ray stops (at 0.28 s). At 0.36 s bending of vertebral column and a tail beat result in second jump. Note that the rate of strong EODs is lower at the onset of the second attack than in the first.

An occasional creeping sequence recorded after the double jump of Fig. 2B is shown in Fig. 6. Three seconds after onset of the first jump, the stunned prey swam erratically below the ray (Fig. 6, 3.00 s); at 5.20 s and after, the prey remained inactive in contact with the ray, which maintained its arched position, resting on the margin of the pectoral fins with the rostral and central parts of the disc raised to form a blind tunnel (Fig. 6, 5.80 and 6.00 s). Four successive creeping responses (Fig. 6, 6.10, 6.60, 7.00 and 7.20 s) resulted in placement of the prey's head in the region of the mouth (Fig. 6, 7.50 s). For each response, the ray *crept* by small rising and falling movements of the anterior part of the disc. When the ray raised the anterior and central parts of the disc forming a narrow blind tunnel, a small water stream was produced which displaced the prey backward; the falling movement of disc and a small tail beat produced a forward movement of the ray. Backward displacement of prey plus forward movement of ray brought the prey beneath the disc. Erratic swimming activity of the prey (Fig. 6, left column, during first creeping response) or forward displacement of the prey, after it had been knocked by the rostrum of the ray (Fig. 6, left column, end of second creeping response), resulted in continued creeping towards the prey. *Suction* occurred as the mouth opened (Fig. 6, left column, first creeping response) and the rostrum of the prey was pulled into the mouth cavity (Fig. 6, left column, end of fourth creeping response). This sequence was successful: contact of prey with the jaws elicited a biting response (Fig. 6, 7.50–8.00 s and left column).

During this creeping sequence, the ray displayed adapted activity elicited by displacement of the prey which occurred 160 ms before the creeping. The prey fell on its left side 160 ms before the first creeping, immediately after a small downward movement of the ray's disc (Fig. 6, left column). Knocking the pectoral fin of the prey during forward displacement of the ray (Fig. 6, 6.80 s) elicited the third creeping response after a latency of 160 ms and also *creeping fixation*, *EOD-set* and *tail beat*, after a shorter latency of 40 ms (Fig. 6, left column, end of second creeping response). Fig. 6, left column, also shows that creep fixation occurs before other creeping responses; this occurs often together with a tail beat and sometimes with an EOD-set. Two consecutive phases, phase 1 (at onset of creeping fixation) and phase 2 (at onset of creep) may be distinguished.

Suction responses followed by biting responses displayed in creeping predation resemble those of the jumping predation.

The swallowing response is elicited when edible food has been retained in the mouth cavity.

The spitting response, in contrast, is elicited by food such as dead fish (*Trachurus*) or living crustaceans (*Macropodia*). The ray vigorously *spits* out these items which are thus apparently unpalatable.

Defensive behaviour

Two types can be distinguished, either defence of the disc or defence of the tail, named according to the locus of the stimulation made by the intruder (Belbenoit, 1981). Defence of the disc was found in embryos ≥ 70 mm, neonates, young and

adult individuals (30 cases observed in detail, independently of several hundred other cases in which the analysis was focused on the EOD characteristics); defence of the tail (107 cases) was observed in two neonates and 11 adults.

Defence of the disc. The disc defensive response (Fig. 7) is elicited by pressing, pinching, prodding or stretching the disc. To a weak stimulation (1–2 point stimuli with a small rod dropping vertically by its own weight from a constant locus) the ray responds with a *pectoral wave* to reject the intruder (this is termed a small disc defensive response). Stronger stimulations (6–10 of these point stimuli) provoke an *immediate tail stroke* which turns the ray to face the intruder together with a *set of EODs* to stun it. *Delayed tail beats* can occur during the next minute, sometimes followed by *burying movements*. In contrast to the tail strokes, tail beats are bilateral movements; they produce a swimming flight in a straight line.

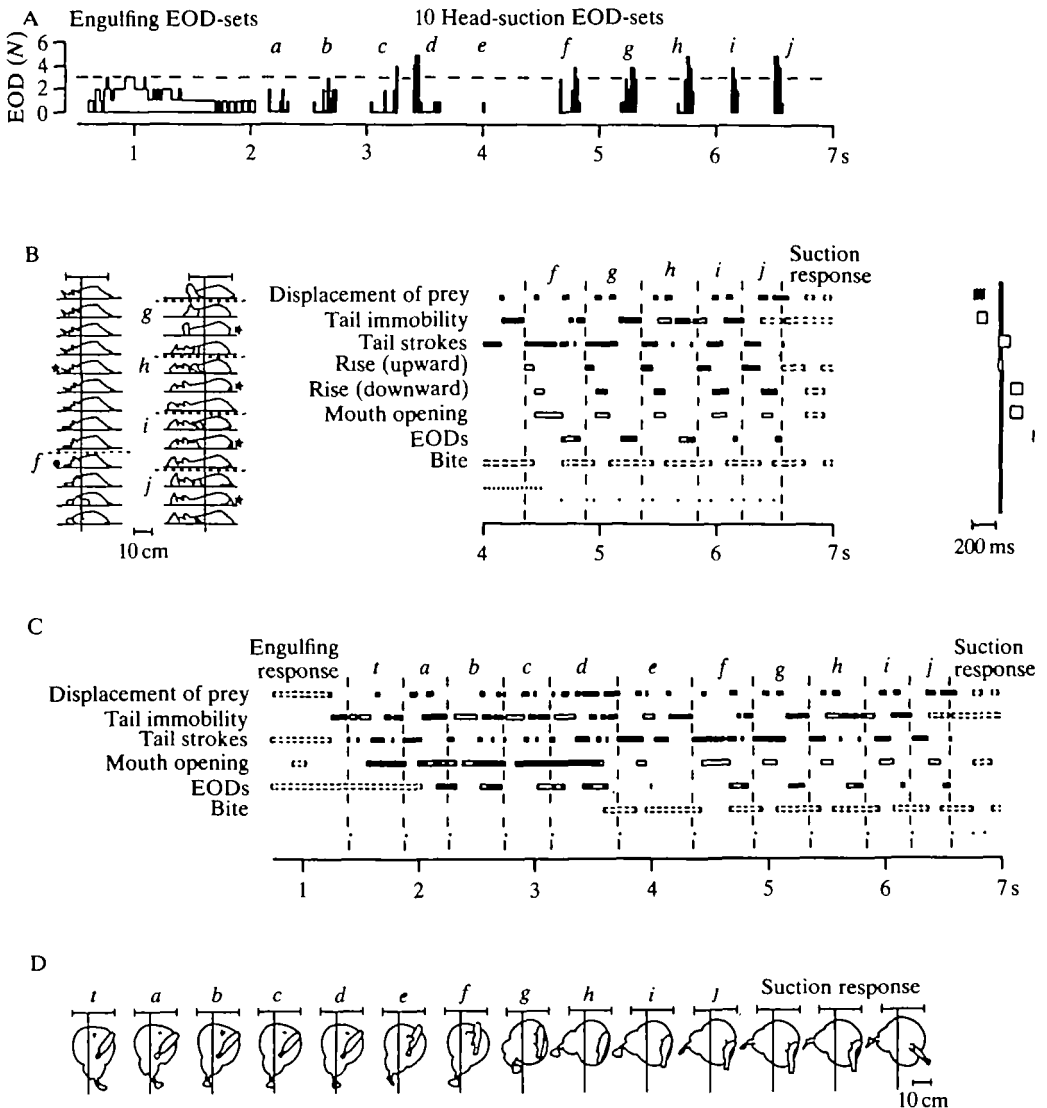


Fig. 4

Defence of the tail. The tail defensive response (Fig. 8) is elicited by pressing or pinching the caudal fin or when rubber or plastic tape bands have produced skin injury of the caudal peduncle. Brief pressure elicits only a *dorsal tail bend*, i.e. a small tail defensive response, which propels the fish upward and results in a complete loop. Such movements can break contact with the intruder.

Maintained pressure, pinch or skin injury elicits a small tail defensive response which is followed by one or several successive large tail defensive responses; the edges of the disc rise and the tail bends dorsally; when this *body bend* is maximal (see Fig. 8) the disc and tail are maintained in this position during several seconds and a *set of EODs* is emitted. In this position, the ray has placed the intruder which caught its tail in the maximum gradient of its EOD field; thus, the ray can successfully shock the intruder.

Variations in predatory and defensive behaviour

Variations in the basic pattern described above were found to be related to variations in the succession of stimuli, the stimulus parameters, and the stage of ontogenetic maturation.

Variations dependent on succession of stimuli

The stimulus–reaction chains of predatory behaviour are affected by the variations in the occurrence of successive stimuli produced by the prey or by a prey as a result of the preceding behaviour.

Fig. 4. Head-suction responses (*a–j*) of *Torpedo marmorata* (390 mm) and transition of this sequence with preceding engulfing and following suction responses which are shown in Figs 3 and 5. Successful attack upon *Dicentrarchus* (145 mm). Temperature = 23°C. The time reference is the onset of attack. (A) Time course of electric emission (ordinate, number of EODs per 20-ms bin) of engulfing and head-suction responses; for recordings see Figs 10 and 12. Onsets of sets *a–j* have been used in B and C as a marker for the analysis of the structure of the head-suction responses. (B) Structure of responses *f–j*, and transitional suction response. Left column, lateral views showing a tail fixation (onset: star) before the tail stroke (onset: dot) of response *f*. Second column, lateral views showing the successive positions of ray at onset of responses *g–j* (under broken lines), at maximum rise of rostrum (stars) and at the EOD onset, during these responses. Third column, diagram showing time course of activities indicated in the column; black bars: observed activities; white bars: inferred activities of responses *f–j*, except for tail immobility where black bars indicate tail fixation preceding the responses and white bars the other periods of immobility; mouth opening is observed or inferred from pattern of prey displacements; activities of biting and suction responses are indicated by bars with broken lines. Dots refer to pictures, in left and second columns. Vertical broken lines: onset of responses. Right column, high reproducibility of onset of motor events (white rectangles) of head-suction responses *f–j* relative to the onset of the EOD-sets; onset of events is given in the same order as in the third column; dark line, onset of responses according to the onset of rises. Cross hatched area gives an estimate of the stimulation 40 ms before onset of tail fixation. (C) Time course of activities for head-suction responses, biting responses and transitions to and from engulfing and suction responses. Same presentation as in B. Observed mouth opening has revealed the transitional head-suction response *t*. Dots refer to pictures in D. (D) Ventral views of ray and prey at onset of head-suction and transitional suction responses, or immediately before and after the mouth opening of the transitional suction response.

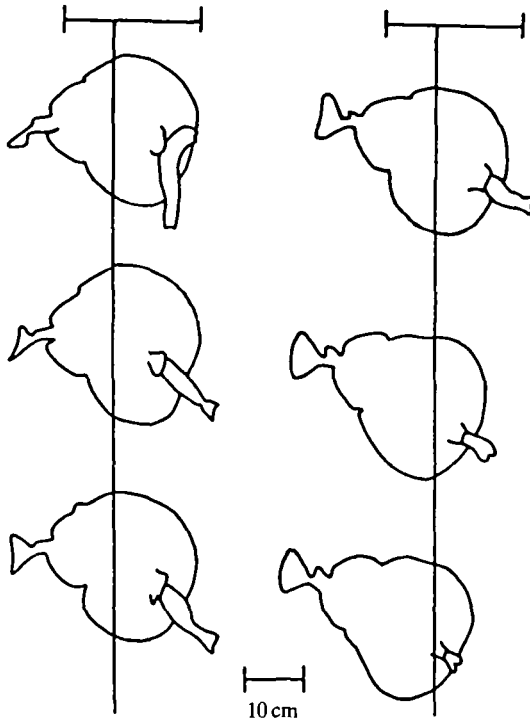
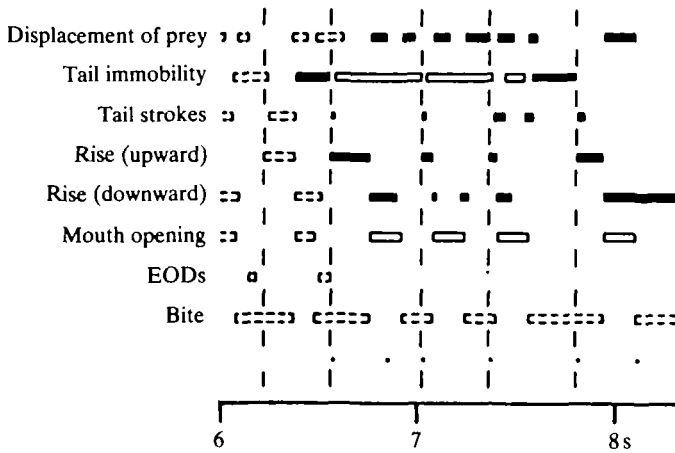


Fig. 5. Suction responses and biting responses displayed during jumping predation; successful attack of adult (390 mm) *Torpedo marmorata* upon *Dicentrarchus* (145 mm). Top: same presentation as in Fig. 4B, third column, except that suction response activities are indicated by black and white bars and that head-suction as well as biting responses are indicated by bars with broken lines. Note that there is no electric activity during alternation of suction/biting responses until the whole prey enters the mouth. Dots refer to pictures below. Bottom: (left and right) sequence of schematic drawing of ventral views of the ray and the prey. Top horizontal and vertical lines indicate ray's position at onset of the first head-suction response.

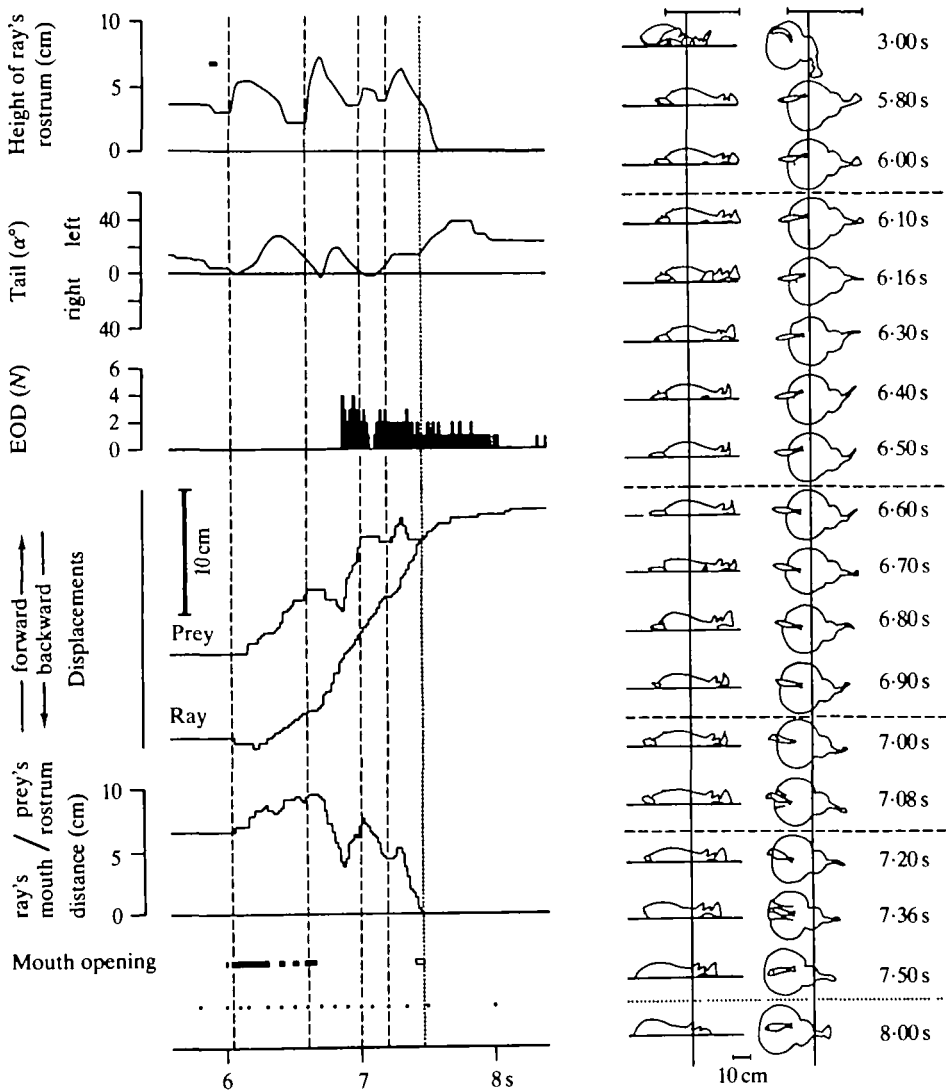


Fig. 6. Creeping responses and biting response of *Torpedo marmorata* (450 mm). This sequence upon *Trachurus* (160 mm) was occasionally recorded with a preceding double jumping response shown in Fig. 2B and with following head-suction, suction and swallowing responses. Right column: schematic drawings of lateral and ventral views of *Torpedo* and prey; four successive creeping responses (below horizontal broken lines) followed by a biting response (below horizontal dotted line) are illustrated. Sequential pictures indicated in s; 0:00 s time reference is the onset of the jumping predation. Top horizontal and vertical lines indicate the ray's position at onset of first creeping response. Left column: events of successive creeping responses. Vertical broken lines indicate onset of each creeping response. Abscissa, time in s. From top to bottom, variations in height of rostral edge of disc; variations in ray's tail angle; occurrence of electric emission (ordinate, number of EODs per 20-ms bin); displacements of the ray and the prey; distance between the mouth of the ray and the rostrum of the prey; occurrence of mouth opening visible on video pictures (black bars) or inferred from onset of biting response (white bar). Dots refer to central and right pictures. Note that black bar above the diagram on height of ray's rostrum, before first creeping, indicates prey falling on its left side.

Incomplete chains of responses are often displayed when the prey has not been caught under the disc (Fig. 1) or has escaped from under the disc; responses which would follow jumping, engulfing or head-suction responses are lacking. Small prey which are suddenly taken up into the mouth cavity during an engulfing response are swallowed directly without occurrence of head-suction and suction responses. Jumping predation without an engulfing response may be observed when the ray has directly captured the prey under the head area of the disc.

Repeated reactions may be elicited by repetition of similar stimuli; repetitive head-suction and suction responses are generally displayed in successful attacks (Figs 4, 5). Repetition of engulfing or swallowing responses is observed less frequently and rarely for jumping responses (Fig. 2B, plus one case directly observed). Occasionally, during the jumping predation, the stunned prey did not come into immediate contact with the disc of the ray, which is required to elicit the next chain of the jumping predation; in this case, repetitive creeping responses were inserted between the jumping and the head-suction responses (Fig. 6).

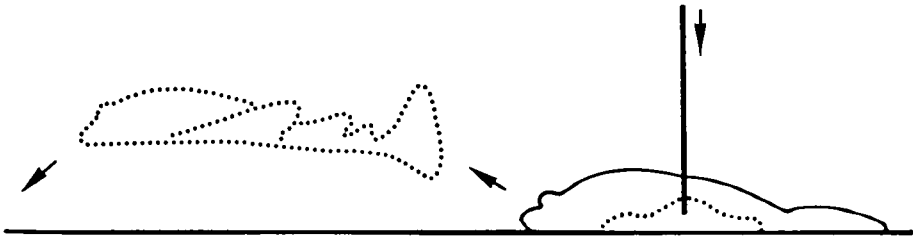


Fig. 7. Defence of the disc of *Torpedo marmorata*. The diagram shows stimulation of pressure with a rod on the disc eliciting a local pectoral wave followed by a swimming flight. These activities are important events of the small and large disc defensive responses.

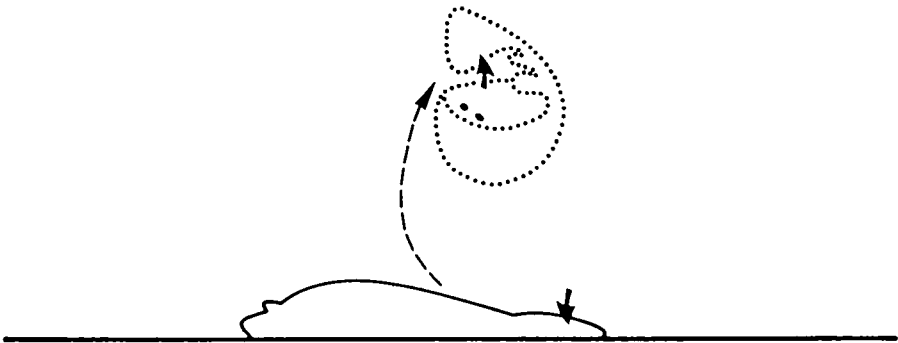


Fig. 8. Defence of the tail of *Torpedo marmorata*. The diagram illustrates small and large tail defensive responses elicited by pressure applied to the caudal fin (small arrow) when the ray is resting. The small response comprises a dorsal tail bend with an upward retraction of the disc which propels the ray upwards. The large response comprises a body bend (tail bending with upward rise of disc edges in 'tea cup' shape) and an electric emission.

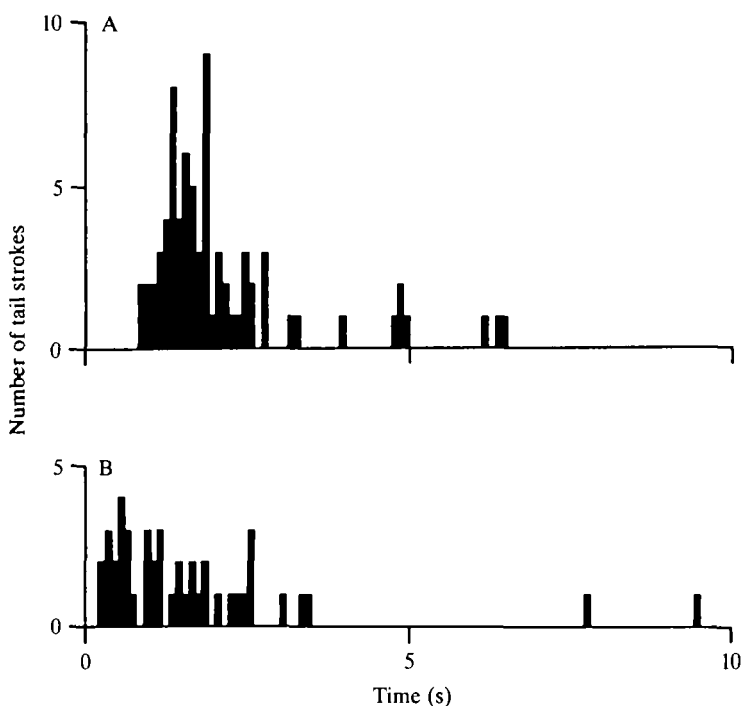


Fig. 9. Tail stroke interval histograms of jumping predations of *Torpedo marmorata* without (A, $N = 74$) and with (B, $N = 44$) prey present under the disc. Analysis of eight attacks of two neonates (120 mm) upon *Pomacentrus* and *Dascylus* of 20–40 mm; 0.1-s bins. Note that activity is increased in the presence of prey, by comparison with activity in the absence of prey.

Responses also vary when successive stimuli have concomitant effects. The tail stroke activity of the jumping predation depends on variations in occurrence of stimuli after onset of attack: the differences provoked in the case of stimulation by prey present under the disc or in the case of absence of such stimulation are shown in Fig. 9. Concomitant responses which occur during the jumping response result in modified motor patterns and particular motor acts which are not observable when each response is displayed alone. As has been indicated above, both 'jump fixation' and 'tail fixation' are observed when two jumps have occasionally collided but not in the case of a single jump (Fig. 2). Tail fixation of the engulfing response phase 1 is never observed when the response is triggered in a resting animal, but only when the response overlaps with a jumping response. Lowering of the rate of the delayed tail strokes followed by an activity rebound, or a stopping of the tail display (Fig. 3) are produced, depending on the motor state of the ray at the onset of the engulfing response. Engulfing response phase 2 and head-suction responses are only found during the jumping predation, i.e. probably after a facilitation by the jumping response (Belbenoit, 1981).

Variations dependent on stimulus parameters

The immediate tail stroke displayed in the jumping, engulfing, head-suction or disc defensive responses varies as a function of trajectory of prey or of the intruder's position and shows ipsilateral stimulus-oriented responses (Figs 1, 2, 3). The locus of the pectoral wave of the disc defensive response also varies as a function of the stimulus site (Fig. 7).

The amplitude of different motor acts of the jumping response (maximum height of jump, number of cycles and total duration of the delayed tail stroke activity) varies as a function of the height of the prey above the bottom at the start of the response (see Belbenoit, 1981). Similarly, the duration of the delayed tail beat activity and the amplitude of burying movements of the disc defensive response vary as a function of the number of mechanical pressure stimuli.

The absence of an expected motor act may depend on a specific parameter of the stimulus. For instance, display of different motor acts of the disc defensive response (trains of EODs, immediate tail stroke, delayed tail beats, burying movements) also vary as a function of the number of mechanical pressure stimuli. The immediate tail stroke of the jumping response is not displayed when the prey (or an inanimate object, Fig. 1B) approaches the ray frontally in the midline of the disc; the burying movements and, more rarely, the delayed tail strokes of the jumping response are not displayed in cases when the prey swims very close to the bottom when approaching the ray. When prey is not present under the disc during delayed activity of a jumping response, contact of the pectoral margin with another *Torpedo* elicits an engulfing response phase 1 with EODs, but contact with an inanimate obstacle elicits an engulfing response phase 1 without EODs (in this latter case it has been observed that the rate of delayed tail strokes is lowered before an activity rebound).

Variations dependent on the ontogenetic maturation

Presentation of defensive or predatory stimuli has no effect in embryos of 50 mm which display regular respiratory and swimming movements; defensive and predatory motor acts can be elicited in older embryonic–neonatal stages, in which the strong EODs mature from the mV range up to a plateau of 50 V. The 60-mm stage is the first at which EODs can be triggered by electric nerve stimulation (Krenz *et al.* 1980) and the 73-mm stage is the first at which sensory stimulations provoke EODs in the mV range (Mellinger *et al.* 1978). At this stage, adequate stimuli can elicit electric activity of the disc defensive response and of the engulfing response phase 1. In embryos of 70 ± 3 mm, all the motor components of the disc defensive response are displayed and cues of the tail defensive responses trigger the tail-bend motor act.

Presentation of jumping response stimuli has no effect in embryos and in immature neonates, and these often remain unresponsive for 2 or 3 months after the Caesarean section. For example, two neonates of the same litter delivered on the 30th of April displayed their first jumping response, respectively, on the 1st and 6th of July; another neonate delivered on the 10th of December displayed its first jumping response on the 17th of March.

At the stage of the first jumping response, neonates are able to give the whole sequence of jumping predation. Events of Fig. 1A (third response of a neonate) and 1B (sixth response of another individual) are comparable with those of Fig. 2 (responses of adults). Linear stimulus-response relationships were found in two neonates (120 mm) without previous predatory experience and in one adult (450 mm) for the relationship height of prey (P)/height of the jump (T) (see Belbenoit & Bauer, 1972, fig. 4; Belbenoit, 1981, fig. 5). If the extreme values of these correlations are expressed relative to the length of the ray, it appears that neonates attack prey swimming in a wider range of relative heights ($P = 0.05-0.5$) than the adult ($P = 0.1-0.2$), but that the range for the relative height of the jump remains almost comparable ($T = 0.2-0.5$ in neonates, $0.3-0.5$ in adults). The engulfing-swallowing responses displayed by neonates are also very comparable with those of adults; for example, a realignment, with catching of the head of the prey, was first observed during the first series of head-suction responses given by a neonate. Nevertheless, head retraction during swallowing, displayed during the same jumping predation, gives evidence of the existence of a small variation which is dependent on development in post-neonatal stages. When inanimate stimuli are presented, the jumping response is considerably less easily triggered in experienced adults than in the neonates.

Characteristics of the electric emission related to different behaviour

Electric repertoire

The sets of strong EODs emitted during the different types of motor behaviour show stereotyped patterns which are generally characteristic of each type of response. The electric activity of jumping predation (Fig. 10) is composed of a succession of EOD-sets emitted during the jumping response, the two phases of the engulfing response and finally the head-suction responses. The successive stereotyped sets are generally separated by long inter-set intervals (Fig. 10, top diagram), thus easily identifiable.

The discharge of the jumping response (Fig. 10a; Belbenoit, 1970, 1979) is generally characterized by a high frequency burst of long duration. Maximal instantaneous frequencies are comparable in adults and in neonates at 21–23°C (350 and 330 Hz, respectively).

Fig. 10b shows a short set of seven strong EODs emitted irregularly and at a low rate during an engulfing response phase 1, displayed in a jumping predation. This emission is more regular if obtained with inanimate objects in a resting animal; the frequency rate is 150–170 Hz at 21–23°C. A study of 244 trains emitted by 16 individuals (315–585 mm) showed that these were generally composed of 1–7 strong pulses (rejecting the two tails of the distribution containing 5% of the data in each) but showed a maximum of 12 strong pulses. The emission during the engulfing response phase 2 is characterized by a long set of strong EODs (Fig. 10c); it differs from the electric activity of the jumping response by its lower rate and its longer duration.

Fig. 10*d* shows a short set of strong EODs emitted during one head-suction response; head-suction EOD-sets are easily distinguishable because they are brief and often of higher frequency than the engulfing EOD-sets (Fig. 4A). This pattern may also be distinguished consistently during audio monitoring and it has been used successfully as a marker for the analysis of the structure of the head-suction responses (Fig. 4B,C), in spite of the diversity of the motor activities.

The train of EODs of the disc defensive response is a short burst generally formed by 1–9 strong EODs (rejecting the two tails of the distribution, containing 5% of the data in each) but may also show a greater number (maximum 15). The frequency is regular (150–170 Hz at 21–23°C). These data were obtained from 151 trains, emitted by 16 individuals of 315–585 mm.

The train of EODs of the tail defensive response is a short burst, often formed by a greater number of EODs than those of the disc defensive response. When examined

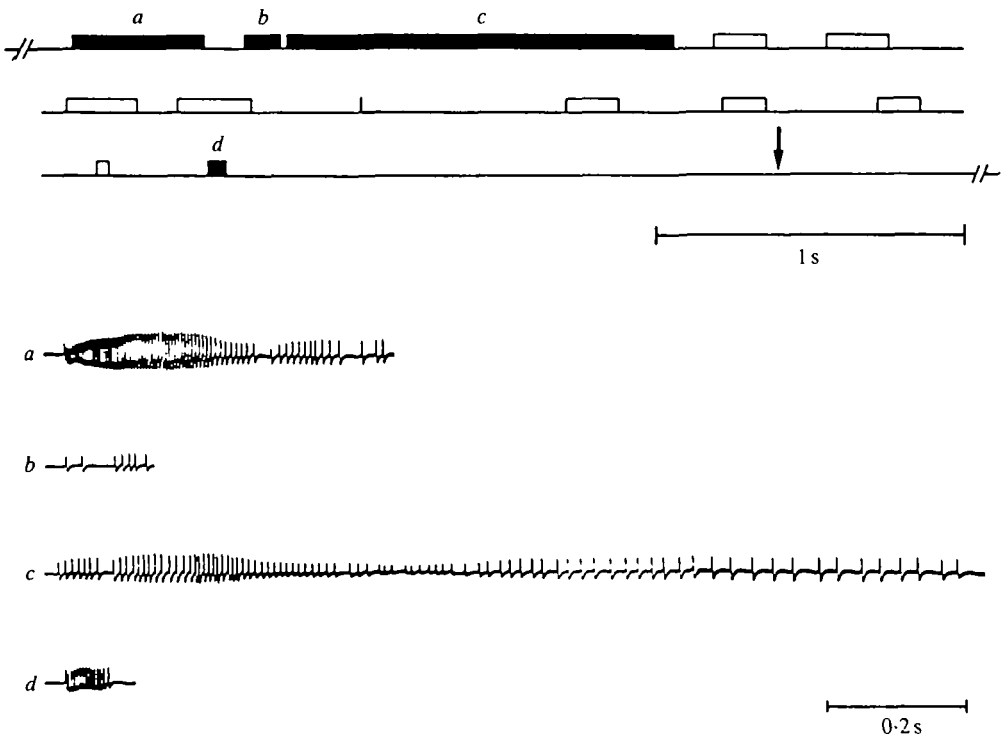


Fig. 10. Top: electric activity sequence during a successful jumping predation of an adult *Torpedo marmorata* (390 mm). The prey, a *Dicentrarchus* (145 mm) was captured in about 8.5 s. The arrow indicates the moment when the entire prey was introduced into the mouth. Filled rectangles represent the electric activity elicited during *a* jumping response, *b* engulfing response phase 1, *c* phase 2, and *d* one of the head-suction responses, respectively. Open rectangles represent electric emission elicited with other head-suction responses. Below: recordings of EOD emission correspond to filled rectangles above (*a*–*d*); temperature = 23°C. Amplitude variations are due to the ray's movement with respect to the recording electrodes.

using the established criteria, emissions of the tail defence, of the disc defence, and of the engulfing response phase 1 of an individual of 340 mm were generally formed of 6–12, 4–6 and 3–5 strong EODs, respectively (total ranges: 3–13 for 20 tail defensive responses, 2–7 for 10 disc defensive responses, 2–5 for 10 engulfing responses phase 1).

Variations in the electric motor acts

Fig. 11 shows EODs of 13 jumping responses emitted by a neonate of 120 mm (Fig. 11A, 1–7) and by an adult of 450 mm (Fig. 11B, 1–6; B 5, EODs of second jump shown in Fig. 2B) at 23–25°C. These sets comprise one or two successive trains; up to three trains have been recorded in another adult. The EOD-sets of Fig. 11 are compared graphically; for each one, the number of strong EODs plotted against time defines a series of points. These series generally show a strong reproducibility which diminishes after 0.1 s of emission. Initial rates are identical (Fig. 11A, 1–3; 11B, 1–4, 6) or are strongly or slightly lowered (Fig. 11A, 7; 11B, 5; Fig. 11A, 4–6, respectively) depending on the time interval from onset of previous electric emission. However, the total duration of 21 jumping sets of EODs emitted by two neonates and five adults shows no correlation with ontogenetic stage or with the time interval from the onset of the previous electric emission. During each set in Fig. 11A,B, EOD rate decreased less rapidly in adults than in neonates, except in the case of second jump B 5. Therefore, the maximal number of EODs per set is generally higher in adults than in neonates.

Fig. 12 shows the successive EOD emissions associated with the 10 head-suction responses analysed in Fig. 4; the EOD variability is considerably greater than in the case of the jumping electric motor act. The head-suction EOD emission of Fig. 12 is composed of 1–18 pulses (median, 12 pulses); its duration varies widely (range, 3–235 ms; median, 150 ms) and EODs are often emitted irregularly. Nevertheless, pulses have a tendency to form one or several bursts, as in the case of the jumping EOD-sets, and most of the series (Fig. 12, *c, d, f–j*) comprise an activity described above as characteristic (Fig. 10*d*). Fig. 12, notably the recordings *c* and *h*, gives evidence for a continuum between usual and occasional patterns.

Several features indicate that the different kinds of electric motor acts of *T. marmorata* show important variations depending on temperature and ontogenetic maturation, as well as on the succession of stimuli.

EOD rate varies markedly with temperature, with a Q_{10} of about 2 between 15 and 30°C (Auger & Fessard, 1928). Accordingly, maximal instantaneous frequencies of 430, 330 and 230 Hz are found at 26.5, 22 and 15°C, respectively, for the jumping EOD-sets.

The ontogenetic maturation intervenes not only in the jumping EODs (see Fig. 11), but in all the EODs emitted during successful predation. Typically a neonate of 120 mm emits up to 66 EODs while an adult of 450 mm emits up to 340 EODs. Furthermore, the number of EODs per successful predation can be predicted from the length of the individual, whatever the particular succession of electric motor acts emitted, if predation is displayed after a long resting interval: a positive

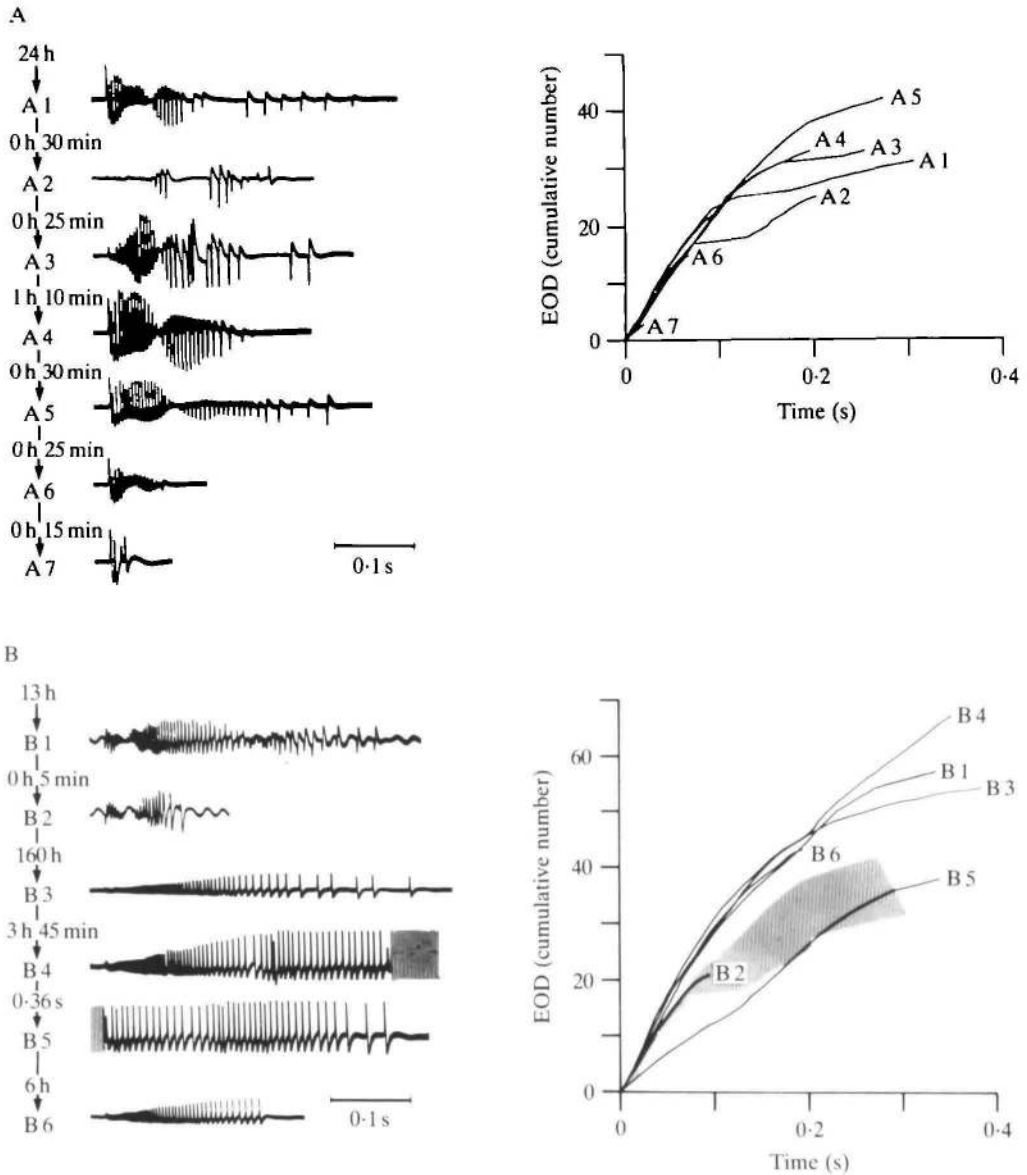


Fig. 11. Electric activity emitted with successive jumping responses of two *Torpedo marmorata*. Time intervals from onset of previous electric emission are indicated; A 1-7, sets of EODs emitted by a neonate (120 mm) preying on *Pomacentrus* and *Dascylus* of 20-30 mm at 23°C; B 1-6, six sets of EODs of an adult (450 mm) emitted while preying on *Mugil* and *Trachurus* (145-160 mm) at 23.5-25°C (B 4 and B 5, EOD activity during the double jumping response shown in Fig. 2B). Note that A 1, 2 show two trains of EODs per set. The smooth amplitude variations were due to the ray's movements with respect to the recording electrodes. Right: cumulative number of EOD pulses in each jumping response plotted against time for each individual. Limits of neonate EOD pattern are shown as a cross-hatched area on the adult diagram. Identical initial rates are found at onset of emission in neonates and adults, except in sets A 7 and B 5. Rate decreases in sets more rapidly in neonates than in adults.

correlation (Bravais Pearson test, $r = 0.82$, $N = 18$, $P < 0.001$) has been established with 15 individuals of 240–470 mm and prey of 50–200 mm (Belbenoit & Moller, 1971). From recordings of immobile individuals with electrodes placed in contact

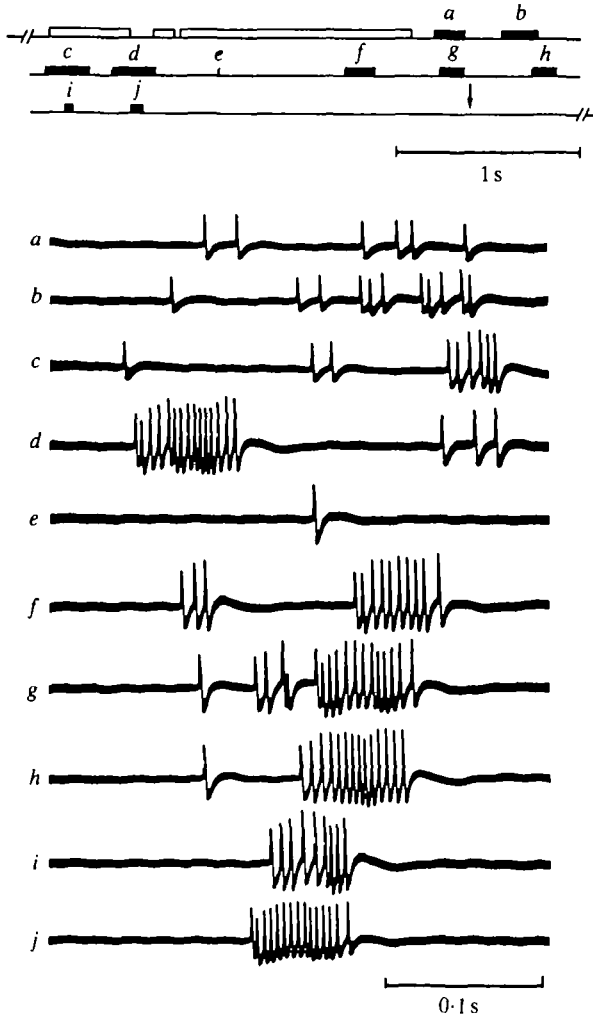


Fig. 12. Electric activity of an adult *Torpedo marmorata* (390 mm) during head-suction responses upon *Dicentrarchus* (145 mm) at 23°C. Top: diagram showing occurrence of sets of EODs (open and filled rectangles); open rectangles, trains of EODs associated with jumping and engulfing responses (see Fig. 10). Filled rectangles (*a-j*), EOD emissions (corresponding oscillograph recordings below) associated with head-suction responses analysed in Fig. 4. Arrow indicates the moment when the entire prey was introduced into the mouth. Below: *a-d*, sets of EODs associated with head-suction responses displayed before prey was caught between the jaws; *e-j*, single pulse or EOD-sets emitted with prey's body or prey's head caught transversely between the jaws. Note the diversity of patterns with a continuum between *j*, defined in Fig. 10*d* as the usual pattern, and the more occasional patterns *e*, *a*. The smooth amplitude variations were due to the ray's movements with respect to the recording electrodes.

with the dorsal and ventral surfaces of one electric organ it is obvious that the EOD-sets may vary during both the disc defensive and the engulfing response phase 1. In embryos, the pulse intensity, the pulse duration and the EOD rate often show large variations within one EOD-set; fusion phenomena and changes in the envelope of the set may occur also (Mellinger *et al.* 1978; Belbenoit, 1979). The variability decreases dramatically in neonates and adults. However, even in adults the pulse intensity of these EOD-sets may sometimes vary.

The fatigue of the EOD rate constitutes a first kind of variation, dependent on a succession of stimuli. In the case of colliding jumps (Figs 2B, 11B, 4–5) or even in the case of successive jumps emitted at intervals of some minutes or tenths of minutes (Figs 11A, 1–7; 11B, 1–2), a fatigue of the EOD rate may be present at the onset of the EOD-emission of the latest jumping response. Furthermore, when two successful jumping predations took place at a short interval, the maximal instantaneous frequency of the EOD was much lower during the different responses of the second predation: for example, 110 Hz *versus* 230 Hz, for the maximal instantaneous frequency of the second and first jumping EOD-sets, respectively (juvenile *T. marmorata*, 360 mm, at 15°C; interval between the attacks, 16.5 s; first attack was one jumping EOD-set of 48 EODs in 0.32 s, plus several engulfing, head-suction EOD-sets, 297 EODs; second attack was one jumping EOD-set of 10 EODs in 0.26 s, plus several engulfing, head-suction EOD-sets, 45 EODs) (see also Belbenoit, 1979).

Another kind of variation, dependent on a succession of stimuli, exists: after triggering of several large tail defensive responses comprising EODs, body bend is elicited without EOD emission; however, electric emission is facilitated when disc defensive or engulfing stimuli are applied: the thresholds of EOD emission of engulfing response phase 1 and disc defensive response are lowered and the number of EODs per train is increased. This was obtained in five individuals of 396–530 mm in which engulfing and disc defensive EODs were triggered at rest or a few seconds to a minute after the body bend. Engulfing activity generally shifted from 1–5 up to 3–8 strong EODs (shift of median, 3 up to 7; shift of maximum, 8 up to 12) and disc defensive activity generally shifted from 1–7 up to 3–8 strong EODs (shift of median, 3 up to 6; shift of maximum, 15 down to 12).

Weapon functions of the electric repertoire and consequences

It has been pointed out above that each set of EODs is designed to shock the prey or the intruder and contributes to specific behaviour, obtained in coordination with the effects of other motor acts.

In adults, effective use of the EODs as a weapon resulting in the immobilization of the victim or its flight, disorientation disorders, breaking of the vertebral column and death has been previously reported as being part of the jumping, engulfing and disc defensive responses (see Wilson, 1953; Fessard, 1958; Belbenoit, 1970; Belbenoit & Bauer, 1972).

Neonates also use EODs as a weapon against prey. The immobilization of a prey by a neonate at the onset of a jumping response has been observed, and this may be

effective from the first EODs of the train of the jumping response. Unsuccessful predation of a neonate has been seen to produce an immobilization of prey at the onset of the attack, followed by a strong bending of the body of the prey; not caught under the disc, the prey remained disorientated, showing disorders of swimming activity and equilibrium.

DISCUSSION

The present results give a detailed account of predatory and defensive behaviour in *Torpedo marmorata*.

Stereotypes of motor behaviour

Observation of body movements, buccal suction and electromotor activity, during jumping and creeping predation and during defence, has shown that these behaviour patterns consist of predictable sequences of events which are consistently displayed in response to a given stimulus. In jumping predation and defence responses, little difference was seen between the responses of adults and of neonates to similar stimuli. Well-documented results on the EOD repertoire (Figs 10, 11, 12) show that the electromotor apparatus responds specifically to different afferents.

A comparison of the behaviour of *T. marmorata* with that of *T. nobiliana* (Wilson, 1953) and *T. torpedo* (Michaelson *et al.* 1979) shows that at least several major elements of the jumping predation are identical in these different species. In addition, jumping responses have been observed by Bray & Hixon (1978) in *T. californica*. Certain motor activities, identifiable as elements of the disc defensive responses, have also been mentioned by Cox & Breder (1943) in *Narcine brasiliensis* and by Roberts (1969) in *T. nobiliana*.

Thus, ontogenetic and taxonomic features are sufficiently consistent to allow the conclusion that predatory and defensive motor activities of torpedinoids are stereotyped, i.e. the expression of motor programmes.

Variability of stereotyped behaviour

(1) Individual experience may produce variability. For example, in numerous adults, jumping responses were triggered less often by inanimate objects. Similarly, the magnitude of delayed tail strokes in the jumping response appears more finely controlled in adults than in neonates.

(2) A large degree of variability was observed in the described motor activities, but in general this could be reduced to dependence on stimulus parameters or to the effects of successive stimuli. Variations in behaviour patterns included oriented responses, stimulus intensity/response magnitude relationships, missing of certain motor acts, incomplete chains of responses and repetition of responses. Certain features, for instance fatigue of the EOD rate, EOD facilitation during disc defence and the engulfing phase 1 caused by previous tail defensive stimulation, and motor acts such as jump fixation depend on interference between different responses. The failure of the electric emission of tail defence is probably due to a habituation

process: this is concluded because tail defence stimuli continue to elicit the associated motor events of the tail defence and to facilitate the engulfing and disc defence EOD emissions, showing that the tail defence sensory receptors are not adapted and the electric system is not fatigued.

Variations in the EOD rate are related to the effects of temperature and to the fatiguability which is dependent on ontogenetic maturation. Tested by the jumping stimulus, the fatigue of the EOD rate was greater after the involvement of several kinds of stimuli than after the involvement of a single jumping stimulus; this supports the conclusion that the 'fatigue' was produced centrally in the electromotor system during the different EOD-sets which preceded the testing response, rather than in the sense organs to the electric system or in the sensory pathways. Variations of other EOD-set characteristics depend on the ontogenetic maturation (Belbenoit, 1979). Pulse intensity variations have been found in adults, at least in some kinds of electromotor acts. As similar features have been found in different species and genera of torpedinoids (Bennett *et al.* 1961; Bennett & Grundfest, 1961; T. H. Bullock, personal communication), it is plausible that pulse intensity variation can exist in all kinds of electromotor acts.

Defensive responses

These responses show a level of complexity comparable with some of the predatory responses, such as the jumping, engulfing or creeping responses, but are very differently organized.

Active movements, rather than an immobile posture, constitute the small disc or tail defensive responses. The small tail defensive response is a plurisegmental spinal response (Szabo, 1965); a similar mechanism could be involved in the small disc defensive response.

Probing function of delayed tail strokes of the jumping response

Analysis of the functional organization of jumping behaviour (Belbenoit, 1974*b*) has shown that the delayed tail strokes of the jumping response could provoke displacement of the prey, and these were thus interpreted as probing motor acts used to explore the substrate and furnish biological cues when prey is present. Further study has revealed that the delayed tail stroke is followed by an engulfing, a head-suction or even by a creeping response, supporting the interpretation that this is a probing tactic.

Such probing motor acts increase the rate of occurrence of stimuli giving information on the position of the prey, which may be important in the triggering of certain responses of the predatory chain after the jump. The chain of responses produced varies widely and depends upon interaction between (1) the endogenous control of the delayed tail strokes and (2) the external stimuli evoked by the prey following delayed tail strokes. However, except in some instances when a prey is present under the disc for a long time, the effects of such external stimuli (tail fixation and lowering of the tail stroke rate followed by an activity rebound, immediate tail strokes) are so slight that the relationship between the intensity of the

original stimulus which triggered the jumping response and the magnitude of the delayed activity of the jumping response is maintained. To account for this, a short-term memory of the magnitude of the input is involved in the control of the delayed tail strokes and burying movements. The input-output dependency in disc defensive response also supports the involvement of such a short-term memory in a centrally generated programme controlling the swimming-burying activities. Occurrence of burrowing-like movements without the presence of sand or mud is consistent with an endogenous control.

Ballistic responses preceded by postural reaction and gating properties of the information processing

Jumping, head-suction and engulfing are oriented responses. The ballistic nature of jumping and engulfing responses has been proposed by Belbenoit & Bauer (1972) and Belbenoit (1981). For the jumping response, this is consistent with the data of Kalmijn & Weinger (1981), who obtained feeding-oriented responses displayed without further course correction in sharks and skates, in response to electrical stimuli. The present results suggest that head-suction and creeping responses are also ballistic responses because they have an organization similar to that of jumping and engulfing responses.

This ballistic interpretation of the observed behaviour is consistent with data on electroperceptive and cutaneous evoked potentials (Platt *et al.* 1974; Bullock, 1979, 1982) showing that in the sensory areas of the brain of *Torpedo* the integrative processes do not allow a permanent survey of the sensory inputs. For example, electroperceptive following generally fails above 8 s^{-1} . In this context, head-suction and creeping chains of responses are assumed to be the result of successive exteroceptive stimuli and constitute repetitive responses of a ballistic nature. The present data show that the ballistic course of jumping, engulfing, head-suction and creeping responses may be interrupted or reset by exteroceptive stimuli.

Our data on EOD emissions show that during a single ballistic response, organized trains or bursts of EODs may be emitted. Thus repetitive reactivation of a simple neuronal mechanism may be involved and this introduces the idea of an endogenous 'resetting' factor.

Involvement of parallel sensory or sensorimotor systems

Complex predatory behaviour is obtained in part by the activation of several sensorimotor systems in parallel. This is obvious in the case of the responses which occur during the delayed tail activity.

A second example of involvement of parallel sensorimotor systems is given by the biting response which occurs together with engulfing, head-suction and suction responses; biting responses require activation of the mesencephalic trigeminal neurones (Roberts & Witkovsky, 1975).

The similarities in locomotor activity during head-suction and suction sequences suggest that the same neuronal circuits may control both kinds of behaviour. The characteristic difference between the behaviour patterns is in the presence or the

absence of EOD (see Fig. 4). This can be explained by the involvement of stimuli of different modalities. While the prey remains outside the mouth, only cutaneous and electroreceptive stimulation may be possible and this elicits the head-suction response associated with EOD; when the prey enters the mouth, as during mouth opening of the transitional suction response shown in Fig. 4, taste buds may be stimulated and the behavioural pattern changes to the suction sequence in which EOD is inhibited; this change may be mediated following stimulation of the taste buds. The parallel gustatory input, which is unnecessary to trigger the response, may provoke a direct inhibition of the electromotor command nucleus (oval nucleus of Szabo, 1954) stronger than the excitatory inputs which this nucleus receives simultaneously from the neurones which control the head-suction response.

Evolutionary relationships between suction of food and EOD activity

Suction of food during mouth opening of engulfing, head-suction and suction responses occurs fairly soon after the onset of these responses. This, and the bifunctionality of the respiratory system, which has been shown to allow both respiratory activity and suction for feeding in sharks and batoids (Moss, 1977), strongly support the idea that these two activities involve a single respiratory cycle controlled by the medullary respiratory centre. The respiratory cycle, as described by Hughes & Ballintijn (1965), starts when the mouth is adducted, with a decrease in volume of the orobranchial and then the parabronchial cavities due to the contraction of certain sets of respiratory muscles; mouth opening follows and suction is produced when the volume of the parabronchial pump is increased by the contraction of other respiratory muscles which are successively activated. Consistent with the respiratory origin of the electric system (Kappers, 1947; Mellinger *et al.* 1978; Fox & Richardson, 1978, 1979), it must be inferred that this effector, which is activated after the onset of mouth opening and suction of food during the head-suction response, was also activated during suction of food in non-electric ancestors of *Torpedo*, i.e. in rhinobatoids. This means that the motor programme which controls the head-suction response is probably an ancestral character.

For the inhibition of EODs by gustatory inputs, two opposing hypotheses may be proposed.

(1) The control of certain respiratory muscles of Elasmobranchii may be inhibited when food contacts taste buds, i.e. when it is no longer necessary to produce such a strong suction effect as when the food was outside the mouth. In this case, the suction response of *Torpedo* may be an ancestral character.

(2) Alternatively, the inhibition of EODs may have been acquired secondarily by torpediniforms. This change would serve to avoid supplementary fatigue of the electric system, when the tetanizing effects of EODs are no longer necessary to capture the prey which has been sufficiently engaged into the mouth cavity. If this is the case, the suction response of *Torpedo* may thus constitute a derived character.

A transition from a respiratory to an electromotor function may have been a continuous process without any functional rupture.

I would like to thank Dr T. H. Bullock for his encouragement and for critical reading of this manuscript, Dr T. Szabo and Professor P. Moller for their detailed comments and advice, Dr K. Grant for correcting the English and for helpful discussions, C. Teyssedre and Dr J. Serrier for valuable suggestions, M. Boudinot for technical assistance, D. Kemenovic for typing the manuscript and the Director and Staff of the Marine Biology Institute at Arcachon, France, for their hospitality and assistance.

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