Animal behaviour

Dynamic visual cues induce jaw opening and closing by tiger beetles during pursuit of prey

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In dynamic locomotory contexts, visual cues often trigger adaptive behaviour by the viewer, yet studies investigating how animals determine impending collisions typically employ either stationary viewers or objects. Here, we describe a dynamic situation of visually guided prey pursuit in which both impending prey contact and escape elicit observable adaptive behaviours in the pursuer, a predatory beetle. We investigated which visual cues may independently control opening and closing of the beetle’s jaws during chases of prey dummies. Jaw opening and closing typically occur when prey is within the 60° binocular field, but not at specific distances, angular sizes or time-to-collision. We show that a sign change in the expansion rate of the target image precedes jaw opening (16 ms) and closing (35 ms), signalling to the beetle that it is gaining on the target or that the target is getting away. We discuss the ‘sloppiness’ of such variation in the lag of the behavioural response, especially jaw closing, as an adaptation to uncertainty about target position due to degradation of the target image by motion blur from the fast-running beetle.

1. Introduction

Animals use visual information about separation from objects in the environment to trigger adaptive behaviours, such as collision avoidance or object interception [1,2]. The information may be spatial, such as absolute or relative separation, or surrogates of distance, such as object size or motion parallax. Temporal information about separation, such as time-to-collision [3–5] or relative retinal expansion velocity [6], are also derived from visual cues. In most cases examined, viewers are typically stationary and objects approach on a collision course, although cases of moving observers approaching stationary targets have been studied [4,6]. In both scenarios, approach velocities are typically constant. We now describe a novel dynamic situation in which an observer chases a moving object and uses dynamic visual cues derived from the constantly changing separation to produce adaptive behaviours.

Tiger beetles (Cicindela spp.) are diurnal, cursorial predators that pursue prey under visual guidance. Their fast running speeds can produce high angular velocities that typically degrade visual contrast enough [7,8] to cause the beetle to stop intermittently to re-localize its prey. When prey has high contrast and/or the pursuit has lower angular velocity, however, the beetle engages in smooth, closed-loop, pursuit [7,9], typically running with its jaws closed. At some time during the chase, the beetle opens its mandibles, likely in anticipation of imminent prey capture. If prey is not contacted, however, the mandibles are closed. In laboratory experiments, we investigated the visual cues preceding jaw opening and closing while beetles continuously chased moving prey dummies.
2. Material and methods

(a) Animals

We used oblique-lined tiger beetles, *Cicindela tranquebarica* (Carabidae), with husbandry protocols as previously described [8]. Beginning three weeks before experimentation, beetles were only fed in the experimental arena until they foraged readily and chased a prey dummy.

(b) Experimental design

Experiments were performed in a cylindrical arena (33 cm diameter × 18 cm height) with walls patterned alternately with black (4 mm) and white (12 mm) vertical stripes illuminated from above by two 45 W fluorescent lamps. Sequences of individual beetles pursuing a prey dummy were recorded from above at 250 fps with 1024 × 1024 resolution using a high-speed camera (*PHANTOM* v. 5.0, AMETEK, USA). The prey dummy was a black plastic bead (4.5 mm diameter) attached to a nylon monofilament moved by hand from above the arena.

(c) Analysis

Recorded pursuit sequences (*n* = 44) by 12 beetles yielded 110 jaw openings and 102 jaw closings. Some sequences had several openings and closings, but data for openings (range = 3–15 per beetle; mean ± s.d. = 9.2 ± 3.8) and closings (range = 3–14 per beetle; mean ± s.d. = 8.5 ± 3.9) were relatively evenly spread across beetles. Videos were analysed in *IMAGEJ* v. 1.46r (Wayne Rasband, NIH, USA). In each frame, eight points were marked: (1) posterior elytral apex, (2) anterior centre of the pronotum, (3 and 4) left and right antennal bases, (5) mid-point between eyes, (6 and 7) left and right antenna tips and (8) centre of prey dummy (electronic supplementary material, figure S1). Transition from fully closed to opened jaws, and centre of prey dummy (electronic supplementary material, Movie S1). The mean absolute angular position of the prey, |θe|, at the time of jaw opening was 25.6 ± 15.4° and at closing was 26.0 ± 20.5°. Jaws were opened or closed at variable distances from the prey (figure 1), and jaws remained opened for variable durations (Mdn = 251 ms, IQR = 208.5 ms; electronic supplementary material, figure S2).

Examination of expansion and contraction of the target image at various lags preceding jaw opening and closing reveals similar functions (figure 2). Both behaviours are preceded by two sign changes in expansion rate and a local inflection. Consider jaw opening (figure 2, left panels). The first sign change around −75 ms is irrelevant for this behaviour, i.e. a target that begins to contract should not signal the beetle to open its jaws. The inflection provides information that the contraction rate is slowing, but the target is still contracting, i.e. getting away, and jaw opening is not adaptive. The final sign change from contraction to expansion informs the beetle that it is gaining on the prey independent of their velocities. The jaws open 16 ms later (range 11.7–19.7, best-fit CI, figure 2a).

Jaw closing follows similar logic. When the jaws are open and the target image changes from expanding to contracting, i.e. target separation is increasing, jaw closing follows 35 ms later (range 32.4–39.0, figure 2b). Jaws are usually opened after a burst of acceleration associated with target expansion (figure 2c), whereas target contraction leads deceleration and jaw closing follows (figure 2d). Cross-correlation of beetle velocity with $\dot{x}$ is broadly tuned around $t = 0$ ms, indicating...
that movement of beetle and prey both drive image expansion (electronic supplementary material, figure S3). The sign change of $a$ also influences time-to-collision, calculated as $a = \alpha / \dot{a}$ [5]. Thus, that variable crosses zero at similar lags to $\dot{a}$ (figure 2), but the data are more scattered. Standard deviation of normalized means of both variables are equal during jaw opening, but higher for time-to-collision during jaw closing (open: mean normalized $a = 0.31 \pm 0.097$, ttc = $0.71 \pm 0.091$; close: $a = 0.53 \pm 0.094$, ttc = $0.52 \pm 0.155$).

4. Discussion

Tiger beetles pursuing prey may continuously open and close their jaws several times as pursuit dynamics lead to expansions or contractions, respectively, of the target image. At jaw opening, the image is typically within 30° of the sagittal midline, which defines the region of binocular overlap [10] and the region bounded by the tips of the beetle’s antennae [8]. Nevertheless, targets are often viewed binocularly during pursuit yet the jaws are not opened. Thus, although a specific target angular position may be necessary for jaw opening, angular position is not sufficient (figure 1), as it is for release of snapping by bulldog ants (Myrmecia gulosa) [11].

Angular size is also not a sufficient trigger (figure 1). When looming objects are likely to be conspecifics of known absolute size, as is the case in intercepting hover flies (Eristalis sp., Volucella pellucens) [12] and evading locusts (Locusta migratoria) [13], threshold values of image size can be an effective trigger. By contrast, tiger beetles are generalist predators that pursue prey of various absolute sizes. Thus, retinal size is an unreliable measure of distance to their prey. Even in cases where target absolute size is predictable and experiments are performed with stationary observers and targets approaching at constant velocity, trigger thresholds are variable, e.g. threshold target size in locusts varies almost threefold (see fig. 3d in [14]).

Determining visual cues and threshold values that trigger the behaviours is difficult and several possible visual cues are closely coupled, because distance and angular size of physical targets are related. For constant approach velocities, expansion rate and distance are related. Time-to-collision is angular size divided by expansion rate. Thus, all four variables are related and a single nervous system can compute many such variables [15]. Yet, determining which one(s) may trigger a specific behaviour is typically not rigorously tested. Moreover, it is not the value of the visual parameter at the time of the behaviour that we seek, but its value at some lag preceding the behaviour without a priori knowledge of that specific sensori-motor delay.

We tried to identify a lag time with reduced variation of specific visual parameters, including expansion rate and time-to-collision preceding jaw movement, but did not find unambiguous trends towards minimized variation at any particular lag. Examination of visual triggers in other systems has fared little better and relatively few researchers [6,16] have attempted to determine which combination of closely related visual cues triggers the behaviour under study. Wagner [6] compared several visual variables to determine which might trigger deceleration of flying houseflies landing on a single-sized stationary target. He proposed that flies use relative retinal expansion velocity (the inverse of time-to-collision) because it had a lower coefficient of variation at different lags before deceleration, although no statistical comparisons were performed. In a study of...
standing house flies escaping from an approaching object, Holmgvist & Srinivasan [16] compared values of related visual parameters at the time of the escape jump. ‘Total temporal contrast’, i.e. change in angular size divided by initial angular size, showed less variation than other variables, yet again, no statistical comparisons were performed. Finding reduced variation in a visual parameter at some lag in flies and not tiger beetles may reflect the broader temporal tuning of the visual guidance system of terrestrial tiger beetles [9], compared with sharper tuning in flies [17].

In dynamic chases by tiger beetles, sign changes in target image expansion precede jaw opening/closing by short lags and better indicate imminent contact or prey escape than a set threshold of expansion or contraction. Jaws are often open while the beetle accelerates, but this is not a prerequisite: they are also opened when the target slows down while the beetle is running at steady or decreasing pace. Jaw closing appears to be a secondary response to target contraction, the primary response being reduction of the beetle’s velocity.

The tiger beetle’s relatively ‘ sloppy’ initiation of jaw closing may be an adaptation to compensate for effects of visual motion blur, which can reduce accuracy of aiming as the beetle pursues its target. As beetles run over prey that they have momentarily lost due to motion blur, they sweep it up with a wide capture basket formed by their open jaws, opened spiny maxillary and labial palpi. This feeding mode is reminiscent of great white sharks, which keep their jaws open while closing in on seals [18], and analogous to ram feeding in larval fish [19], where increases in mouth radius make up for errors in aiming. With distance to prey fluctuating quickly during sinusous chases, it is important for the tiger beetle to ensure that the jaws are open when there is a chance of contacting prey.

Data accessibility. Data deposited in the dryad repository: http://doi.org/10.5061/dryad.83452 [20].

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References