

RESEARCH ARTICLE

Behavioural responses to infrasonic particle acceleration in cuttlefish

Maria Wilson^{1,2,*}, Jens Ådne Rekkedal Haga² and Hans Erik Karlsen²

ABSTRACT

Attacks by aquatic predators generate frontal water disturbances characterised by low-frequency gradients in pressure and particle motion. Low-frequency hearing is highly developed in cephalopods. Thus, we examined behavioural responses in juvenile cuttlefish to infrasonic accelerations mimicking main aspects of the hydrodynamic signals created by predators. In the experimental set-up, animals and their surrounding water moved as a unit to minimise lateral line activation and to allow examination of the contribution by the inner ear. Behavioural responses were tested in light versus darkness and after food deprivation following a 'simulated' hunting opportunity. At low acceleration levels, colour change threshold at 3, 5 and 9 Hz was 0.028, 0.038 and 0.035 m s⁻², respectively. At higher stimulus levels, jet-propulsed escape responses thresholds in daylight were 0.043, 0.065 and 0.069 m s⁻² at 3, 5 and 9 Hz, respectively, and not significantly different from the corresponding darkness thresholds of 0.043, 0.071 and 0.064 m s⁻². In a simulated hunting mode, escape thresholds were significantly higher at 3 Hz (0.118 m s⁻²) but not at 9 Hz (0.134 m s⁻²). Escape responses were directional, and overall followed the direction of the initial particle acceleration, with mean escape angles from 313 to 33 deg for all three experiments. Thus, in the wild, particle acceleration might cause escape responses directed away from striking predators but towards suction-feeding predators. We suggest that cuttlefish jet-propulsed escape behaviour has evolved to be elicited by the early hydrodynamic disturbances generated during predator encounters, and that the inner ear plays an essential role in the acoustic escape responses.

KEY WORDS: *Sepia officinalis*, Cuttlefish, Hearing, Infrasound, Predator–prey interaction, Striking predator, Suction feeding

INTRODUCTION

The large and highly developed eyes of cephalopods, as well as their ability to undergo rapid camouflage colour changes, are important for surviving encounters with predators (Hanlon and Messenger, 1988; Langridge, 2009; Langridge et al., 2007). In darkness or murky water, however, the use of vision is limited and other sensory modalities such as hearing and lateral line sensing become more important (Stewart et al., 2013). Attacks by several important cuttlefish (*Sepia officinalis*) predators, such as fish [e.g. seabass (*Dicentrarchus* sp.)] and sea mammals [e.g. bottlenose dolphin (*Tursiops* sp.)] (Hanlon and Messenger, 1988; Kier and Leeuwen,

1997), typically generate close-range hydrodynamic flow fields dominated by low-frequency pressure and particle acceleration gradients, with most energy in the infrasonic frequency range (<20 Hz) (Bleckmann et al., 1991; Enger et al., 1989; Stewart et al., 2014; Wainwright et al., 2007; Werth, 2006).

The attack phase of a bass or a dolphin can be divided into two phases, namely the initial approach phase and a later suction-feeding phase (Wainwright et al., 2007; Werth, 2006). The initial approach by a predator generates a frontal bow wave characterised by particle acceleration directed away from the predator and an associated pressure increase (Stewart et al., 2014). When the predator is close to the prey, an engulfment attempt is performed by suction feeding, where the prey is drawn into the mouth by a rapid expansion of the volume of the oral cavity of the predator. This produces a frontal flow field, consisting of an initial particle acceleration towards the predator, and an associated pressure decrease (Wainwright et al., 2007; Werth, 2006). Abrupt changes in pressure gradients and accelerations may be used by prey to detect the attacking predator. In this context, a successful escape and avoidance will rely on the precise timing of whether and when the prey should respond to the hydrodynamic signal generated during either the early approach phase or the later hydrodynamic signal generated during suction feeding. This decision process may vary between species and will be influenced by a number of factors, including predator species/type and predator density, as well as internal condition within an individual such as the speed of sensory processing and escape responses (Lima and Dill, 1990; Ydenberg and Dill, 1986). An empirical model by Holzman and Wainwright (2009) suggests that approaching predatory bluegills (*Lepomis macrochirus*) are detected primarily based on their suction-induced disturbance rather than the bow wave-induced disturbance by different copepod species. Conversely, zebrafish (*Danio rerio*) larvae exhibit an escape response following the detection of the early bow wave of the approaching predator (Stewart et al., 2013).

Cephalopods detect low-frequency sound with their best sensitivity below ~20 Hz (Mooney et al., 2010; Packard et al., 1990; Williamson, 1988; Williamson and Budelmann, 1985), using the accelerometer-like statocyst organs of their inner ear (Kaifu et al., 2007; Mooney et al., 2010; Packard et al., 1990; Samson et al., 2014; Williamson, 1988; Williamson and Budelmann, 1985). The hair cells of statocysts are polarised and direction sensitive, supporting the notion of directional hearing in cephalopods (Budelmann, 1979; Budelmann and Williamson, 1994). In addition, cephalopods have epidermal lines on their head and arms containing hair cells that detect local water movements relative to the skin of the animal (Budelmann and Bleckmann, 1988). Field observations of cuttlefish exhibiting anti-predator displays, in the absence of visual stimuli, suggest that acoustic signals may play an important role in predator detection (Hanlon and Budelmann, 1987). Furthermore, the frequencies of optimal sensitivity of the inner ear, statocyst organs coincide with the frequency range of

¹Department of Biology, University of Southern Denmark, 5230 Odense M, Denmark. ²Department of Biosciences, Faculty of Mathematics and Natural Sciences, University of Oslo, 0315 Oslo, Norway.

*Author for correspondence (maria.wilson@biology.sdu.dk)

 M.W., 0000-0003-0187-0713

the main acoustic energy generated during predator attacks. How cuttlefish respond to isolated hydrodynamic signals, specifically particle acceleration versus pressure phase generated during predator attacks, has to our knowledge not been studied in detail. In addition, it is unknown whether predator-induced whole-body acceleration, and thereby inner ear activation, is sufficient to support directional and adaptive jet-escape behaviours.

Studies addressing behavioural responses of common cuttlefish to the isolated visual appearance of real predators have been conducted both in the field (Hanlon and Messenger, 1988) and in the laboratory (Langridge, 2009; Langridge et al., 2007; Staudinger et al., 2013). The anti-predator responses of cuttlefish (and many other cephalopods) can be categorised as either primary or secondary defences (Hanlon and Messenger, 1988, 1996). The primary defence consists of cryptic behaviour involving rapid colour changes serving to camouflage the animal against its background, thereby reducing the probability of detection by predators. If these cryptic behavioural responses fail, then secondary defences are employed in the form of either a stay or flee response. The stay behaviour includes acute body pattern changes to disrupt the attack phase, whereas the flee behaviour consists of jet-propulsed escapes, which may be accompanied by the release of ink (Hanlon and Messenger, 1988, 1996).

In the present study, we tested the behavioural responses in cuttlefish exposed to infrasonic signals mimicking key aspects of the hydrodynamic signatures generated by predators in the initial approach phase and in the final prey-capture phase (suction

feeding). In the experimental set-up, the cuttlefish and surrounding water moved as a unit, thus allowing us to examine the contribution made by the inner ear to avoidance responses.

MATERIALS AND METHODS

Animals

Nine juvenile common cuttlefish (*Sepia officinalis* Linnaeus 1758) aged between 10 and 12 weeks and with a mean mantle length of 4.3 ± 0.5 cm were used in the experiment. Cuttlefish were obtained from the Øresund Aquarium, University of Copenhagen, Denmark, and transported to the Drøbak Marine Biological Station, University of Oslo, Norway, where they were kept in 70-litre glass aquaria supplied with natural seawater (33–35‰) at 18–20°C. The photoperiod was maintained at 12 h:12 h, and cuttlefish were fed a mix of opossum shrimps (*Praunus flexuosus*) and other prawns (*Crangon crangon*, *Palaemon adspersus*, *Palaemon elegans*) twice daily. Following a one month acclimation period, experiments were conducted from July to September 2013.

Experimental set-up

The experimental set-up followed that described in previous studies (Heuch and Karlsen, 1997; Karlsen, 1992; Karlsen et al., 2004). In brief, the set-up consisted of a thick-walled (3 cm) Perspex chamber (inner dimensions of 55×27×14 cm) suspended by four steel wires attached to a solid steel frame (Fig. 1). The frame was mounted on a 150 kg concrete block resting on a 12 cm-thick base of dry sand to dampen noise from the surroundings. The test chamber was sealed

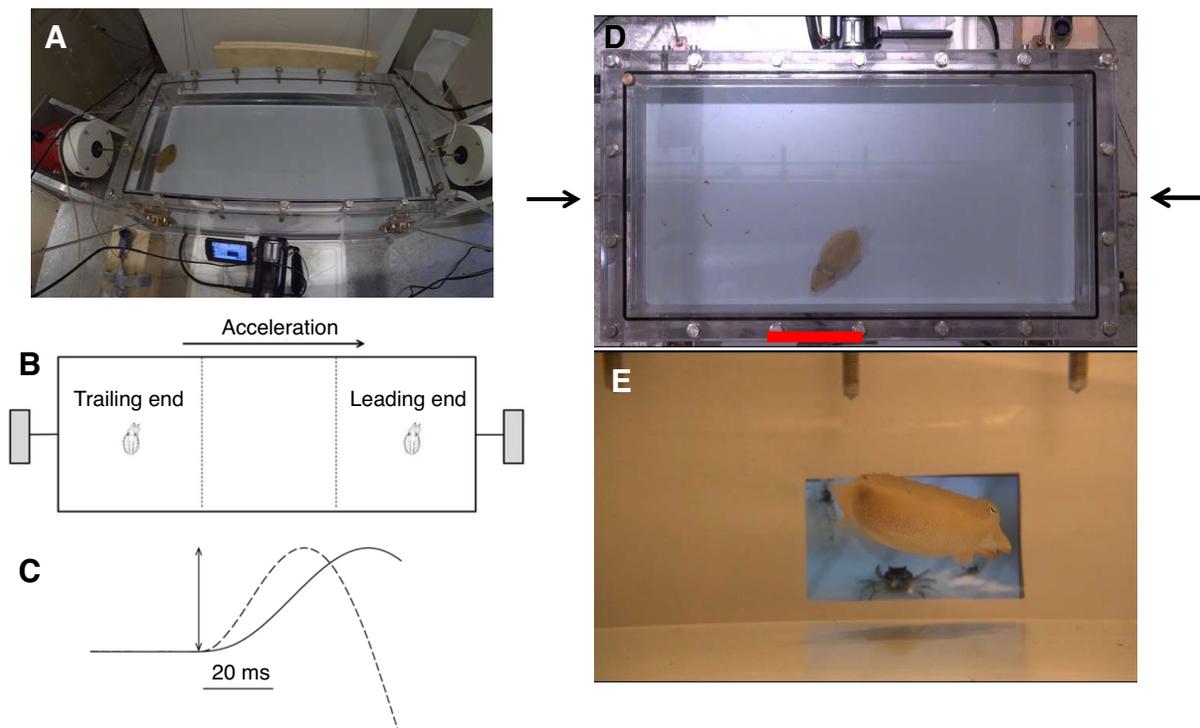


Fig. 1. The experimental set-up and waveform of infrasonic stimulus. (A) The experimental chamber (inside dimensions 55×27×14 cm) suspended by four metal wires and with one shaker attached to each end wall by metal rods. Test animals were unconstrained and exposed to the infrasound stimulus when inside the trailing or leading end as illustrated in (B). (C) Measured initial acceleration (solid line) of the test chamber and initial pressure (broken line) at the trailing end wall for the 5 Hz stimulus. In the leading end, the pressure stimulus waveform was inverted. The first 55 ms of the stimulus waveforms are shown. All colour and fast jet responses occurred within this time frame. The arrow indicates the peak-to-peak amplitude of acceleration signal and the 0–peak initial amplitude of the pressure signal. Stimulus waveforms created at 3 and 9 Hz were essentially similar in shape. (D) Top view of the test chamber. The red bar indicates the position of the screen with a video sequence of moving prey items. Arrows indicate acceleration from either the left or right (E) side view of the test chamber with a cuttlefish paying attention to the moving prey (experiment III).

with a transparent Perspex lid and locking screws, and filled in such a way that no air bubbles formed within the chamber. A small flow of seawater circulated within the chamber during the experiments.

The water-filled test chamber and experimental animals were accelerated by driving voltage waveforms delivered to two electromechanical vibrators (V20, Data Physics Corp., San Jose, CA, USA) firmly secured to the concrete base of the set-up and attached to each end wall of the test chamber via steel rods. The waveform to one of the vibrators was inverted, allowing the vibrators to work in a push and pull mode. Voltage waveforms were generated by Spike software version 7.2 (Cambridge Electronic Design Limited, Cambridge, UK) and a 500 kHz and 16 bit D/A–A/D converter (Micro 1401 mkII, Cambridge Electronic Design Limited, Cambridge, UK). Before reaching the vibrators, the driving voltage waveform passed an attenuator (LAT-45, Leader Electronics Corp., Yokohama, Japan) for stimulus-level adjustments and finally a custom-built DC-power amplifier (40 W) set to fixed gain. To avoid any disturbance of the animals during the experiments, the test chamber was located in a separate, dedicated room, remotely operated from a control room. The animals were continuously monitored by live view on a computer screen.

Stimulus waveforms

The driving voltage waveform used in the experiment was a single cycle of a ramp-shifted sinusoid waveform (described in Karlsen, 1992) of 5, 10 and 20 Hz. This type of driving waveform was employed to generate a transient-free initial acceleration of the test

chamber (Fig. 1C). The set-up behaved as a forced pendulum oscillator with a resonant frequency of ~ 3.8 Hz. Therefore, the initial rise in the chamber acceleration was reduced compared with the driving voltage waveform, and frequency analysis showed that the main energy content was at 3 Hz in the period from stimulus onset until the initiation of escape behaviour when the driving waveform was 5 Hz. Driving waveforms of 10 and 20 Hz caused initial accelerations of the test chamber with peak energy levels at 5 and 9 Hz, respectively. Particle acceleration levels reported here refer to amplitude rms (root mean square) values.

At the onset of acceleration of the test chamber, a linear pressure gradient was created with increased pressure (compression) in the lagging end and a corresponding pressure decrease (rarefaction) in the leading half of the chamber (Fig. 1). Thus, the hydrodynamic signature of an approaching predator was mimicked in the lagging end of the chamber and a suction-feeding predator was mimicked in the leading end of the chamber (Fig. 2A). The pressure component in the centre remained unchanged while maximum and minimum pressures developed at the end walls. A water movement relative to the chamber is necessary to support the pressure changes, with a maximum value in the chamber centre and a zero value at the end walls. Assuming rigid chamber walls and a sinusoidal acceleration of the test chamber, the maximum relative particle acceleration (A_{\max}) in the chamber centre can be calculated by the equation:

$$A_{\max} = \rho a L^2 \omega^2 / 8K, \quad (1)$$

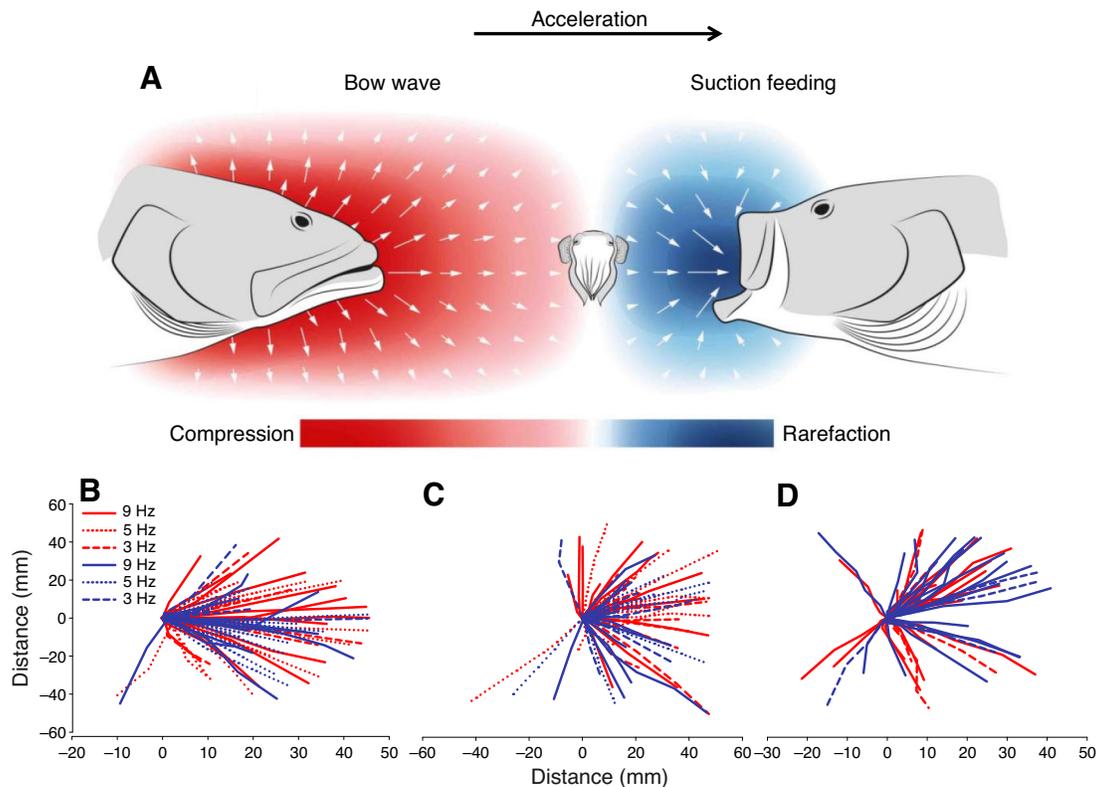


Fig. 2. Cuttlefish jet-propulsed escapes to hydrodynamic predator signatures. (A) Schematic illustration of the two main modes of aquatic predator attacks: the bow wave of a striking predator to the left and a suction-feeding predator to the right. Colour code depicts pressure gradients and a vector grid depicts the scaled fields of particle acceleration created by predators. Illustration: V. Mischitz/M. Wilson/J. Haga/H.E. Karlsen. CC BY 4.0. (B–D) The initial components of all fast startle jet-propulsed escape responses of cuttlefish when exposed to acceleration combined with compression (red tracks) or rarefaction (blue tracks) for experiment I (B, $N_{\text{compression}}=32$, $N_{\text{rarefaction}}=36$) experiment II (C, $N_{\text{compression}}=38$, $N_{\text{rarefaction}}=31$) and experiment III (D, $N_{\text{compression}}=24$, $N_{\text{rarefaction}}=24$). All tracks start with the cuttlefish head positioned in 0,0.

Table 1. Measured acceleration values [root mean square (rms) in m s^{-2}] of the test system and the associated pressure changes (rms in Pa) at the leading (rarefaction) and trailing (compression) ends of the system at 3, 5 and 9 Hz

3 Hz			5 Hz			9 Hz		
Acceleration (m s^{-2})	Pressure (Pa), trailing	Pressure (Pa), leading	Acceleration (m s^{-2})	Pressure (Pa), trailing	Pressure (Pa), leading	Acceleration (m s^{-2})	Pressure (Pa), trailing	Pressure (Pa), leading
0.012	0.360	-0.346	0.012	0.453	-0.611	0.017	1.360	-1.541
0.028	0.712	-0.712	0.025	0.917	-1.172	0.030	3.172	-2.719
0.057	1.438	-1.489	0.051	2.191	-2.547	0.064	5.891	-6.072
0.119	3.981	-3.162	0.096	4.942	-4.738	0.134	12.054	-12.054

where ρ is water density, a is the amplitude of chamber acceleration, L is the length of the test chamber, ω is the angular frequency of the chamber acceleration and K is bulk modulus of water.

At a chamber acceleration of 0.1 m s^{-2} , the maximum relative particle acceleration in the chamber centre was $\sim 5 \times 10^{-6} \text{ m s}^{-2}$. At this stimulus level, the peak pressures at the end walls of the test chamber were $\sim 25 \text{ Pa}$, and the corresponding amplitude of particle acceleration due to the compressibility of water is $\sim 10^{-3} \text{ ms}^{-2}$ at 9 Hz (R. R. Hansen, A. F. Berthelsen and H.E.K., unpublished). Thus, the acceleration experienced by a cuttlefish within the test chamber was determined by the overall chamber acceleration, and was insignificantly affected by the position of the cuttlefish within the test chamber.

The experimental set-up was calibrated by accelerometers (EGCS-A2-2, Measurement Specialties, Hampton, VA, USA; sensitivity 2475 mV g^{-1}) attached to each of the steel rods connecting the electromechanical vibrators to the test chamber, thus measuring the overall chamber acceleration. Pressures developing at different positions within the test chamber were measured with a hydrophone (Sensor SQ03, Sensor Technology Limited, Collingwood, Canada; sensitivity $148 \text{ dB re. } 1 \mu\text{Pa V}^{-1}$). The accelerometers and hydrophone were connected to the D/A–A/D converter and all signals recorded by the Spike software. The chamber was accelerated from left to right and from right to left (Fig. 1) in a random manner and at a final ratio of 0.89. The horizontal background acceleration noise level of the experimental system has been determined earlier to be below 10^{-6} m s^{-2} in the frequency range 0.1–200 Hz when measured in 1/3 octave bands (Karlsen et al., 2004).

Experimental protocol

Cuttlefish were exposed to infrasonic stimuli under three different conditions. Experiment I was conducted in daylight to test for changes in skin pattern and colour and jet-escape trajectories in response to infrasonic stimuli. Experiment II was conducted in darkness with three 850 nm infrared lights sources (model 995JH, Kinapriner) and only jet-escape trajectories were studied. Experiment III was conducted in daylight, where cuttlefish were food deprived for 24 h and shown a short video sequence of live decapod prey items (Fig. 1D,E). The video sequence was shown for 2 min followed by a 2 min pause. Cuttlefish are highly visual

predators (Hanlon and Messenger, 1996) and, as soon as the video with prey items appeared, the test animals positioned themselves in front of the video screen trying to capture the prey on the screen. Infrasonic stimulation was performed during the same time period as the video sequence, when the cuttlefish was paying close attention to the moving prey. There was no sign of habituation to the video sequence. In experiment III, the test animals were thus in a food-deprived hunting mode, which potentially would cause an attention shift and affect the acoustic jet-escape behaviour. Behavioural response thresholds for colour change or jet-propulsed escape response were calculated as the medium acceleration at 3, 5 and 9 Hz.

Animals were tested one at a time in the experimental test chamber and exposed to the experimental conditions for a maximum of 24 h. Each cuttlefish was used only once in each of the three experiments with a minimum of 1 week between testing. The test session in experiments I and II consisted of a random order of exposures to the infrasonic frequencies at 3, 5, and 9 Hz at four different exposure levels (Table 1) in the trailing and leading ends of the test chamber. In experiment III, cuttlefish were exposed to infrasonic frequencies at 3 and 9 Hz at the same four exposure levels as for experiments I and II. Not all experimental animals were exposed to the full set of acoustic stimulations, as summarised in Table 2. The time between tests varied from 15 to 25 min. Behavioural responses were recorded with a Sony HD camera (ExmorR, HDR-CX740VE, Sony Corp., Tokyo, Japan) in 1920×1080 pixel frames at either 25 or 50 fps. The video camera filmed from above through a small hole in a top plate positioned horizontally 1.3 m above the test chamber.

The onset of the driving voltage was synchronised by a LED bulb. The LED light was fully shielded from the test animals inside a non-translucent socket and positioned in the right corner of the camera view. It reached full strength within 1 ms, and thus identified stimulus onset in the video recordings and analysis.

All experiments were conducted in accordance with the Norwegian Animal Welfare Act of 1974, the Regulation of Animal Experimentation of 1996 and approved as field experiments at the Marine Biological Station Drøbak by the University of Oslo, Animal Welfare Unit (ref. 155 UiO – Biological Institute). All of the cuttlefish were handled with the utmost care and

Table 2. Number of cuttlefish used in the three experiments, number of exposures and number of jet responses at a specific frequency in compression and rarefaction mode

Experiment	3 Hz			5 Hz			9 Hz		
	No. of cuttlefish	No. of exposures	No. of jet responses	No. of cuttlefish	No. of exposures	No. of jet responses	No. of cuttlefish	No. of exposures	No. of jet responses
I	7/6	26/22	16/13	8/8	32/32	15/19	7/7	28/28	5/4
II	6/6	22/19	13/12	5/4	17/13	15/11	5/7	16/23	10/8
III	8/8	16/12	19/20	–	–	–	5/5	27/28	5/4

Data represent the number of cuttlefish, exposures and jet responses in compression/rarefaction mode.

performed in the behavioural experiments without any signs of injuries.

Data analysis

Escape responses were unaffected by the experimental test chamber being initially driven from left to right or from right to left. Thus, escape behaviours when the chamber was driven from right to left were turned 180 deg. As a consequence, all jet-escape responses were plotted as if all stimulus accelerations were from left to right, corresponding to a striking predator attacking from the left. The direction of the initial stimulus acceleration was therefore 0/360 deg. Cuttlefish jet response trajectories were determined by single frame video analysis in ImageJ (1.47) using the MTrackJ plugin in ImageJ (Meijering et al., 2012). Tracking was done for the first 160 ms from behaviour onset or occasionally until the cuttlefish touched the side wall of the test chamber. The initial angle of the cuttlefish pre-stimulation was calculated as the angle between the midline of the cuttlefish in the frame before sound exposure and the initial stimulus of 0/360 deg. The escape angle was calculated as the angle between the midline of the cuttlefish at time 160 ms (or the last frame where tracking was possible) and the stimulus direction.

Statistical analyses were performed using Matlab 8.2 (MathWorks Inc., Natick, MA, USA), R (The R project for Statistical Computing) and PAST3 (version 1.0.0.0) (Hammer et al., 2001). We used a non-parametric Hodges–Ajne (H–A) omnibus test (Zar, 1999) to test for a significant directionality of the escape angles as well as to test for a random initial orientation of the cuttlefish before sound exposure, and a non-parametric Wheeler–Watson’s test to test for differences in escape angle distributions between compression and rarefaction at the different test frequencies in the three experiments. Generalised linear mixed models (GLMM) in R were used to correlate the characteristics of colour change probability and jet-escape response probability, with frequency, stimulus phase, acceleration level, light regime and food level. Mixed models were used because data obtained from the same cuttlefish were not independent; thus, cuttlefish identification was treated as a random variable. In addition, a non-parametric Mann–Whitney *U*-test was conducted to test for differences in median acceleration levels, defined as response thresholds ($\alpha=0.05$ for all tests).

RESULTS

Infrasonic sensitivity

All cuttlefish settled almost immediately after swimming from the transfer jar into the test chamber, and in the time following they swam calmly around, exploring their new environment. Testing was initiated after ~2 h of acclimation. In experiment I, conducted in daylight at low acceleration levels of 0.01–0.03 m s⁻², cuttlefish

showed different forms of colour changes. These sometimes involved an intensification of a disruptive skin pattern with transverse and longitudinal light and dark components, while at other times an asymmetrical mantle bar clearly signalled towards the initial stimulus acceleration direction. At higher acceleration stimulus levels in the range 0.05–0.25 m s⁻², cuttlefish displayed blanching and performed rapid jet-propulsed escape responses. At the highest stimulus level, jetting was sometimes also associated with release of ink and, accordingly, acceleration levels above 0.25 m s⁻² were thus generally avoided in order to prevent unnecessary stress on the animals and contamination of the surrounding water.

Median particle acceleration thresholds for colour changes (experiment I) and for jet-propulsed escape responses (experiments I, II and III) at the three different test frequencies are given in Table 3 and Fig. 3. Colour change was most accurately supported by an additive logistic mixed effects model with acceleration level as a single fixed parameter (corrected Akaike information criterion, AICc=200.4) (Fig. 3C). Including frequency and pressure phase (i.e. testing in the compression as opposed to the rarefaction test chamber halves), the model showed that these factors had no significant effects (AICc=117.7) (Table 4).

The jetting response was most accurately described by a mixed effects model with acceleration level and hunting mode as fixed parameter values (AICc=209.9) (Fig. 3D). Predicted acceleration thresholds for jetting behaviour were reduced by 2.5 dB in animals in the food-deprived hunting mode when compared with the control. Adding pressure phase and light level data to the model also showed that these parameters had no significant effect on jetting probability (AICc=213.4) (Table 4).

A Mann–Whitney *U*-test was conducted to compare the median acceleration threshold levels at the three test frequencies (Table 3). There were no significant differences at the three frequencies between experiments I and II (Table 3), whereas in experiment III, the median acceleration threshold at 3 Hz was significantly higher compared with both experiments I and II. At 9 Hz, there was no significant difference, despite the fact that the median acceleration thresholds at 9 Hz in experiment III (0.134 m s⁻²) are almost twice as high as the acceleration thresholds in experiments I (0.069 m s⁻²) and II (0.064 m s⁻²) (Fig. 3B).

Directional response

Body orientations of the cuttlefish immediately before exposure were not significantly different from a uniform (i.e. random) distribution based on an H–A omnibus test (experiment I, $P=0.81$; experiment II, $P=0.82$; experiment III, $P=0.74$). Contrary to this, stimulus-induced jet-propulsed escape responses in the cuttlefish were highly directional, and overall followed the initial acceleration vector irrespective of the pressure phase as well as the light versus

Table 3. Median acceleration thresholds for colour change and jet response at 3, 5 and 9 Hz

	Colour change		Jet-propulsed escape response								
	Experiment I		Experiment I		Experiment II		Experiment III				
	Acceleration threshold (m s ⁻²)	<i>N</i>	Acceleration threshold (m s ⁻²)	<i>N</i>	Acceleration threshold (m s ⁻²)	<i>N</i>	Acceleration threshold (m s ⁻²)	<i>N</i>	I vs II $ Z $; P	I vs III $ Z $; P	II vs III $ Z $; P
3 Hz	0.028 (0.014; 0.039)	7	0.043 (0.039; 0.046)	5	0.043 (0.028; 0.047)	7	0.118 (0.072; 0.119)	3	0.00; 0.86	2.00; 0.044*	1.76; 0.048*
5 Hz	0.038 (0.032; 0.045)	8	0.065 (0.051; 0.072)	8	0.071 (0.045; 0.092)	8	–	–	0.06; 0.95	–	–
9 Hz	0.035 (0.03; 0.047)	7	0.069 (0.064; 0.099)	7	0.064 (0.050; 0.125)	7	0.134 (0.067; 0.169)	8	0.26; 0.79	1.29; 0.20	1.36; 0.17

Values in parentheses are the lower and upper quartiles. Medians from experiments I, II and III at the different frequencies were compared using a Mann–Whitney *U*-test (final three columns). *Significant difference based on a $P<0.05$. *N*=sample size. I, experiment I; II, experiment II; III, experiment III.

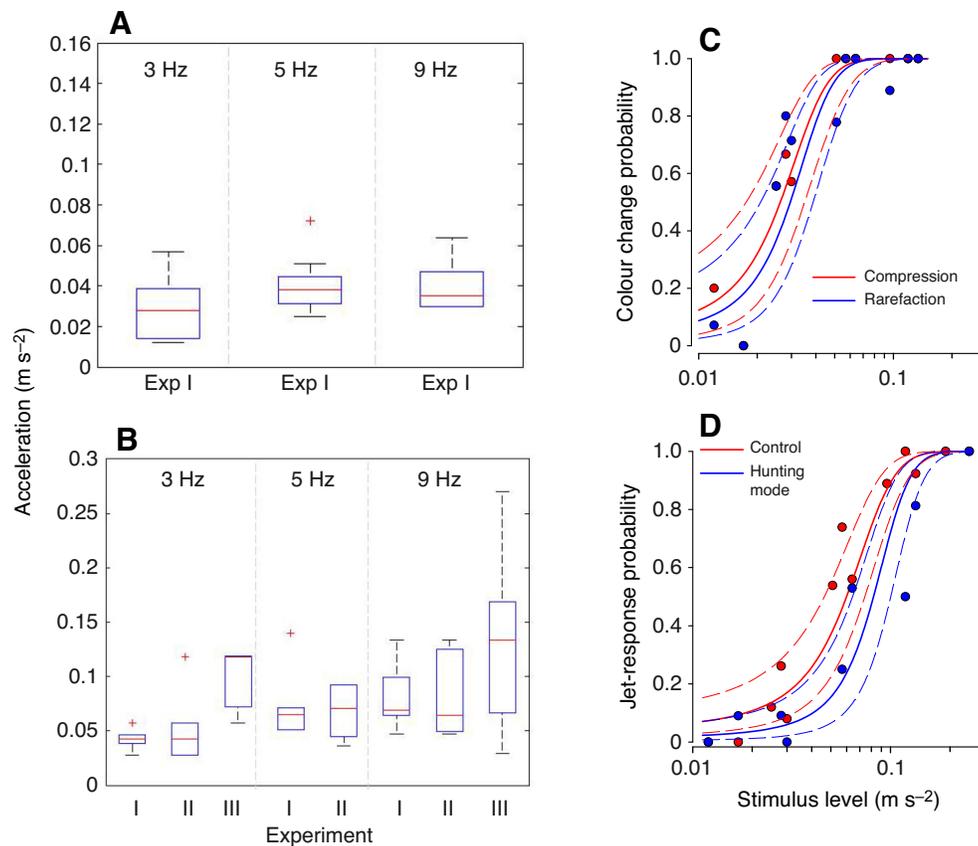


Fig. 3. Median behavioural acceleration threshold. (A,B) Median acceleration thresholds for colour change (A) and jet response (B). The middle line in the box represents the median, the lower box bounds the first quartile, the upper box bounds the third quartile, whiskers are 1.5× the interquartile range and crosses are outliers. Acceleration thresholds were most accurately supported by additive logistic mixed effects with a significant effect of the stimulus acceleration level on both colour change and jet responses and no effect of pressure phase. (C,D) Predicted probability and 95% confidence intervals for colour change (C) and jet-escape response (D) as a function of acceleration level, based on most supported logistic mixed effects models. A summary of GLMM is provided in Table 3.

darkness and food-deprived hunting mode test conditions (Figs 2 and 4). The mean escape angle for the three different treatments and different frequencies are given in Table 5. There was significant directedness at all frequencies in the three experiments except at 3 Hz for both compression and rarefaction in experiments I and III, and rarefaction in experiment II, which could be explained by the low sample size (Table 2). There was no significant difference in distribution between compression and rarefaction at the different test frequencies in experiment I (Mardia–Wheeler–Watson: 3 Hz: $w=0.8$, $P=0.67$; 5 Hz: $w=0.56$, $P=0.76$; and 9 Hz: $w=0.54$, $P=0.76$), in experiment II (Wheeler–Watson: 3 Hz: $w=0.66$, $P=0.72$; 5 Hz: $w=1.15$, $P=0.56$; and 9 Hz: $w=3$, $P=0.22$), nor in experiment III (Wheeler–Watson: 3 Hz: $w=0.38$, $P=0.83$; and 9 Hz: $w=0.3$, $P=0.86$). Because there was no effect of pressure phase on escape angle, escape angles during compression and rarefaction were combined in Fig. 4. The overall mean escape angle for all escape

trajectories in experiment I was 351 deg (334 deg, 11 deg), 359 deg (337 deg, 22 deg) in experiment II and 30 deg (360 deg, 71 deg) in experiment III.

DISCUSSION

The suspended experimental test chamber allowed us to expose cuttlefish to an initial transient-free and directional infrasonic particle acceleration associated with either a pressure increase or decrease (Figs 1 and 2A). Following stimulus onset, a significant linear pressure gradient developed inside the test chamber. However, as the cuttlefish was free to move with the surrounding water, and as the frontal part of the cuttlefish (containing the inner ear and the superficial lateral line analogue) is soft tissue and not a rigid body, we are confident that the pressure gradient was not relative to the skin surface. The possibility for activation of superficial mechanoreceptors was thus

Table 4. Fixed-effects parameter estimates for generalised linear mixed models (GLMM) fitted to predict cuttlefish colour change probability in the leading and the lagging half of test chamber for experiment I (AICc=117.7) and cuttlefish jet-propulsed escape response probability for all experiments (AICc=213.4)

Parameter	Threshold	Estimate	s.e.	Z-value	P-value
(Intercept)	Colour change	-2.08	0.93	-2.24	0.0251
Acceleration level		127.86	24.68	5.18	$2.21 \times 10^{-7***}$
Frequency		-0.21	0.11	-1.82	0.0686
Pressure phase		-0.59	0.52	-1.15	0.2519
(Intercept)	Escape response	2.65	0.60	-4.46	$8.07 \times 10^{-16***}$
Acceleration level		53.77	5.86	9.18	$<2 \times 10^{-16***}$
Frequency		-0.09	0.06	-1.45	0.16
Pressure phase		-0.13	0.30	-0.43	0.70
Hunting mode		-1.08	0.45	-2.43	0.02*
Light level		-0.06	0.35	-0.18	0.86

Random effects: cuttlefish identification. *** $P < 0.001$. * $P < 0.05$.

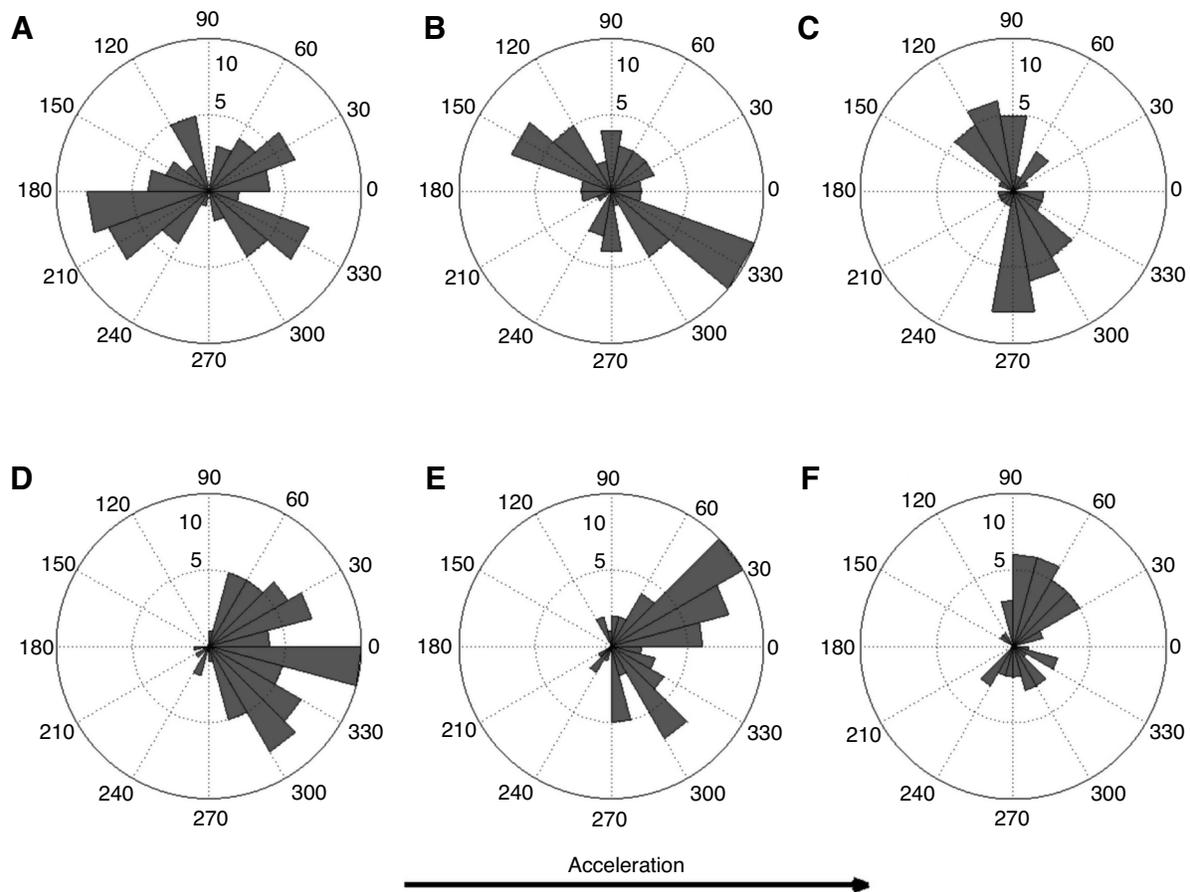


Fig. 4. Polar histograms showing initial angles of cuttlefish before exposure relative to the stimulus direction and escape angles for all jet responses performed. (A–C) Initial angles before stimulus direction. (D–F) Escape angles for the jet responses. (A,D) Experiment I, (B,E) experiment II and (C,F) experiment III. There were no significant differences in distribution between compression and rarefaction at the different test frequencies in the three experiments (Mardia–Wheeler–Watson: $P > 0.2$ for all). The pre-stimulation orientation was not significantly different from a uniform distribution (H–A omnibus test for directedness; $P > 0.5$ for all). Responses are plotted as if the acceleration is always from right to left (arrow). Concentric circles represent a frequency of 5. Bin frequency is 10 deg.

minimal, as has been shown for the teleost species roach (*Rutilus rutilus*) tested in the same experimental set-up (Karlsen et al., 2004). Complete blocking of the lateral line system in this fish did not affect acoustic startle response probabilities or directionalities at infrasonic frequencies. In addition, care was taken to eliminate the possibility for any visual cues above and around the test chamber, and observed escape behaviours in light and darkness were similar. We thus conclude that the observed and analysed behavioural responses were elicited and driven by activation of the inner ear statocyst organs.

The driving voltage waveforms employed in the experiments were chosen in order to create a low-frequency pulse stimulation,

which mimicked key aspects of the hydrodynamic near-field generated by the two generalised types of predators: the approaching predator and the suction-feeding predator. The applied stimulus waveforms were simplified signals compared with the many real signals aquatic prey are exposed to. In nature, several factors will affect the hydrodynamic signatures such as predator species and size, in addition to external factors, e.g. if the surrounding water is calm or turbid. Furthermore, the position in the water column where the interaction takes place is important for the signatures; is the interaction in the pelagic layers or close to any boundary surfaces? We thus recognise that under natural conditions the hydrodynamic fields produced by predators may involve the

Table 5. Mean escape angle in all three experiments and results of a non-parametric Hodges–Ajne (H–A) omnibus test for directedness

	Experiment I		Experiment II		Experiment III	
	Escape angle	H–A omnibus P -value	Escape angle	H–A omnibus P -value	Escape angle	H–A omnibus P -value
3 Hz compression	327 (282, 12)	0.31	334 (306, 362)	0.25	51 (321, 140)	0.31
3 Hz rarefaction	33 (319, 359)	0.31	29 (354, 85)	0.31	48 (319, 138)	0.94
5 Hz compression	339 (319, 359)	<0.05	355 (332, 379)	<0.01	–	–
5 Hz rarefaction	312 (293, 331)	<0.05	358 (340, 376)	<0.01	–	–
9 Hz compression	356 (344, 8)	<0.001	21 (8, 35)	<0.01	32 (5, 70)	0.21
9 Hz rarefaction	313 (288, 338)	<0.05	350 (323, 377)	<0.01	42 (1, 83)	<0.05

Values in parentheses are the lower and upper quartiles.

activation of both the inner ear and skin mechanoreceptor systems. However, we have shown here that information from the statocyst organs alone may provide cuttlefish with sufficient information to execute directional jet-propulsed escapes to evade striking predators.

Studies on visual interactions between cuttlefish and predators have shown that cuttlefish use various forms of anti-predatory responses, dependent on the size and type of predator (Langridge, 2009; Langridge et al., 2007; Staudinger et al., 2013). The hydrodynamic displacement field created by predators can also give important information about the size and type of predator (Hanke and Bleckmann, 2004; Kier and Leeuwen, 1997; Niesterok and Hanke, 2013; Oufiero et al., 2012). We found that cuttlefish exhibited intensity graded anti-predator responses when exposed to infrasonic pulses, mimicking the central hydrodynamic signatures of predator attacks. Our findings are in accordance with established ethograms of visually based anti-predatory responses in cuttlefish (Hanlon and Messenger, 1988). At the lowest intensity, some of the cuttlefish exhibited an asymmetrical mantle bar, signalled towards the stimulus direction. The same type of coloration has been seen in free-living cuttlefish when approached by a fish that does not constitute a threat (Hanlon and Messenger, 1988). At higher intensities, simulating a nearby or larger predator, cuttlefish display a rapid escape response using jet propulsion sometimes combined with inking.

Acoustic sensitivity in cephalopods increases towards lower frequencies (Kaifu et al., 2008, 2011; Mooney et al., 2010; Williamson and Budelmann, 1985). At 3 Hz, a median colour change or jet-propulsed escape response was obtained at a particle acceleration level of $2.8 \times 10^{-2} \text{ m s}^{-2}$ and $6.9 \times 10^{-2} \text{ m s}^{-2}$, respectively, under daylight. The threshold for colour change was thus ~ 6 dB lower than for abrupt jet-propulsed escape response (Fig. 3A,B), which is to be expected because higher acceleration levels mimic larger or nearby threats. Packard et al. (1990) found decreasing auditory threshold levels towards lower frequencies in cuttlefish, reaching $2.3 \times 10^{-3} \text{ m s}^{-2}$ in the infrasonic frequency range at 1–3 Hz in conditioned cuttlefish. There is an order of magnitude difference in the auditory thresholds found by Packard et al. (1990) and the behavioural thresholds found in the current study. These differences are most likely a result of differences in experimental procedures. Packard et al. (1990) used classical conditioning and the staircase technique to determine absolute hearing thresholds in cuttlefish by conditioning individuals to associate a short-duration, single-frequency sound stimulus to a mild electric shock. In contrast, we used unconditioned cuttlefish to find the innate behavioural response threshold. A recent study conducted by Samson et al. (2014) tested behavioural responses of cuttlefish exposed to pure tone signals at 80–1000 Hz. They found best sensitivity at 150 Hz with threshold level as low as $4 \times 10^{-4} \text{ m s}^{-2}$ for an unconditioned behavioural response, which is an order of magnitude below the thresholds found by Packard et al. (1990). It should be noted that the infrasonic thresholds used by Packard et al. (1990) were limited by background noise levels at the test site. Thus, the studies by Packard et al. (1990) and Samson et al. (2014) are both consistent with cuttlefish having a highly developed, low-frequency hearing, which extends to a few hundred Hz, i.e. comparable to what has been documented in fish sensitive to particle acceleration only (see Sand and Karlsen, 2000).

The ability to detect infrasound seems to be widespread in the aquatic environment and has been found in several distantly related aquatic species, including copepods (Budelmann and Williamson, 1994; Heuch and Karlsen, 1997; Williamson, 1988; Williamson and

Budelmann, 1985), cephalopods (Packard et al., 1990), and both cartilaginous (Casper and Mann, 2007) and bony fishes (Karlsen, 1992; Karlsen et al., 2004; Sand and Karlsen, 2000). Playback studies that exposed Atlantic salmon (*Salmo salar*), European silver eels (*Anguilla anguilla*) and roach (*R. rutilus*) to infrasound found that these fish species, like cuttlefish, exhibit a strong avoidance response with little or no sign of habituation (Karlsen et al., 2004; Knudsen et al., 1992, 1994; Sand et al., 2000). Although cephalopods and bony fishes are distantly related, there is a spatial overlap in habitats and in the predators they are exposed to (Packard, 1972). It is, therefore, not surprising that we find a convergent evolution of escape behaviours in response to infrasonic stimuli in the two animal groups. The overall ability to detect infrasound might therefore be important in predator avoidance in the aquatic environment, especially when the use of other sensory modalities such as vision is limited (Karlsen et al., 2004; Wilson et al., 2013).

The jet-propulsed escape responses of cuttlefish were studied under different external scenarios. Conducting an escape response is always a trade-off between the risk of being eaten and the energy expended in undertaking rapid escape responses, which could have otherwise have been used to engage in other activities such as mating or finding food (Lima and Dill, 1990; Ydenberg and Dill, 1986). Therefore, the response depends on the animal's perception of the predation risk where external factors might have a significant influence on the threshold for conducting an escape response or not (Lima and Dill, 1990; Ydenberg and Dill, 1986). This effect has been observed in a study on escape responses on male nocturnal moths that were exposed to intense ultrasonic signals mimicking an approaching predatory bat (Skals et al., 2005). The authors found an increase in threshold for a behavioural response of up to 40 dB when moths were exposed to female pheromones (simulating a mating opportunity) at the same time as ultrasonic signals emitted compared with the isolated ultrasonic signal. This suggests that a moth's reaction to the predatory threat constitutes a sensory conflict and the decision to conduct an escape response is a trade-off depending on the relative intensity of the input to the central nervous system (CNS) from not only the hearing sense but also other sensory modalities (Skals et al., 2005). In the current study, we deprived the cuttlefish of food for 24 h and tested the behavioural responses to simulated predatory attacks at the same time as prey items were shown on a screen (stimulating a hunting opportunity). Similar to the moth, there was an increase in threshold but only by ~ 6 dB. This increase was significant at 3 Hz but not at 9 Hz, which could be explained by the low sample size and large variation between individuals. An alternative explanation could be that the threshold for making an escape response based on input from the statocyst organ gives a stronger signal to the CNS compared with inputs from other sensory modalities, which might have a weak influence on the escape response threshold. This is intuitively appealing, because a wrong decision in an encounter with a predator can have fatal consequences, whereas missing one opportunity to feed or mate has less effect on the animal's overall fitness (Lima and Dill, 1990; Ydenberg and Dill, 1986).

When cuttlefish performed fast jet-propulsed escape responses, they followed the direction of the initial particle acceleration vector, irrespective of whether the particle acceleration was associated with a pressure increase or decrease (Figs 2B–D and 4). This type of behaviour would take them away from striking predators but direct them towards and into the mouth of suction feeders. We, therefore, suggest that the early phase of an attack by a striking predator is the primary cue used by cuttlefish to detect approaching predators.

Whether or not a prey should respond to the early warning signals (bow wave) or the later warning signals (the suction) of a predatory attack might depend on several conditions, e.g. the speed of the sensory and muscular systems of the prey. If the processing time of the system is slow, responding to the early signals of the nearby threat might be an advantage. Conversely, for those aquatic organisms (e.g. some species of copepod), having a very short latency response time (1.5 ms) from when the sensory input is received to when the contraction of the muscles begins (Lenz et al., 2000), responding to the late warning signal might be just in time while also preventing unnecessary escape reactions. The latency response time of the cuttlefish statocyst system when exposed to infrasound is between 37 and 56 ms (M.W., J.Å.R.H., H. B. Schack and H.E.K., unpublished). This is ~10 times slower compared with the copepod and, therefore, responding to the early warning signals might be linked to the processing time of the sensory and muscular systems of the cuttlefish.

Our findings are in accordance with studies on teleost fish, which in general show acoustic startle behaviours directed away from the acoustic source (Eaton et al., 1995, 1997). It has been suggested that fish with inner ears stimulated by particle acceleration and indirectly by pressure changes are able to distinguish their startle behaviour between the opposing hydrodynamic signatures of approaching and suction feeding. This is in addition to, or under conditions of, where the use of other sensory modalities might be limited (Eaton et al., 1995; Guzik et al., 1999). Roach can detect both particle acceleration and the pressure phase components of acoustic signals and, therefore, have the ability to discriminate between pressure phases. When it was studied in the same experimental set-up as in the present study, it also showed infrasonic startle escapes in the same direction as the initial particle acceleration (Karlsen et al., 2004). However, startle behaviour in this species was unexpectedly inhibited when the initial pressure phase was a rarefaction (Karlsen et al., 2004).

For both the cephalopod species in the present study and the few fish prey species that have been studied, it appears that responding to the early phase of the predatory attack has played a significant role in the evolution of behavioural responses compared with the final stage of a predatory attack, even though suction feeding is the most widely used mechanism of prey capture in aquatic vertebrates (Wainwright et al., 2007). This is intuitively appealing because it provides prey with more time to optimise behavioural responses in situations where time is paramount. However, more observations across several taxa are needed to conclude whether or not this type of behaviour is a general response pattern when exposed to a hydrodynamic flow field from approaching and/or suction-feeding predators. It could be a general phenomenon, because it has been observed that as a counter strategy some predators reduce the bow wave by opening the mouth before getting within suction distance, which apparently enables them to get close enough to engulf prey without alerting the prey, even if it comes at the expense of a reduced strength of the suction motion performed (Gemmell et al., 2014).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: M.W., H.E.K.; Methodology: M.W., J.Å.R.H., H.E.K.; Software: M.W., J.Å.R.H.; Formal analysis: M.W., J.Å.R.H., H.E.K.; Investigation: M.W., J.Å.R.H., H.E.K.; Resources: M.W.; Data curation: M.W.; Writing - original draft: M.W.; Writing - review & editing: M.W., J.Å.R.H., H.E.K.; Project administration: M.W.; Funding acquisition: M.W.

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