

Escape manoeuvres in the spiny dogfish (*Squalus acanthias*)

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Summary

The locomotor performance of dogfish during escape responses was observed by means of high-speed video. Dogfish show C-type escape responses that are comparable with those shown previously in teleosts. Dogfish show high variability of turning rates of the anterior part of the body (head to centre of mass), i.e. with peak values from 434 to 1023 deg. s⁻¹. We suggest that this variability may be due to the presence of two types of escape manoeuvres, i.e. responses with high and low turning rates, as previously found in a teleost species. Fast responses (i.e. with high maximum turning rates, ranging between 766 and 1023 deg. s⁻¹) showed significantly higher locomotor performance than slow responses (i.e. with low maximum turning rates, ranging between 434 and 593 deg. s⁻¹) in terms of distance covered, speed and acceleration, although no differences were found in the turning radius of the centre of mass during the escape

manoeuvres. The existence of two types of escape responses would have implications in terms of both neural control and muscular activation patterns. When compared with literature data for the locomotor performance of bony fishes, dogfish showed relatively low speed and acceleration, comparable turning rates and a turning radius that is in the low part of the range when compared with teleosts, indicating relatively high manoeuvrability. The locomotor performance observed in dogfish is consistent with their morphological characteristics: (1) low locomotor performance associated with low thrust developed by their relatively small posterior depth of section and (2) relatively high manoeuvrability associated with their high flexibility.

Key words: dogfish, elasmobranch, escape response, locomotion, *Squalus acanthias*, kinematics, swimming, manoeuvrability.

Introduction

Kinematics and performance during unsteady swimming manoeuvres in fish have been investigated by various authors, especially within the context of predator–prey interactions (Rand and Lauder, 1981; Webb and Skadsen, 1980; Webb 1984a, 1986a,b; Nemeth, 1997; Harper and Blake, 1991; Domenici, 2001). The ability of fish to escape from predators may depend upon a variety of parameters, including distance–time variables (such as speed and acceleration; see Domenici and Blake, 1997, for a review), manoeuvrability (Howland, 1974; Webb, 1976; Weihs and Webb, 1984; Nissanov and Eaton, 1989; Domenici and Blake, 1993), timing (Dill, 1974; Webb and Zheng, 1994; Domenici, 2002) and trajectory of escape (Blaxter et al., 1981; Eaton and Hackett, 1984; Domenici and Blake, 1993).

Escape responses in fish are usually mediated by the Mauthner neurons, although alternative pathways may exist (Eaton et al., 1984). Escape responses are usually divided into two main stages based on kinematics (stage 1 and stage 2), which correspond to consecutive body contractions, beyond which the locomotor behaviour is highly variable (Weihs,

1973; Webb, 1976, 1978a). Typically, during stage 1, fish bend into a ‘C’ shape (hence the term C-start) due to a unilateral contraction of the body musculature (although bilateral muscular activity in stage 1 was recently found in *Polypterus senegalus*; Tytell and Lauder, 2002), while stage 2 corresponds to the return flip of the tail (Weihs, 1973; Domenici and Blake, 1997). Jayne and Lauder (1993) show that the onsets of muscular activity are synchronous on one side during stage 1, whereas the contralateral muscular activity (i.e. during stage 2) are propagated posteriorly. Recent work by Hale (2002) has shown that escape responses (in the muskellunge, *Esox masquinongy*) may also involve simultaneous muscle activity anteriorly on one side of the body and posteriorly on the opposite side (S-starts). Earlier work has shown that, in some species (e.g. angelfish, *Pterophyllum eimikei*, knifefish, *Xenomystus nigri*), stage 2 may be a coasting phase (Domenici and Blake, 1991; Kasapi et al., 1993) and stage 2 electromyogram (EMG) activity may be absent in some cases (Tytell and Lauder, 2002). Past work on schooling fish (herring, *Clupea harengus*) has shown that escape responses

may show short (~20 ms) and long (~100 ms) latencies in reaction to a stimulus, associated with fast and slow head turning rates, respectively (Domenici and Batty, 1994). In herring, proximity to neighbours in the school may induce long latency responses, although long latencies were also sometimes observed in solitary individuals (Domenici and Batty, 1994, 1997). It is not known if other species of fish, including dogfish, present a similar dichotomy of responses to that observed in herring.

While previous work has investigated a variety of fish species of various forms and sizes, little is known about the fast-start behaviour of chondrichthyans in general (Hale et al., 2002). Nevertheless, various species of elasmobranchs, including embryos of spiny dogfish, possess Mauthner cells (Bone, 1977; Zottoli, 1978; Stefanelli, 1980). Based on functional morphology, the spiny dogfish would be expected to show relatively low acceleration performance, as high acceleration is dependent on a large body depth placed posteriorly (Webb, 1984a). On the other hand, given their relatively high flexibility (Alev, 1977), spiny dogfish can be expected to perform well in terms of manoeuvrability, i.e. to show a tight turning radius and high turning rate when compared with other fish.

As far as we are aware, the present study is the first kinematic investigation of escape responses in chondrichthyans. The aims of this study were twofold: to investigate the pattern of variation in turning rates in dogfish and to compare the kinematics and the performance of the spiny dogfish with those of previously studied teleosts.

Materials and methods

Study animals

Spiny dogfish (*Squalus acanthias* L.), were collected by trawls on the southeast side of San Juan Island, Washington, USA. Experiments were performed on five specimens (mean total length 58.6 ± 4.6 cm; mean \pm S.E.M.). Fish were transported to Friday Harbor Laboratories, where they were held in 4 m-diameter outdoor tanks with flow-through seawater at $12 \pm 1^\circ\text{C}$. Fish were maintained in the tanks for two weeks prior to the experiments. Fish were fed every other day with frozen fish (locally caught) but were starved at least 24 h prior to experiments.

The position of the centre of mass of the fish when stretched straight (CM) was determined on one euthanized 60 cm specimen, previously frozen in order to be stiffened and balanced. A long pin was placed transversely through the body of the fish at the position at which the fish was balanced in the horizontal plane. This position was measured and calculated to be 33% of the total length.

High-speed videography

Single fish were transferred to a 4 m-diameter experimental outdoor tank (height 1.1 m) filled with water to a depth of 60 cm, of the same shape and size as, and adjacent to, the holding tank. Transferral time was therefore minimized and

the dogfish did not appear to be stressed by showing high-speed response nor an increase in ventilation after transferral but rather swam at low speed as in the holding tank. Water temperature in the filming tank matched that of the holding tanks (i.e. $12 \pm 1^\circ\text{C}$). Square reference panels (5 cm squares) were laid on the bottom of the tank, approximately at the centre of the tank. Escape responses were elicited by manually thrusting a 2 m-long pole (diameter 3 cm) towards the body of the dogfish, from outside the tank. This proved to be the most effective means of eliciting an escape response in the dogfish, and a similar method has been used in escape response studies of other fish (Harper and Blake, 1990). In no instance did the pole actually touch the dogfish. Prior to being stimulated, the dogfish were cruising undisturbed at low speed. To avoid any wall effects (Eaton and Emberley, 1991), fish were only startled when they were at least two body lengths from the nearest wall. Fish were allowed to acclimate for at least 30 min prior to being startled. Three responses for each of the five individuals were filmed, using a minimum interval of 30 min between trials. Filming rate was $500 \text{ frames s}^{-1}$, using a Redlake Motionscope PCI-8000S digital high-speed camera positioned 2 m above the filming tank. All escape responses obtained were analyzed. Video sequences were exported as AVI files and compressed using Cinepak Codec compression software. Sequences were calibrated from the filming reference grid and analyzed using WINanalyze automated tracking program. The X, Y coordinates of the CM of the fish when stretched straight (Webb, 1976; the point on the midline, at $0.33 L$ from the tip of the head) and tip of the rostrum were digitized for each escape sequence. The CM of the shark was located on the video by measuring the length of the midline from the tip of the rostrum to 0.33 of body length.

The characteristics of the stimulus were measured in 2-D, i.e. in the horizontal plane, the main plane of stimulus motion. Stimulus speed was calculated based on the distance covered by the stimulus tip during the 25 ms preceding the escape response onset. Stimulus distance was calculated as the shortest distance between the stimulus and the body of the fish at the onset of the response. Stimulus angle was calculated as the angle between the tip of the head of the fish, the tip of the stimulus and the centre of mass of the fish (Domenici and Blake, 1993). Therefore, a frontal stimulus, in line with the head, would correspond to 0° , while a posterior stimulus would correspond to 180° . Stimulus position at the time of response was calculated based on the position of the tip of the stimulus relative to the fish's body. If the point on the body that was closest to the stimulus was half-way along the body, a $0.5 L$ (body length) was assigned. Stimuli near the head approached $0 L$, while tail stimuli approached $1 L$. In addition, the swimming phase of the fish was defined as in Blaxter and Batty (1987) and Domenici and Batty (1994), i.e. whether the tip of the tail was oriented away or towards the stimulus in the frame before response onset. Tail tip orientation was scored as +1 (tail tip oriented away from the stimulus) and -1 (tail tip oriented towards the stimulus).

Data analysis

Durations

Stage 1 (S1) duration was defined as the time between the first detectable reaction of the fish and the change in direction of turning by the anterior part of the body (snout to the centre of mass), following Kasapi et al. (1993) and Domenici and Blake (1997). Stage 2 (S2) duration was defined as the time between the end of stage 1 and the subsequent change in direction of the anterior part of the body following Kasapi et al. (1993) and Domenici and Blake (1997). Total duration was defined as the sum of stage 1 and stage 2 durations. In addition, stage 1 duration was also measured in four fish while making spontaneous turns ('routine turns') without being startled.

Angles

Stage 1 angle was determined by the rotation of a line passing through the centre of mass and the snout between the beginning of the response and the end of stage 1. Stage 2 angle was determined by the rotation of a line passing through the centre of mass and the snout between the end of stage 1 and the end of stage 2. Since stage 2 rotation is in a direction opposite to that of stage 1, stage 2 angle bears a negative sign. In addition, stage 1 angle was also measured in four fish while making spontaneous turns ('routine turns') without being startled.

Head turning rate

Head turning rate was defined as the angular velocity of the line linking the tip of the snout and the centre of mass (Domenici and Blake, 1997). Head turning rate was derived from the raw angle data with a five-point smoothing regression (Lanczos, 1956). Mean stage 1 head turning rate (corresponding to the ratio of stage 1 angle/stage 1 duration) and maximum stage 1 and stage 2 head turning rates were measured.

CM turning rate

The rate of turning, during stage 1, of the centre of mass of the fish when stretched straight (CM) was calculated by measuring the arc of the turn of the CM divided by stage 1 duration.

Turning radius

Turning radius was measured as the radius of the path of the centre of mass throughout stage 1, following Domenici and Blake (1991). Turning radius was measured in lengths (*L*), since previous authors have shown that turning radius is a constant proportion of fish length (Webb, 1976).

Distance–time variables

Distance–time variables were measured based on the displacement of the CM. Cumulative distance, speed and acceleration were derived from the distance–time data by using a five-point smoothing regression (Lanczos, 1956). Distance–time variables were measured using two procedures: throughout the duration of the response (d_R , cumulative distance; U_R , maximum speed; A_R , maximum acceleration, where subscript R stands for response) or within a fixed time

(i.e. 288 ms, the mean of the pooled fast-start duration of both slow and fast responses; d_T , cumulative distance; U_T , maximum speed; A_T , maximum acceleration, where subscript T stands for time). This latter procedure was adopted following previous authors (Webb, 1976; Domenici and Blake, 1991) to avoid any performance bias due to differences in fast-start duration. In addition, the speed immediately prior to the fish's first detectable reaction was measured for all the escape responses.

Results

Escape responses consisted of C-starts, i.e. with the body bent in the characteristic C-shape at the end of stage 1 (Figs 1, 2). Dogfish show high variability of turning rates of the anterior part of the body (head to centre of mass), as shown in Figs 1, 2. This variability can be appreciated by inspecting the relationship between stage 1 angle and stage 1 duration, as well as the maximum S1 head turning rates (Figs 3, 4A). We suggest that the observed variability in the relationship

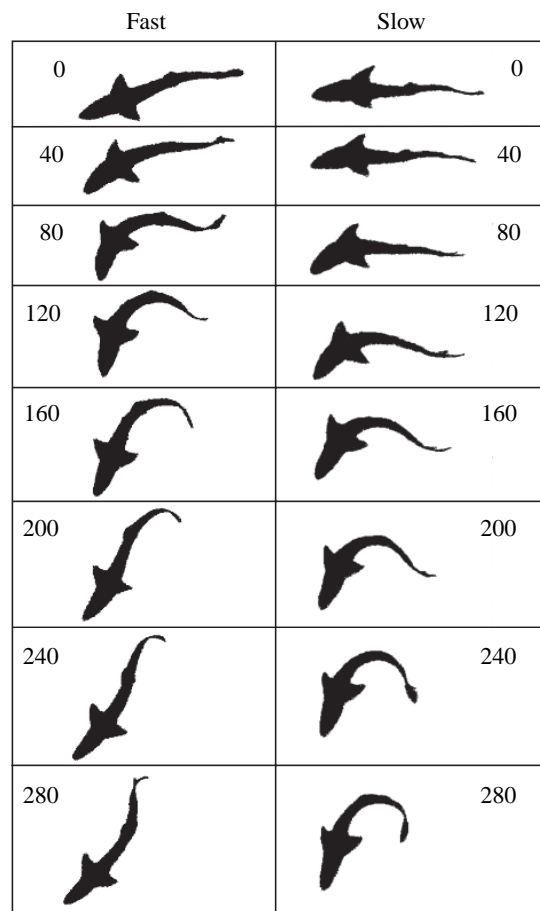


Fig. 1. Silhouettes of dogfish fast-starts. The first 280 ms of a fast response (left panels) and a slow response (right panels) are shown. Numbers indicate time in ms after the onset of the response. Note the faster rate of bending in the fish on the left panels when compared with the right panels, i.e. the fish's shape in the fast response after 120 ms is similar to the fish's shape after 200 ms in the slow response.

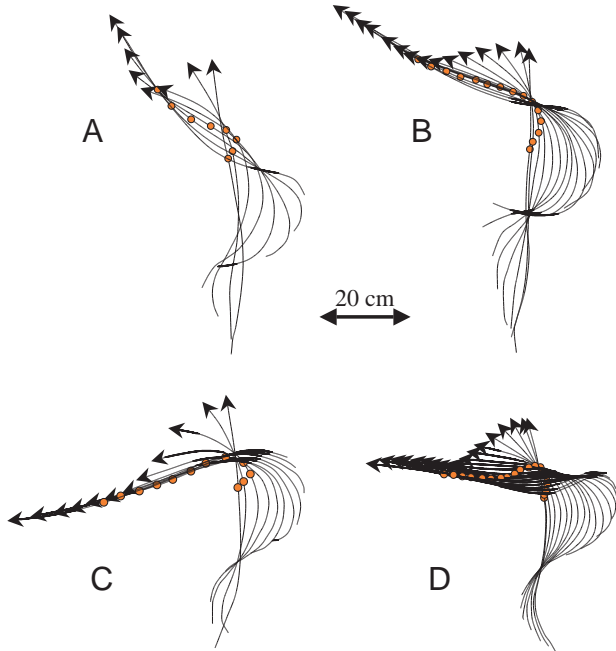


Fig. 2. Midline and centre of mass (red circles) of the fish at 40 ms intervals from the onset of the response. Head is indicated by the arrow. A and B correspond to the fast and slow responses, respectively, shown in Fig. 1. C and D show large turns achieved by fast and slow responses, respectively. Note the longer time taken by fish in B and D in order to achieve a similar stage 1 angle as A and C, respectively.

between stage 1 angle and stage 1 duration and in head turning rates may be due to the presence of two types of escape response, as shown by Fig. 3, where escape responses occupy two distinct regions of the graph, and Fig. 4A, where a bimodal pattern appears. On the basis of these observations, we have therefore divided escape responses into two groups (types) of fast-starts, with significantly different slopes of the regression lines for the relationship between S1 angle and S1 duration (Fig. 3; ANCOVA, line A vs line B, $P < 0.005$; line A, $Y = 0.40 + 10.8X$, $P < 0.001$, $r^2 = 0.91$, $N = 7$; line B, $Y = 0.17 + 17.4X$, $P < 0.001$, $r^2 = 0.92$, $N = 8$). Each of the two regressions differed from the linear relationship derived for routine swimming turns (line C, $Y = 0.15 - 34X$, $P < 0.05$, $r^2 = 0.90$, $N = 4$) (ANCOVA, A vs C, difference in slope $P < 0.01$; B vs C, no difference in slope, $P > 0.4$; difference in intercept $P < 0.0001$). Similarly, the frequency distribution of maximum S1 head turning rates (Fig. 4A) presents a bimodal pattern of distribution, where a large range of turning rate values occurs, i.e. with the maximum values being more than twice as high as the minimum values. Stage 1 head turning rates ranged between 434–593 and 766–1023 deg. s^{-1} (maximum values for slow and fast responses, respectively) and between 211–322 and 408–507 deg. s^{-1} (mean values for slow and fast responses, respectively). Therefore, two types of fast-start, defined as fast and slow responses (i.e. with high maximum S1 head turning rates, $> 750 \text{ deg. s}^{-1}$, and with low maximum S1 head turning rates, $< 600 \text{ deg. s}^{-1}$, respectively) were considered, and the

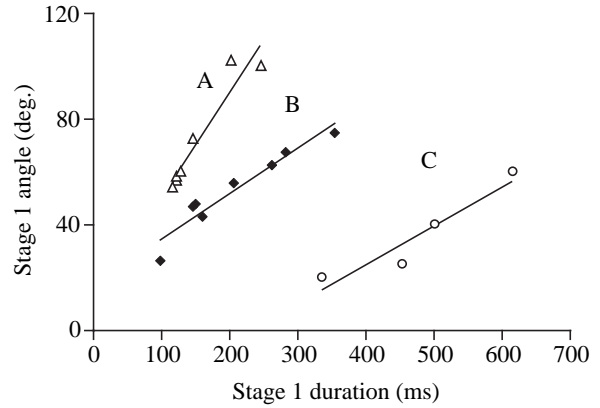


Fig. 3. The relationship between stage 1 angle and stage 1 duration in fast responses (open triangles), slow responses (filled diamonds) and routine turns (open circles). (A) $Y = 0.40 + 10.8X$, $P < 0.001$, $r^2 = 0.91$, $N = 7$; (B) $Y = 0.17 + 17.4X$, $P < 0.001$, $r^2 = 0.92$, $N = 8$. (C) $Y = 0.15 - 34X$, $P < 0.05$, $r^2 = 0.90$, $N = 4$.

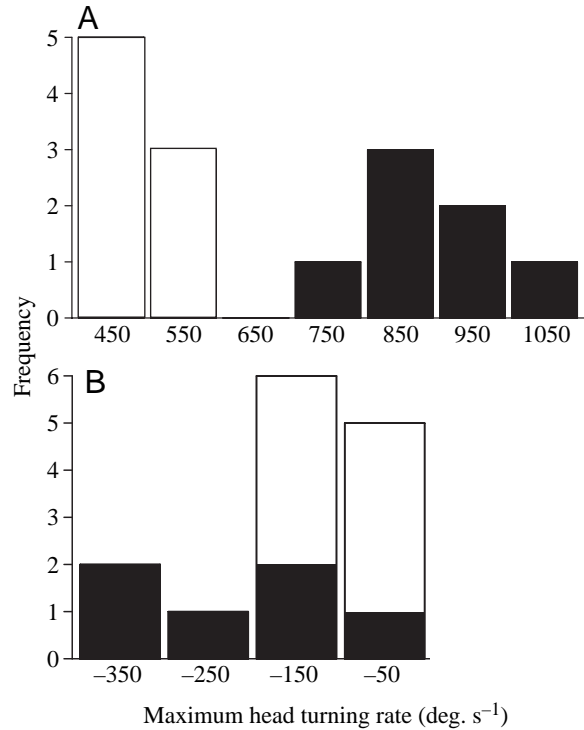


Fig. 4. Frequency distribution of maximum head turning rates during stage 1 (A) and stage 2 (B). Stage 1 distribution shows a bimodal pattern, where slow (open bars) and fast (filled bars) responses are present, in line with Fig. 1. The distribution of stage 2 maximum head turning rate shows that slow (open bars) and fast (filled bars) responses overlap.

differences between them were tested. Both mean and maximum stage 1 head turning rates (mean head turning rates 471 ± 12 and $268 \pm 14 \text{ deg. s}^{-1}$; maximum head turning rates 889 ± 38 and $499 \pm 20 \text{ deg. s}^{-1}$ in fast and slow responses, respectively; Table 1) were statistically different when comparing slow and fast responses, as expected by the bimodal distribution found (Fig. 4A).

t-tests were used in all comparisons, except when the variances of the two samples were significantly different (*F*-test), in which case a Mann–Whitney test was used. *N* for all tests was 8 (slow responses) or 7 (fast responses), except where noted due to the absence of stage 2 in one response (see below). The mean speed prior to the response was 0.29 ± 0.02 and $0.26 \pm 0.04 \text{ m s}^{-1}$ (mean \pm S.E.M.) in slow and fast responses, respectively (no statistical difference; *t*-test, $P > 0.1$; $N = 8$ and $N = 7$, respectively). Stimulus characteristics and swim phase at the time of response onset did not differ between escape type (Table 2).

Stage 1 duration did not differ between response types (Table 1). Stage 2 was present in all but one response (a fast response), which was therefore considered to last until the end of stage 1. In this case, this response was removed from the analysis of stage 2 variables, i.e. stage 2 duration, stage 2 angle, maximum stage 2 head turning rate (Table 1). Total duration did not differ between response types while stage 2 duration did (Table 1). The stage 1 angles (positive values) of the two response types showed no statistically significant differences while stage 2 angles (negative values) did (Table 1).

Maximum stage 2 head turning rates were statistically different (-236 ± 52 and $-99 \pm 21 \text{ deg. s}^{-1}$ in fast and slow responses, respectively; Table 1). A frequency distribution plot (Fig. 4B) shows that maximum stage 2 head turning rates overlap considerably. CM turning rates were significantly different ($P < 0.001$; Table 1). Mean turning radii were $0.074 \pm 0.007 L$ (body length) and $0.060 \pm 0.006 L$ in slow and fast responses, respectively. These values did not differ significantly (Table 1) and the mean value for the pooled responses was $0.067 \pm 0.005 L$ ($N = 15$). The minimum turning radius measured was $0.041 L$.

The relationship between mean S1 head turning rate and CM turning rate was not significant within either fast or slow responses ($P > 0.1$ in both cases; Fig. 5A). CM and mean S1 head turning rates were significantly related to stage 1 duration only for slow responses (mean S1 head turning rate $Y = -0.36 + 342X$, $r^2 = 0.64$, $P < 0.05$, $N = 8$; CM turning rate $Y = 1.63 + 1044X$, $r^2 = 0.61$, $P < 0.05$, $N = 8$; Fig. 5B). U_T was not significantly related to mean S1 head turning rate and CM turning rate of slow and fast responses ($P > 0.01$ in all cases; Fig. 5C).

All distance–time variables were significantly higher in fast than in slow responses (Table 3), whether measured within fast-start duration (d_R , U_R , A_R) or within a fixed time (i.e. 288 ms, the pooled fast-start duration of both slow and fast responses; d_T , U_T , A_T). Fig. 6 shows examples of speed and head S1 turning rate profiles of a fast and a slow response. Nevertheless, despite being significantly different, distance–time variables did not form the bimodal distribution found with S1 head turning rates, and the data for fast and slow responses showed a slight overlap in the distribution (Fig. 7).

Fast and slow responses were shown by all individuals tested. Since each fish was tested three times in succession with at least a 30 min interval between trials, the possibility that trial number had an effect on the type of fast start was tested by assigning a score to each fast-start of the series, i.e. 1 to the

Table 1. Fast-start duration, turning angles, turning rates and turning radius for slow and fast responses (means \pm S.E.M.)

Escape type	S1 duration (ms)	S2 duration (ms)	Total duration (ms)	S1 angle (deg.)	S2 angle (deg.)	Mean S1 t. rate (deg. s ⁻¹)	Max. S1 t. rate (deg. s ⁻¹)	Max. S2 t. rate (deg. s ⁻¹)	CM t. rate (deg. s ⁻¹)	T. radius (L)
Slow	207.3 \pm 30.3	74.2 \pm 14.6	281.5 \pm 34.9	53.1 \pm 5.4	-5.0 \pm 2.0	268 \pm 14	499 \pm 20	-99 \pm 21	706 \pm 63	0.074 \pm 0.007
Fast	154.6 \pm 18.9	164.3 \pm 29.7 [#]	295.4 \pm 41.4	72.2 \pm 7.8	-20.6 \pm 4.8 [#]	471 \pm 12	889 \pm 38	-236 \pm 52 [#]	1221 \pm 83	0.060 \pm 0.006
Test	NS	$P < 0.05^*$	NS	NS	$P < 0.05^*$	$P < 0.0001$	$P < 0.0001$	$P < 0.05^*$	$P < 0.001$	NS

*Indicates Mann–Whitney test; all other tests are *t*-tests. $N = 8$ for fast responses; $N = 7$ for slow responses, except where noted by # ($N = 6$).

Table 2. Stimulus characteristics (means \pm S.E.M.)

Escape type	Stimulus speed (m s ⁻¹)	Stimulus distance (cm)	Stimulus angle (deg.)	Stimulus position (L)	Swim phase (score)
Slow	0.76 \pm 0.14	9.3 \pm 1.7	70.3 \pm 17.0	0.23 \pm 0.07	0.25 \pm 0.37
Fast	0.75 \pm 0.17	13.2 \pm 1.9	96.3 \pm 20.6	0.43 \pm 0.14	0.14 \pm 0.40
Test	NS	NS	NS	NS	NS*

*Indicates Mann–Whitney test; all other tests are *t*-tests. *N*=7 for slow responses; *N*=8 for fast responses.

first escape response triggered, and 2 and 3 to the second and third escape responses, respectively. The results show that no effect of trial number on response type was present (Mann–Whitney test, $P>0.5$).

In order to account for individual variation, paired *t*-tests were carried out using one type of response (fast and slow), randomly chosen for each individual. The results are in line with those presented above. Significant differences were found for stage 1 head turning rates (mean, $P<0.0001$; maximum,

$P<0.0001$), CM turning rates ($P<0.05$) and for all the distance–time variables within a fixed time (d_T , $P<0.05$; U_T , $P<0.05$; A_T , $P<0.005$). Performance to the end of the fast start was different in terms of U_R ($P<0.01$) and A_R ($P<0.05$). Similarly, paired *t*-tests did not detect any significant differences between stimulus characteristics, swim phase or fish speed before stimulation.

Discussion

Response types

Escape responses have been classified into various types by different authors (C- and S-start; Webb, 1976; Hale, 2002; single bend and double bend responses; Domenici and Blake, 1991; slow and fast responses; Domenici and Batty, 1994). A classification into response types could imply opposite extremes of a gradient of responses or, alternatively, two distinct types, which may be due to distinct behavioural patterns, neural commands and muscle activation patterns. Our results suggest that dogfish employ C-shape escape responses similar to those previously observed in teleosts (e.g. the tracings in Fig. 2 are comparable with those shown by Webb, 1976; Domenici and Blake, 1991). We also suggest that dogfish may employ two different response types, which are characterized by two distinct rates of turning of the anterior part of the body (Figs 3, 4), as found previously in a teleost (Domenici and Batty, 1994, 1997). Although no overlap in the maximum S1 head turning rates and in the stage 1 angle/stage 1 duration relationship is apparent, our results are not a definite demonstration that two distinct behavioural patterns of escape

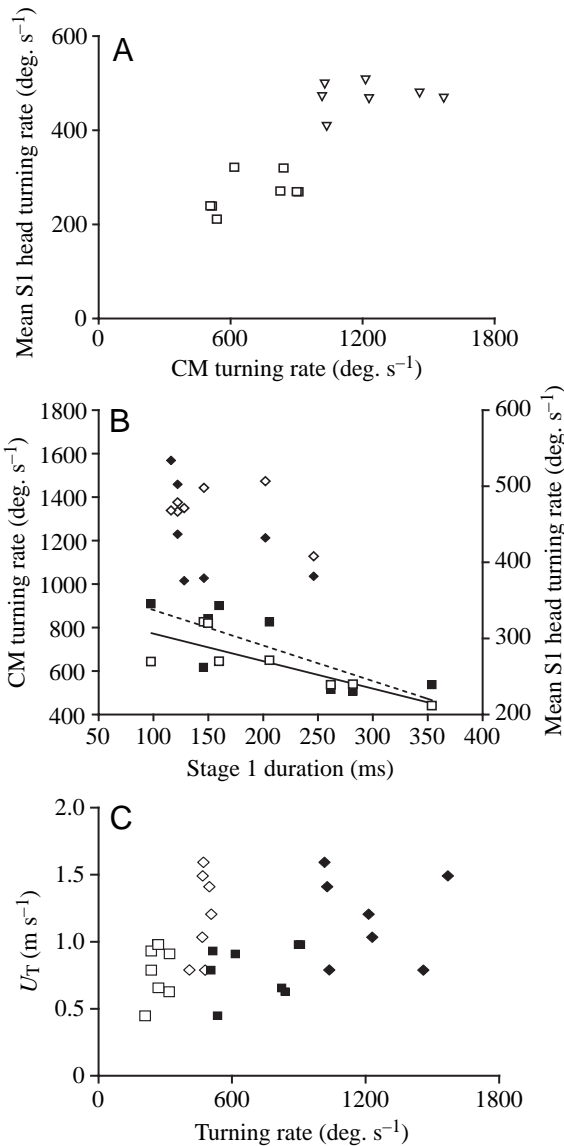


Fig. 5. (A) The relationship between mean S1 head turning rate and centre of mass (CM) turning rate (open squares, slow responses; filled triangles, fast responses). (B) The relationship between turning rates and stage 1 duration (filled diamonds, CM turning rate in fast responses; filled squares, CM turning rate in slow responses; open diamonds, mean S1 head turning rate in fast responses; open squares, mean S1 head turning rate in slow responses). The dotted line represents the regression between CM turning rate in slow responses and stage 1 duration ($Y=1.63+1044X$; $r^2=0.61$; $P<0.05$; $N=8$). The continuous line represents the regression between mean S1 head turning rate in slow responses and stage 1 duration ($Y=-0.36+342X$; $r^2=0.64$; $P<0.05$; $N=8$). (C) The relationship between speed (U_T) and turning rates (filled diamonds, CM turning rate in fast responses; filled squares, CM turning rate in slow responses; open diamonds, mean S1 head turning rate in fast responses; open squares, mean S1 head turning rate in slow responses).

Table 3. Distance–time variables for slow and fast responses (means \pm S.E.M.)

Escape type	d_R (m)	d_T (m)	U_R (m s ⁻¹)	U_T (m s ⁻¹)	A_R (m s ⁻²)	A_T (m s ⁻²)
Slow	0.167 \pm 0.012	0.171 \pm 0.015	0.80 \pm 0.07	0.79 \pm 0.07	19.4 \pm 1.5	18.8 \pm 1.8
Fast	0.264 \pm 0.041	0.279 \pm 0.031	1.17 \pm 0.13*	1.19 \pm 0.12	31.5 \pm 3.3	31.1 \pm 3.5
Test	$P<0.05^*$	$P<0.01^*$	$P<0.05$	$P<0.05$	$P<0.005^*$	$P<0.01$

*Indicates Mann–Whitney test; all other tests are t -tests. $N=8$ for fast responses; $N=7$ for slow responses.

responses exist in dogfish, since it is possible that a larger sample size may reveal responses with intermediate head turning rates. In addition, EMG studies would be necessary in order to provide a close examination of the motor pattern before and during the response and to test the possibility that variation in motor pattern before the response may have an effect on turning rate.

Similar to our results, Domenici and Batty (1994, 1997) found that herring showed slow and fast head turning rates, which were both distinct from the head turning rates of routine turns. They also found that slow head turning rate responses were associated with longer response latencies than fast head turning rate responses. For any given stimulus distance, slow responses were more frequent in schooling than in solitary fish (Domenici and Batty, 1997), suggesting that schooling may raise the threshold for initiation of fast escape responses, inducing longer latencies and slower responses that are more appropriate in reducing the possibility of collision with neighbouring fish. Our present work suggests that the presence of fast and slow responses may not

be limited to highly gregarious teleost fish (although dogfish can also be found in groups; Lythgoe and Lythgoe, 1971) but may be a more widespread phenomenon of escape types that may be worth investigating further in other species. As suggested by Domenici and Batty (1994, 1997), the two response types may be associated with different neural commands. Nissanov et al. (1990) found that escape responses triggered by electrical

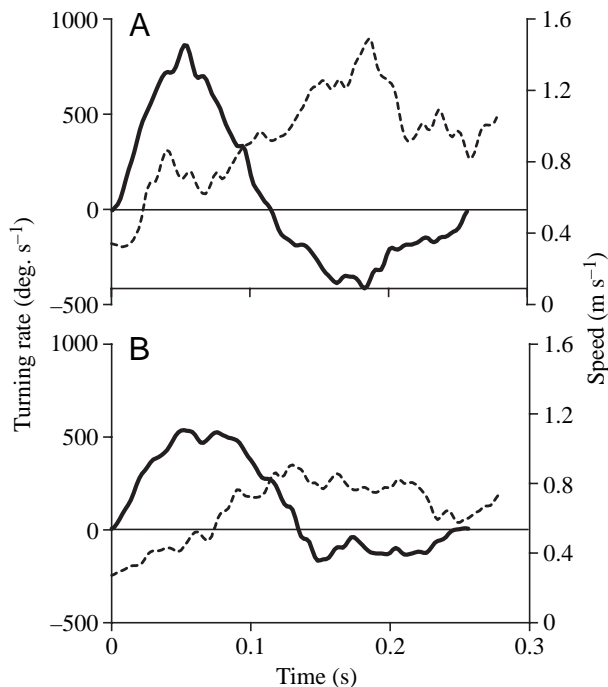


Fig. 6. Examples of performance in fast (A) and slow (B) responses. Head turning rates (continuous lines) and speeds (dotted lines) are shown. Time '0' indicates the beginning of the escape response. In both responses, stage 1 and stage 2 end when the turning rates cross zero, at approx. 0.12 s and 0.25 s, respectively.

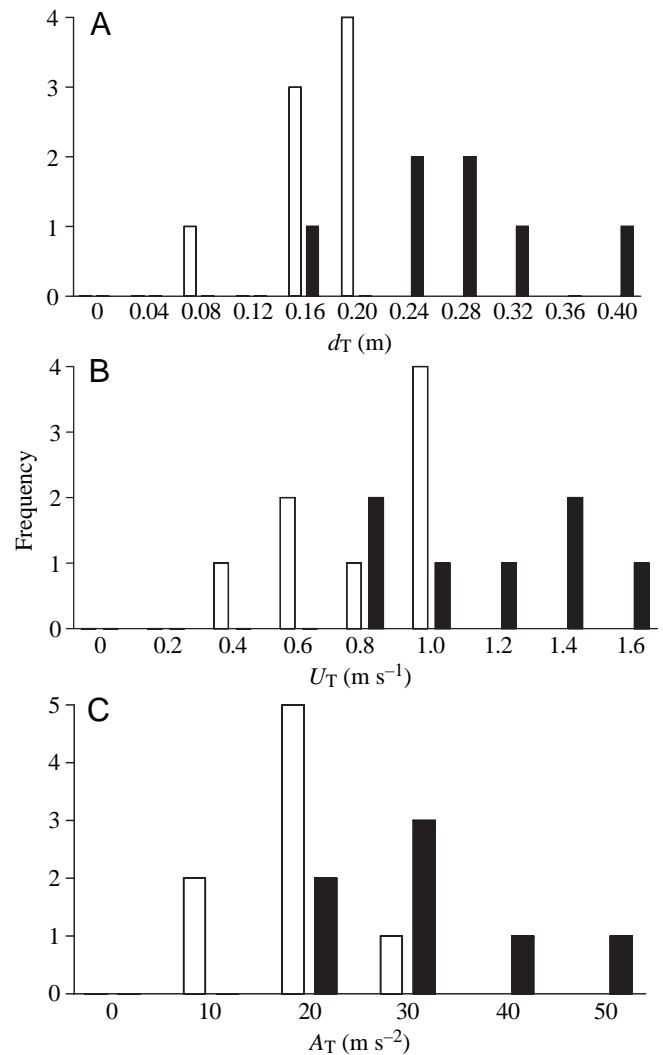


Fig. 7. Frequency distributions of distance-derived performance in slow (open bars) and fast (filled bars) responses. (A) Cumulative distance (d_T); (B) maximum speed (U_T); (C) maximum acceleration (A_T). While fast responses show significantly higher performance in all these variables (Table 3), the values for slow and fast responses overlap in the distributions.

stimulation of single Mauthner cells (M-cells) showed a slower head turning rate than sensory-evoked responses, where both M-cells and parallel reticulospinal circuits were triggered. It is therefore possible that fish may employ fast and slow responses that may be associated with different neural commands, similar to the finding by Nissanov et al. (1990). In addition, the two response types may reflect different muscle contraction speeds and activation patterns.

Domenici and Batty (1997) associated the occurrence of different turning rates to stimulus distance. Here, stimulus characteristics did not differ between responses with different turning rates (Table 2). However, since the stimulus was not a transient one, unlike Domenici and Batty's work, we could not test if turning rates were related to latencies. Previous authors have also investigated the effect of swim phase of the fish prior to stimulation on escape responses. Sillar and Roberts (1988) found that escape responses were gated in tadpoles, i.e. they were inhibited when the body flexure was towards the stimulus. Blaxter and Batty (1987) found that swim phase had an effect on the direction of escape in herring, while Domenici and Batty (1994) found no effect of swim phase on the escape responses of herring. In the present study, swim phase has no significant difference between response types. In addition, response type was not related either to the order of stimulation or to specific individuals. Therefore, the factors affecting turning rates are still unclear, and they may be related to both the internal state (motivation) of the animal and some yet to be measured stimulus characteristics.

Other response types observed by previous authors include single and double bend responses (Domenici and Blake, 1991) and C- or L- (i.e. unilateral bend) and S-start responses (Webb, 1976; Hale, 2002). Domenici and Blake (1991) and Kasapi et al. (1993) classified single and double bend responses on the basis of the absence/presence of stage 2. In the present study, all responses but one (a fast response) showed the presence of stage 2. However, various responses (five in total, both fast and slow) showed small stage 2 angles ($<2^\circ$) associated with short stage 2 durations (<50 ms). Therefore, in dogfish, the intensity of stage 2 appears to correspond to a gradient, from low intensity (and absence of reversal of head direction, in one case) to higher intensities (i.e. maximum stage 2 angle near 30°), and neither stage 2 angle nor stage 2 duration show clear bimodal patterns of distribution (not shown). Similarly, no bimodal pattern in maximum stage 2 head turning rate between response types was found (Table 1; Fig. 4). Foreman and Eaton (1993) also found that the intensity of stage 2 (measured as the EMG integral) showed a gradient, from a minor EMG (or even complete absence of a signal) to a high-intensity EMG signal. Given the overlap in stage 2 variables, we suggest that the hypothesized distinction between fast and slow responses would not correspond to the distinction between double bend and single bend responses. Similarly, Domenici and Blake (1991) found no differences in the relationship between stage 1 angle and S1 duration (equivalent to head turning rate) of single and double bend responses.

Webb (1976) divided fast-starts in trout into L- (later called

C- by most authors; see Domenici and Blake, 1997) and S-starts, based on the fish's body form at the end of stage 1. More recently, Hale has found that different EMG patterns and kinematics were present during the C and S escape responses of pike (Hale, 2002). In the present study, no S-start was observed in dogfish, although this may be due to the relatively low sample size used. It is possible that the presence of S- and C-starts in fish escape responses may be species-specific, where sit-and-wait predators such as pike, which use fast-start in line as a predator attack, may also use in-line (S-starts) fast-starts as escape responses.

Performance differences between slow and fast responses

The two response types showed non-overlapping values of stage 1 head turning rates (both maxima and means). Stage 1 head turning rate was almost twice as high in fast compared with slow responses. Such differences were not associated with different stage 1 angles. While a tighter turning radius might be expected in fast responses, differences were not significant. CM turning rates were also higher in fast response. Maximum stage 2 head turning rates differed between fast and slow responses, similar to stage 2 duration and angle. This suggests that the intensity of stage 2 is stronger in fast responses, although values of stage 2 maximum head turning rates overlapped with those of slow responses.

All distance-derived variables were higher in fast than in slow responses. While this is to be expected because locomotor performance is related to muscle contraction speed (Wardle, 1975), this is the first demonstration that higher turning rate can lead to higher locomotor performance. The distribution pattern of distance-derived performance is, however, not bimodal, unlike for head turning rates (Fig. 7). Therefore, it is possible that overlapping turning rates during stage 2 (Fig. 4B) may account for some degree of overlap in the performance between the two escape types considered.

If the possibility that dogfish possess two types of escape responses is confirmed, this would mean that they can employ a two-gear system with which they respond to startling stimuli. Such a system would allow them to react using different response intensities and, therefore, energetic costs, perhaps depending on the degree of the perceived threat. As suggested above, this system does not appear to be graded, possibly as a result of neuromuscular design features. Domenici and Batty (1994, 1997) found that herring, a teleost with Mauthner neurons (Meredith, 1985), show such response types (i.e. high and low head turning rate responses), both differing from routine turns. Therefore, it is possible that a two-gear system may be a common feature of the escape responses of many fish, including teleosts and chondrichthyans, regardless of the presence of the Mauthner system.

The relationship between mean S1 head turning rate and CM turning rate was investigated. The turning rate of the head and that of the CM should be related (Domenici, 2001), particularly if the anterior part of the animals is relatively rigid and if the CM and the head start off in line and end up in line with the swimming trajectory of the fish. While previous authors

working on aquatic vertebrates have investigated either the head turning rates (Eaton et al., 1981; Domenici and Batty, 1994, 1997; Spierts and van Leeuwen, 1999; Budick and O'Malley, 2000; Walker, 2000) or CM turning rates (Gerstner, 1999; Fish et al., 2003), the relationship between these two variables has never been tested. Our results show that head and CM turning rates are not related within each escape type. However, fast responses show higher head and CM turning rates than slow responses. The order of magnitude is similar for maximum S1 head turning rate and CM turning rate (Table 1). This implies that the overall expectation of similar magnitude is confirmed. However, CM and head turning rates must be relatively decoupled from each other since they are not significantly related within each fast-start type considered.

Turning rates decrease with stage 1 duration only in slow responses, while they are not related to stage 1 duration in fast responses. This result may imply differences in the temporal patterns of turning rate in slow and fast responses, possibly related to differences in the neural commands. Speed (U_T) is not affected by turning rates in either fast or slow responses, although fast responses show higher speed and turning rates than slow responses. Therefore, while CM and head turning rates may be rough predictors of locomotor performance when applied to all responses, detailed analysis of the kinematics of the whole body may be necessary in order to unravel the relationship between kinematics and performance of each response type.

Comparison with other species

Based on morphological features, we expected dogfish to exhibit relatively tight turns, because of their relatively high flexibility (Aleev, 1977), and relatively low locomotor performance during fast-start, due to their relatively low body depth posteriorly (Webb, 1978a, 1984a). As shown by Brainerd and Patek (1993), high flexibility during fast-starts may be associated with number of vertebrae. Spiny dogfish have more vertebrae (72 precaudal vertebrae; Springer and Garrick, 1964) than many of the teleosts whose turning radius has been investigated (reviewed by Domenici and Blake, 1997; e.g. *Salmo gairdneri*, 60–66 vertebrae; *Esox lucius*, 57–65 vertebrae; *Coryphaena hippurus*, 31 vertebrae; *Thunnus albacares*, 39 vertebrae; www.fishbase.org). However, recent work by Kajiura et al. (2003) shows that vertebral count did not have significant effects on flexibility during unsteady manoeuvres in three cartilaginous fishes, while cross-sectional shape did. Therefore, high flexibility in dogfish may be related to body shape and other factors such as the stiffness of the intervertebral tissue. Our results confirmed the expectations based on functional morphology arguments. Fig. 8 shows the turning radius of dogfish in comparison with those of teleost fish and other vertebrates, based on data reviewed by Domenici (2001). This figure is based on mean values. The value for dogfish (0.067 L) is in the low part of the range when compared with other aquatic vertebrates and it is similar to that of a manoeuvre specialist such as angelfish (0.065 L ; Domenici and Blake, 1991). The minimum turning radius achieved during a single event can also be considered a relevant measure of maximum

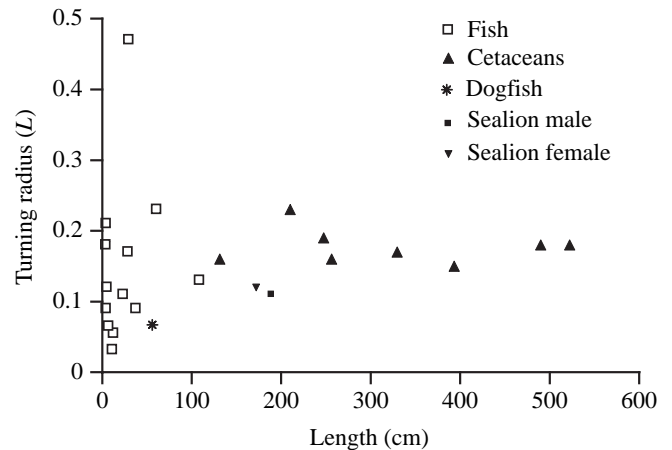


Fig. 8. Turning radius in dogfish compared with the turning radius of other vertebrates. All data are means, except for data on sealion, which are means of the 20% smallest radii. Data on fish are based on Domenici (2001), Gerstner (1999) and Walker (2000). Data on cetaceans are based on Fish (1997), as reported by Domenici (2001). Data on sealion are from Fish et al. (2003). Modified from Domenici (2001).

performance during a single event. The minimum turning radius measured in a single event is 0.041 L in dogfish. Other vertebrate species show relatively small minimum turning radius during a single event, i.e. sealion (0.09 L ; Fish et al., 2003), four species of coral reef fishes (0–0.09 L ; Gerstner, 1999), boxfish (0.0005 L ; Walker, 2000). Although these studies were not based on escape responses, they show that minimum turning radius in certain manoeuvre specialists such as coral reef fishes can be even tighter than that shown by dogfish. The ability to turn along tight paths can be of fundamental importance during predator–prey relationships (Howland, 1974; Webb, 1976), particularly for species living in structurally complex environments (Domenici, 2003). Dogfish are benthic fish that may live in groups on various types of bottoms (sand and mud, rocky bottoms; Wetherbee et al., 1990; Masuda and Allen, 1993). Predators of dogfish may include larger elasmobranches (Harvey, 1989; Stillwell and Kohler, 1993). Dogfish are mainly piscivorous (Tanasichuk et al., 1991; Beamish et al., 1992). High manoeuvrability in dogfish may, therefore, be advantageous during predator–prey encounters, both as predators and prey. The tight turning radius of dogfish may be due to their high flexibility when compared with teleost species (Aleev, 1977). This is in contrast with pelagic fish such as tuna, with very rigid bodies, whose turning radii are an order of magnitude higher than that of dogfish (i.e. 0.47 L ; Blake et al., 1995). In addition, dogfish appear to move their pectoral fins asymmetrically during turning (P. Domenici, personal observation) and this behaviour may aid in producing a tight turning radius, although whether such a movement is active or passive remains to be ascertained. Eaton and Hackett (1984) suggested that escape responses in most fish are associated with abducting their pectoral fins against the body, with a few exceptions such as in the hatchet fish. However, other species appear to fold out their pectoral fins (Kasapi et al.,

1993; Domenici and Blake, 1997). Therefore, the role of specific pectoral fin movements during the escape response of different fish species is an area that needs further attention.

Turning rate is another relevant measurement of manoeuvrability in fish, as it can be used to evaluate agility defined as the ability of a fish to quickly reorient its body (Webb, 1994). Turning rate decreases with fish length (reviewed in Domenici, 2001). Domenici (2001) includes values only for fish up to about 30 cm, although values for other vertebrates (cetaceans) in excess of 1 m are included. Therefore, the value predicted for a 58 cm dogfish based on fig. 7 of Domenici (2001) needs to be considered with caution as it comprises both teleosts and cetaceans, as well as head and CM turning rates. Nevertheless, a 58 cm dogfish is predicted to show a mean turning rate of $\sim 800 \text{ deg. s}^{-1}$, which is within the same order of magnitude as our results for CM and S1 head turning rates of fast responses (Table 1), while values for slow responses are somewhat lower. Therefore, dogfish appear to be capable of escaping using similar rates of bending as would be predicted for other vertebrates of a similar size, although comparable data (in terms of size) for fish are lacking. Therefore, considering both turning radius and turning rates as measures of manoeuvrability, dogfish appear to perform relatively well, although not exceptionally, when compared with other aquatic vertebrates.

Distance–time performance in dogfish appears to be lower than that of most teleost species (Domenici, 2001). Temperature can have an effect on fast-start performance (Webb, 1978b). The temperature used in our study is within the range used in other studies (Domenici and Blake, 1997), although slightly higher than the average of previous fast-start studies (approximately 16°C from Domenici and Blake, 1997) and therefore it is possible that low temperature may account in part for low performance. The speed of both fast and slow responses appears to be considerably lower than those reported in other studies, which include teleosts of sizes similar to the dogfish. According to fig. 1 of Domenici (2001), a 58 cm-long fish should have a maximum speed of $\sim 3 \text{ m s}^{-1}$, which is considerably higher than the speeds reported here (1.19 and 0.79 m s^{-1} for fast and slow responses, respectively). In addition, it is important to consider that, in most other performance studies, fish performed escape responses from a standing start (e.g. trout, pike, angelfish), while dogfish start from a swimming speed of $\sim 0.27 \text{ m s}^{-1}$. Dogfish can swim at speeds faster (e.g. 1.9 m s^{-1} for a 47 cm dogfish reported by Aleev, 1977) than those reported here, although it may take them a few tail beats in order to get to such speeds. As was found for speed, acceleration in our study appears to be at the lower end of the range when compared with other studies (Domenici and Blake, 1997; Domenici, 2001), being 31 and 19 m s^{-2} for fast and slow response, respectively, while it ranges from ~ 20 to $>150 \text{ m s}^{-2}$ in other studies on teleosts reviewed by Domenici (2001). Size is unlikely to be the reason for such a low performance, there being no evidence of an effect of size on acceleration across fish species (Domenici, 2001), and, indeed, acceleration may increase with size within a single species in relation to changes in morphology resulting from ontogeny

(Wakeling et al., 1999; Hale, 1999). Low locomotor performance in dogfish escape responses is most likely related to their relatively small body depth posteriorly, compared with accelerator specialists such as pike and angelfish, whose large posterior depth allows for high thrust generation during fast-start manoeuvres (Harper and Blake, 1990; Domenici and Blake, 1991).

The present results suggest that two escape types may occur in the dogfish. From these results and other recent studies (Tytell and Lauder, 2002; Hale, 2002; Hale et al., 2002) it is becoming apparent that escape responses can be highly variable both within and across species. Some of this variability may be due to flexibility in the neural and muscular systems, although in some cases, as in the fast and slow escape responses observed in the dogfish, discrete behaviours and therefore differential neuromuscular control may be the basis for kinematic differences. Future studies, integrating kinematics and neuromuscular data, should be aimed at studying the variability of escape responses (e.g. by using a variety of species and different stimulus characteristics) in order to further our understanding of the functional basis of both graded and discrete categories of escape behaviours.

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