ZOOLOGY

Piscivorous cyprinid fish modulates suction feeding kinematics to capture elusive prey

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ABSTRACT

Previous studies have shown that evasive prey generally elicit a different kinematical pattern of prey capture from suction feeding fish compared to non-evasive types of prey. However, no evidence exists that predatory fish can modulate their prey capture kinematics in response to whether or not an elusive prey performs an escape response. Here, we analyse prey capture kinematics of a specialist piscivore (asp, *Aspius aspius*) during feeding on untethered, live goldfish, which regularly displayed escape attempts when attacked by the asp. Significant modulation occurred in function of the escape attempts of prey: mouth opening was prolonged and increased in magnitude, and one individual also showed an increased hyoid depression when feeding on prey trying to escape. As the orientation of the prey with respect to the predator prior to the start of mouth opening was related to the probability of observing an escape attempt, asp could theoretically perform this type of modulation by *a priori* choosing a pre-programmed motor pattern. However, since contact between the prey and the asp's mouth appeared to be a factor improving the timing of mouth closing, this fine-tuning of prey capture kinematics is more likely to be caused by reflexive neural feedback control.

1. Introduction

An important aspect of the feeding success of predators that feed on a variety of different prey is the capacity to adjust their prey capture strategy in function of prey type, because the ability of a predator to use different feeding methods will increase the range of prey types it can efficiently handle (Elshoud-Oldenhave, 1979; Liem, 1979, 1980; Nemeth, 1997b; Frost and Sanford, 1999; Liem and Summers, 2000; Bolnick and Ferry-Graham, 2002). For example, the ability of suction feeding fishes to modulate prey capture kinematics when feeding on non-evasive prey versus evasive prey is well documented: the latter prey type elicited faster attacks (Vinyard, 1982; Norton, 1991), longer activity of the feeding muscles (Sanderson, 1988), higher intra-oral suction pressure (Nemeth, 1997a) or larger expansions of the mouth cavity (Ferry-Graham et al., 2001; Coughlin and Strickler, 1990). The non-evasive prey, on the other hand, can be captured more easily (Vinyard, 1982; Aerts, 1990). Interestingly, it has been demonstrated that the Sacramento perch (*Archoplites interruptus*) can learn to distinguish evasive from non-evasive prey, and adjust prey capture behaviour accordingly, in about 20 encounters (Vinyard, 1982).

However, capturing a certain type of prey considered to be intrinsically capable of escaping may not always require the same strategy (Ferry-Graham et al., 2001). We may expect a different pattern of prey capture kinematics in predators whether its prey attempts to escape during the capture event or not. To capture a prey that starts an escape response, the suction feeder should theoretically suck in an additional amount of water (corresponding to the distance travelled by the prey away from the mouth) and mouth closing should be postponed (corresponding to the time delay of the prey entering the mouth). Consequently, if suction feeding predators would possess the capacity to evaluate *a priori* whether or not the prey will attempt to escape, they could probably enhance their feeding efficiency by modulating prey capture kinematics accordingly. As an alternative to this classical theory of pre-strike information determining the kinematical pattern chosen by the suction feeder from its repertoire, Aerts (1990) showed that the suction feeding kinematics of cichlid fish are probably subjected to neural feedback control triggered by the prey entering the mouth.

The hypothesis that suction feeders can modulate prey capture kinematics in function of prey escape attempts has been tested previously for the cheeklined wrasse, *Oxycheilinus digrammus* (Ferry-Graham et al., 2001). In that study, no significant differences in prey capture kinematics could be distinguished in strikes with and without an escape response. However, *O. digrammus* is not specialised in capturing evasive prey, since it is a

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generalistic suction feeder with a widely diverse diet ranging from elusive crustaceans and fishes to prey attached to the coral reef (Westneat, 1995). In the present study, we test the above hypothesis for the asp *Aspius aspius* (Teleostei: Cyprinidae), a specialist piscivore (Kottelat and Freyhof, 2007). In case of significant modulation in function of prey escape attempts, we will further evaluate whether visual, pre-strike information can explain the asp's modulation, or whether a neural feedback control mechanism is likely to be involved.

2. Materials and methods

2.1. Study animals

Two adult *A. aspius* L. 1758 specimens were caught in the river Waal (The Netherlands), and were kept in individual 140 l aquaria (1.0 m × 0.4 m × 0.3 m) at a temperature between 15 and 20 °C, and a 12 h:12 h light:dark photoperiod. The aquaria were aerated and equipped with circulation pumps. Cranial lengths (lower jaw tip to posterior edge of the operculum in lateral view) and total lengths were 86.3 mm and 475 mm (individual A), and 83.2 mm and 432 mm (individual B), respectively. The individuals were fed live goldfish (60–70 mm total length), which were unrestrained in their movement in order to mimic the natural situation as closely as possible. To prevent saturation, the animals were only fed during the weekly recording sessions.

2.2. Kinematical analysis

A. aspius capturing live goldfish were recorded with a Redlake MotionScope M3 (Redlake Digital Imaging Systems, IDT Vision, Tallahassee, FL, USA) high-speed camera (1280 × 1024 pixels) at 250 or 500 Hz. Three arrays of 8 ultrabright, red LEDs provided the necessary illumination. Only the prey capture sequences in which the fish approached the prey along a plane approximately perpendicular to the axis of the camera lens, and in which minimal or no roll or yaw could be discerned during prey capture, were used for further analysis.

Because prey were not tethered, only a small percentage of all feeding trials could be analysed. Despite these practical limitations, we managed to analyse 24 prey captures (10 without escape attempt and 5 with escape attempt for individual A, 6 without escape attempt and 3 with escape attempt for individual B). An escape attempt was defined as a situation where a tail beat was observed that caused propulsion away from the mouth of the predator. This implies that when the prey could only perform the first phase of a C-start (body curving) before being sucked into the mouth of the predator, the feeding sequence was considered not to include an actual attempt to escape.

Ten anatomical landmarks were digitised frame-per-frame on the video images using Didge software (Alistair Collum, Creighton University, Omaha, NE, USA), following the position of the eyes of predator and prey, the lower and upper jaw tips, the hyoid tip, the operculum and the neurocranium (Fig. 1). The *x* and *y* coordinates of these landmarks enabled us to calculate kinematical profiles of the mouth opening, hyoid depression, neurocranium rotation, opercular rotation in the sagittal plane, and a relative measure of opercular abduction (i.e., the posterior-to-anterior displacement of the opercular ridge landmark; Fig. 1). From these kinematical profiles, 10 derived variables were calculated: 1 = maximal mouth opening, 2 = mouth opening duration, 3 = peak instantaneous mouth opening velocity, 4 = duration of the mouth being opened >95% of maximum mouth opening, 5 = maximum hyoid depression, 6 = peak instantaneous hyoid depression velocity, 7 = total neurocranium rotation, 8 = total operculum abduction (i.e., maximal posterior-to-anterior
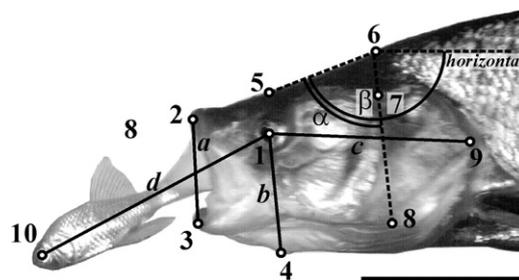
Fig. 1. Anatomical landmarks (numbers) and calculated kinematical variables (letters) that were used to quantify prey capture kinematics in *A. aspius* feeding on goldfish prey. The digitised anatomical landmarks are: 1 = centre of the eye, 2 = rostral tip of the premaxilla, 3 = posterior tip of the lower jaw, 4 = tip of the hyoid, 5 = skull roof dorsal of the eye, 6 = skull roof at the level of the supra-occipital bone, 7 = approximate opercular–neurocranium joint, 8 = ventral tip of the operculum, 9 = caudal tip of the operculum, 10 = centre of the eye of the prey. The kinematical variables calculated from these landmarks are: a (distance 2–3) = mouth opening, b (distance 1–4) = hyoid depression, c (distance 1–9) = distance between the eye and the opercular ridge, d (distance 1–10) = eye-to-eye distance between predator and prey, α (angle between 7–8 and 5–6) = opercular rotation in the sagittal plane, β (angle between 5–6 and the horizontal) = neurocranium angle. Scale bar = 50 mm.

displacement of the opercular ridge landmark), 9 = total opercular rotation, and 10 = eye-to-eye distance between predator and prey at the start of mouth opening. The start of mouth opening was set as time = 0.

2.3. Prey orientation

To allow for testing whether the possibility of the prey to display an escape attempt depends on the prey orientation with respect to the predator right before suction starts, the three-dimensional position of the prey with respect to the predator was estimated. Since only lateral projection images were available, the yaw angle of the prey was estimated based on the prey length and its length shown in lateral projection on the video image (van den Berg, 1994). The following three variables were used to quantify the three-dimensional position of the prey with respect to the asp (Fig. 2): pitch angle (−180° to 180°), yaw angle (−180° to 180°), and the 3D-angle between the midsagittal axes of predator and prey (0–180°). Because of symmetry, statistics were performed on the absolute values of pitch angle and yaw angle.
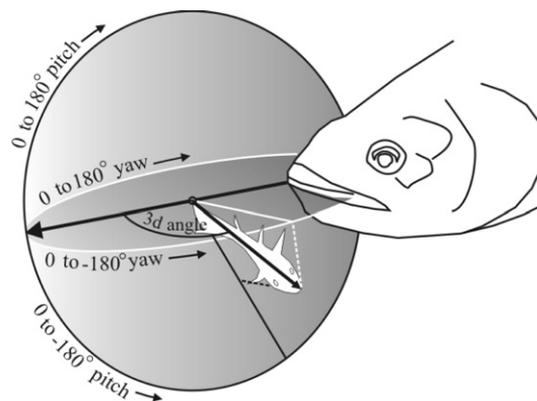
Fig. 2. Variables used to quantify prey orientation. The centreline (large arrow extending from the mouth) is parallel to a line through the midsagittal plane that runs through the middle between the caudal tips of the opercula, the middle between the eyes and the upper jaw tip, and includes the tail tip of the prey fish. The pitching plane corresponds to the midsagittal plane of the predator and runs through the centreline. The yawing plane is the frontal plane of the predator and runs through the centreline. Pitch and yaw angle of the prey are the projection angles of the prey midline onto the respective planes. The 3D angle is defined as the angle between the centreline and the prey midline.

Table 1
Kinematical variables (mean ± SEM) for *Aspius aspius* capturing prey that did or did not show an escape attempt.

Variable	Individual A		P t-test	P ANCOVA	Individual B		P t-test	P ANCOVA
	Escape attempt (N = 5)	No escape attempt (N = 10)			Escape attempt (N = 3)	No escape attempt (N = 6)		
Maximal mouth opening (mm)	35.7 ± 1.2	33.6 ± 0.4	**0.031**	0.26	31.3 ± 0.7	25 ± 4	**0.003**[a]	**0.030**
Mouth opening duration (s)	0.054 ± 0.008	0.041 ± 0.003	**0.048**	0.47	0.111 ± 0.017	0.12 ± 0.04	1	1
Peak instantaneous mouth opening velocity (m s^{-1})	0.73 ± 0.12	0.86 ± 0.07	1	0.90	0.30 ± 0.04	0.30 ± 0.07	1	0.090
Duration of mouth opened >95% of maximum (s)	0.052 ± 0.010	0.025 ± 0.02	**0.028**[a]	**0.018**	0.079 ± 0.019	0.029 ± 0.005	**0.006**	0.080
Maximum hyoid depression (mm)	39.9 ± 0.6	42.4 ± 1.0	1	1	32.9 ± 0.7	29.3 ± 0.6	**0.006**	**0.047**
Hyoid depression duration (s)	0.050 ± 0.010	0.054 ± 0.006	1	1	0.115 ± 0.017	0.11 ± 0.03	0.46	1
Peak instantaneous hyoid depression velocity (m s^{-1})	0.93 ± 0.17	0.87 ± 0.08	0.36		0.30 ± 0.05	0.37 ± 0.08	1	0.14
Neurocranium rotation (°)	8.7 ± 0.5	14 ± 2	1[a]	1	7.2 ± 0.6	8 ± 4	1[a]	0.15
Operculum abduction (mm)	5 ± 2	6 ± 2	1	1	5 ± 5	4.1 ± 0.7	0.083[a]	1
Operculum rotation (°)	8.1 ± 0.5	9.1 ± 1.4	1[a]	1	7.9 ± 1.9	5.7 ± 0.6	0.39	0.17
Predator–prey distance at start of mouth opening (mm)	67 ± 7	51 ± 6	0.16	NA	66 ± 3	41 ± 3	**0.0004**	NA

Bold values indicate *P* < 0.05.

[a] *t*-test for unequal variances.

2.4. Statistics

To test whether the *A. aspius* individuals showed differences in prey capture kinematics between strikes with and without prey escape attempt, Student's *t*-tests were performed on the data from each individual. We chose individual-based statistics as the number of individuals was (for practical reasons) limited, which would result in low statistical power after accounting for inter-individual variation. Additionally, to account for variation in predator-to-prey distance at the start of mouth opening and its effect on prey capture kinematics, an analysis of covariance (ANCOVA; prey distance as a covariate) was performed to test whether differences in prey capture kinematics between strikes with and without prey escape attempt could also be observed independently of potential differences in initial prey position in the two classes of prey behaviour.

In all cases, the Kolmogorov–Smirnov test was applied to test for a normal distribution. In case of a significant deviation from normality, a natural logarithmic transformation was applied. In case of non-homogeneity of variances, a *t*-test for unequal variances was performed. Since it was explicitly hypothesised that head expansion magnitude, velocity and duration should be higher when there is an escape attempt of the prey, *t*-tests on these kinematical variables were one-tailed. On the other hand, differences in prey orientation were tested based on the two-tailed *t*-distribution. All statistics were performed using Statistica 5.0 (StatSoft Inc., Tulsa, OK, USA).

3. Results

3.1. Prey capture kinematics

Prey capture kinematics of *A. aspius* followed the typical pattern of teleost fishes described by Lauder (1985) (Figs. 3 and 4). After the prey fish was released into the aquarium, it was quickly approached (swimming speeds approximately 0.5 m s^{-1}). Mouth opening started (*t* = 0 ms) together with, or was shortly followed by, neurocranial rotation (*t* = 3 ± 13 ms) and hyoid depression (*t* = 11 ± 17 ms; mean ± standard deviation). Rotation of the opercula in the sagittal plane (7.9 ± 3.3°) coincided with mouth opening. A rostrocaudal wave of expansion was observed in the timing of the peak magnitudes of mouth opening (*t* = 74 ± 6 ms), depres-

sion of the hyoid (*t* = 86 ± 6 ms) and abduction of the opercula (*t* = 160 ± 102 ms).

3.2. Kinematical modulation

As predicted, both individuals showed a significantly increased mouth opening in case a prey escape attempt was observed (+6%, *P* = 0.031, and +28%, *P* = 0.003 for individuals A and B, respectively) (Table 1). The duration of the maximal mouth-opening plateau (>95% of maximum) more than doubled for prey captures in which prey tried to escape, compared to feeding trials without a discernible prey escape attempt (+106%, *P* = 0.028, and +140%, *P* = 0.006 for individuals A and B, respectively). No significant increases were found in mouth opening velocity, duration and velocity of hyoid depression, neurocranial elevation magnitude, opercular abduction and sagittal plane opercular rotation (Table 1 and Fig. 3).

Additionally, both individuals showed a different response to prey escape behaviour in two of the measured kinematical variables. In individual A only, mouth opening duration (from start to maximum) was significantly longer for prey captures in which prey attempted to escape (+32%, *P* = 0.048). In individual B only, hyoid depression magnitude was significantly higher when feeding on prey that tried to escape (+12%, *P* = 0.006).

Since the distance of the prey from the mouth of the asp at the start of mouth opening was larger during strikes where the prey was able to perform an escape attempt (see Table 1 and Section 3.3), some of the above-mentioned kinematical differences could be a response of the predator to differences in prey distance. After accounting for variation in prey distance, significant kinematical differences were still observed in each of the two individuals (ANCOVA, Table 1): longer duration of the maximal mouth opening plateau for individual A (*P* = 0.018), greater maximal mouth opening and maximum hyoid depression for individual B (*P* = 0.03 and 0.047, respectively).

3.3. Prey orientation and prey escape potential

Comparing the position of the centre of the prey (middle between head tip and tail tip) with respect to *A. aspius* for feeding trials with and without prey escape attempts indicated prey showed an escape response when they were further away from the
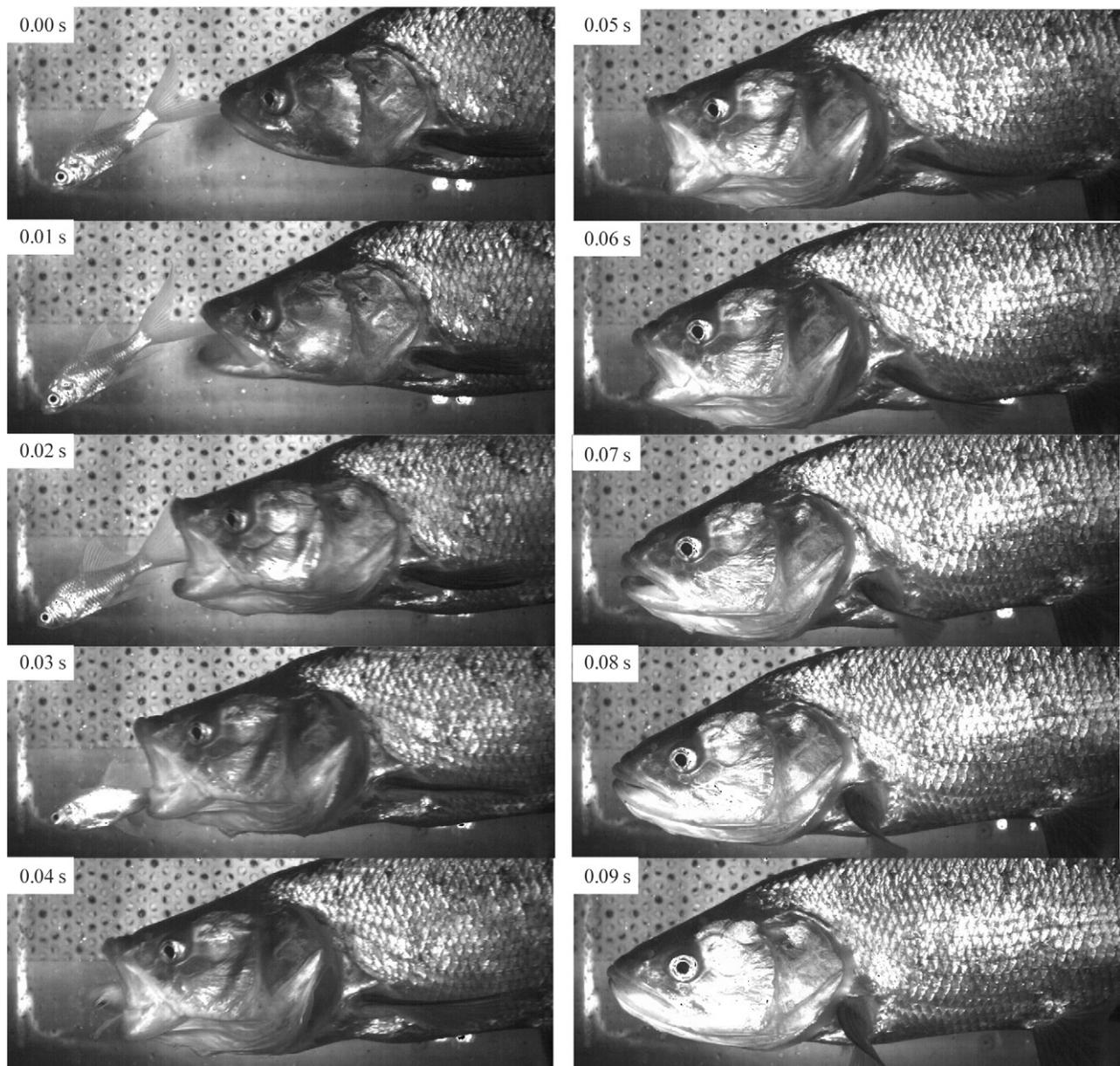
Fig. 3. Selected high-speed video frames for an *A. aspius* individual (cranial length 86.3 mm) capturing a goldfish starting an unsuccessful escape attempt after approximately 0.02 s.

predator at the start of mouth opening: at a distance of 40 ± 4 mm (mean $\pm$ SEM) for prey captures with escape attempt vs. 29 ± 3 mm without prey escape attempt ($P = 0.041$). The estimated pitch angles ($39 \pm 16°$ versus $111 \pm 15°$; $P = 0.006$), yaw angles ($39 \pm 14°$ versus $97 \pm 16°$; $P = 0.028$), and 3D angles ($48 \pm 12°$ versus $101 \pm 11°$; $P = 0.007$) of the prey with respect to the predator (see Fig. 2 for definitions) at the start of mouth opening were significantly lower for strikes eliciting prey escape attempts (Fig. 5).

4. Discussion

In contrast to *Oxycheilinus digrammus*, a species with a relatively diverse diet (Ferry-Graham et al., 2001), our results showed that the specialist piscivore *A. aspius* is capable of modulating prey capture kinematics in function of the escape behaviour of a live goldfish prey (Table 1). Mouth opening was prolonged, and increased in magnitude when prey initiated swimming activity away from the mouth of the predator. One individual also showed an increased

magnitude of hyoid depression when feeding on prey starting an escape response. These results show that prey capture kinematics can differ significantly with an "evasive" type of prey, depending on the specific behaviour of the prey at the instant of attack.

The observed prolonged mouth opening in *A. aspius* when feeding on prey trying to escape shows strong similarity with the observations on the perch *Perca fluviatilis* (Osse, 1969), the pikeperch *Stizostedion lucioperca* (Elshoud-Oldenhave, 1979) and the cichlid *Astatotilapia elegans* (Aerts, 1990). These studies found that for clearly miscalculated attacks, after a normal initial expansion of the buccal cavity, a prolongation of the abducted state of the head occurred. This led to the hypothesis that the expansive phase is subjected to an inhibiting neural feedback control, which is triggered by the entering prey (Aerts, 1990). However, since no further evidence has been found for this hypothesis ever since, the classical idea, that rapid suction strikes are pre-programmed stereotyped events that proceed to completion once initiated regardless of sensory input, still holds (Nauwelaerts et al., 2009).
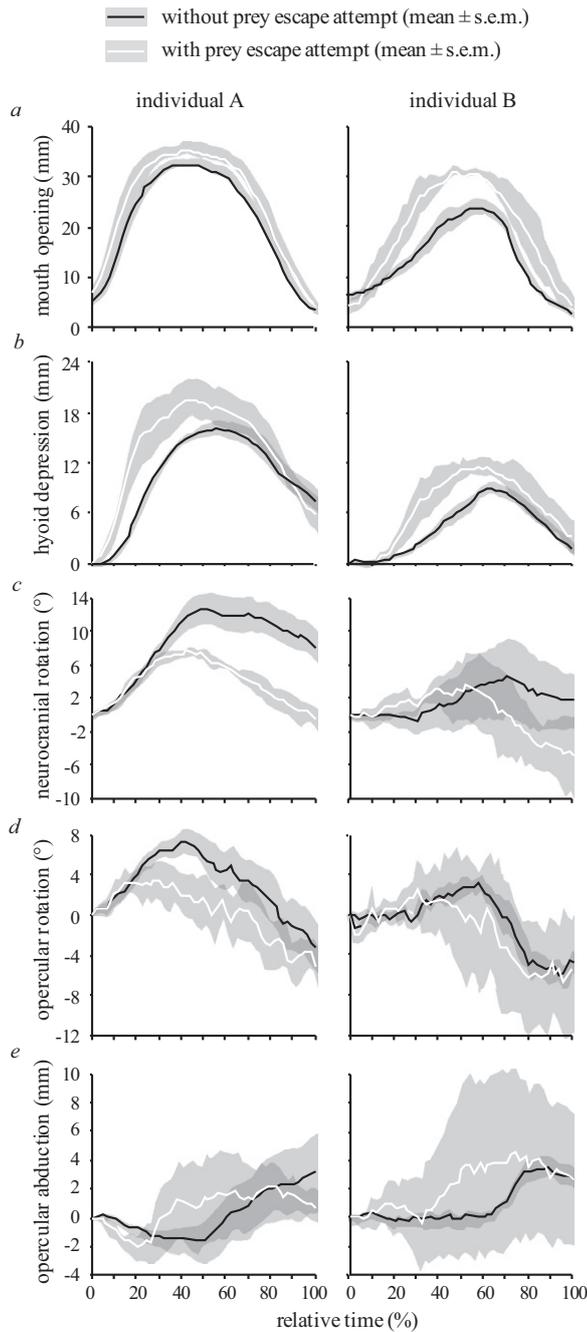
Fig. 4. Mean kinematical profiles during feeding trials with and without a prey escape attempt (see legend above graphs). 0% relative time (*x*-axis) corresponds to the start of mouth opening, and 100% corresponds to the instant when the mouth is fully closed again. Note the relatively longer duration of near-maximum mouth opening (a), and larger hyoid depression (b) when capturing prey that tried to escape. Note also that a relatively large trial-to-trial variation was observed in the kinematics of neurocranial rotation (c), opercular rotation (d), and opercular abduction (e).

Fig. 5. Three-dimensional arrow representation of the midline of the prey (pointing rostrally) with respect to the predator in lateral view (top) and ventral view (bottom) at the start of mouth opening. Prey that showed an escape attempt are indicated by ∗ at their midline vector tip (and represented as white arrows), others are indicated by ○ (and represented as grey arrows).

fact that this condition is fulfilled does not prove that the pre-programmed motor pattern theory applies here. Consequently, it is still possible that *A. aspius* only relies on sensory information *during* feeding to nearly instantaneously adjust its prey capture kinematics accordingly.

One of the assumptions of the peripheral neural feedback hypothesis for nearly instantaneous prey capture modulation (Aerts, 1990) is that the predator must be capable of sensing the prey entering the mouth. For *A. aspius* feeding on the relatively large goldfish, the most likely type of sensory information are tactile stimuli by the prey on the lips or mouth of the suction feeder: physical contact between the fins or body of the goldfish and the borders of the mouth of the asp could be observed in about 60% of the recorded prey capture events ($N = 35$, including videos not suitable for detailed kinematical analysis). For each of these events, we determined the time when the prey had fully entered the mouth, as well as the time when mouth closing started. The results showed a strong correlation between the two ($R^2 = 0.95$), suggesting an overall accurate timing of mouth closing (Fig. 6a). However, when we separated the events with and without prey contact with the mouth, a significantly earlier mouth closing was observed relative to the time of the prey entering the mouth (Fig. 6b; $P = 0.0022$) in cases where prey contact with the mouth occurred. This indeed suggests the presence of modulation based on neural feedback control during prey capture in *A. aspius*.

This relatively early mouth closing when the prey touches the mouth valves or lips of the predator (Fig. 6b) may also explain the difference in mouth opening and closing kinematics between feeding events with and without a prey escape attempt (Table 1 and Fig. 4). It has already been discussed above how prey orientation differed between feeding trials with and without prey escape attempt: prey oriented with a large 3D-angle between their midline and the midsagittal axis of the asp had little chance of displaying an escape attempt (Fig. 5). Probably as a result of this

Do the presented data of *A. aspius* support the presence of pre-programmed motor patterns for both situations (i.e. prey showing an escape attempt or not)? To choose the appropriate motor pattern, the predator must be able to distinguish both situations *before* initiating suction. Since the orientation of the prey with respect to the predator just before mouth opening appears to be related to the probability of observing an escape attempt (Fig. 5), it indeed seems possible that *A. aspius* can "predict" the escape behaviour of the prey by evaluating the prey's orientation. However, the

Fig. 6. Relationship between timing of mouth closing and time at which the prey passes the mouth aperture (a), and the difference between these two variables depending on whether or not the prey makes contact with the lips or mouth of the predator, or whether or not there is a prey escape attempt (b). In (a), strikes with observed mouth–prey contact are discerned by triangles, while strikes without mouth–prey contact are represented by circles. Strikes with and without prey escape attempt can be discerned by the filled and open symbols, respectively. The points below the line with slope = 1 in (a) indicate that the mouth starts to close before the prey has fully entered the mouth. A significantly earlier mouth closing is observed in case the prey contacted the predator's mouth (panel b, left column; $P = 0.0022$), but no significant difference was noted in mouth closing timing relative to prey entering time between trials with and without a prey escape attempt (panel b, the two columns to the right; $P = 0.81$).

difference in orientation, prey showing an escape attempt seldom touched the sides of the mouth (26%, $N = 19$), while prey contact was more frequently observed when there was no escape attempt (57%, $N = 14$). Consequently, since contact between the prey and the mouth of the predator occurs less frequently in case of an escape attempt, it is not impossible that neural feedback based on tactile stimuli is responsible for the observed prolonged mouth opening when feeding on prey trying to escape. Since maximal hyoid depression is typically reached after the start of mouth closing, the same inhibiting neural feedback control could also explain the increased hyoid depression magnitude observed in one of the two individuals when feeding on prey trying to escape (Table 1).

The efficiency of reflexive neural feedback modulation during a very short event such as suction feeding in fish (e.g., less than 0.1 s from the start of mouth opening to full recovery in the asp; Fig. 3) has been questioned because of the reaction latency when responding kinematically to an external stimulus (Nauwelaerts et al., 2009). By approximation, the time between the goldfish prey touching the mouth of *A. aspius* and the start of mouth closing was 18 ± 6 ms (mean $\pm$ SD; $N = 13$). This falls within the range of latencies measured for escape responses of fish, which

vary from 5 to 40 ms among different species (Eaton and Hackett, 1984). A relatively large fish like the grey mullet *Mugil cephalus*, for example, showed escape response latencies (18.1 ± 13.7 ms; Turesson and Domenici, 2007) that are similar to the reaction times estimated for our asps. In addition, mechanical stimuli generally result in shorter escape latencies than visual stimuli (Eaton and Hackett, 1984), which makes tactile information about the prey's position ideal for quickly modulating prey capture kinematics by neural feedback control. For the jaw-adductor muscles in humans, peripherally induced additional muscle activity has also been observed to follow about 20 ms after the onset of an external force exerted on the jaw during mouth closing (Ottenhoff et al., 1993). Consequently, it seems feasible that tactile contact with the prey triggers mouth closing in asp feeding on elusive prey.

Although the role of control has been traditionally ascribed to the nervous system, the dynamics of the mechanical system itself can sometimes lead to an efficient control system (Full and Koditschek, 1999). Steadily running cockroaches, for example, immediately self-correct after lateral force perturbation due to the altered leg moment arms (Kubow and Full, 1999). This 'mechanical feedback' resulting in a zero-delay response can also result from muscle's intrinsic force–length and force–velocity properties (so-called 'preflex'; Loeb et al., 1999). In the present case of prey capture in *A. aspius*, it might be possible that the force of the prey impacting the asp's lower jaw causes additional lower jaw depression. In turn, the jaw-closing muscles (which are probably active at the final instants of the mouth-opening phase) would generate higher passive, elastic forces because of their increased length, as well as higher active forces due to a more pronounced excentric contraction regime. Theoretically, this could explain our observation of earlier jaw closing in case of the prey impacting the lower jaw. However, contact between the goldfish prey and the lower jaw was mostly with the goldfish's fins, which probably resulted in negligibly lower jaw depression forces: there were no signs in our kinematical data of mouth-opening acceleration at the instant of prey contact. Additionally, a preflex response would follow the mechanical perturbation immediately, while we observed an average latency of 18.1 ms between prey contact and the onset of mouth closing. Consequently, a mechanical, preflexive control is improbable here.

Our study could not strictly rule out one of the two hypotheses explaining this modulation from a neuromotorical point of view (i.e. *a priori* choosing one of the pre-programmed motor patterns and/or neural feedback control). However, in case the proposed inhibiting neural feedback control mechanism (Aerts, 1990) is used by the asp as suggested by our data (Fig. 6), the necessity to *a priori* choose the appropriate motor pattern from the animal's repertoire (e.g., asp predicting the goldfish escape potential based on prey orientation) becomes superfluous: mouth closing will automatically be postponed since the escape attempt of the prey inevitably results in later contact with tactile receptors of the mouth or internal buccal surface, so there is no need to anticipate potential prey escape attempts. Therefore, the presented data on the timing of mouth closing in asp (Fig. 6) indicate that neural feedback control is more likely to explain the observed modulation than the classical theory of suction strikes being pre-programmed neuromotoric events.

Acknowledgements

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