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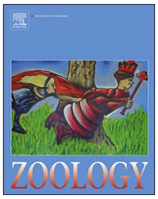

Head stabilisation in fast running lizards

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ABSTRACT

The cyclic patterns of terrestrial animal locomotion are frequently perturbed in natural environments. The terrain can be complex or inclined, the substrate can move unexpectedly and animals can misjudge situations. Loosing stability due to perturbations increases the probability of capture by predators and decreases the chance of successful prey capture and winning intraspecific battles. When controlled corrective actions are necessary to negotiate perturbations, animals rely on their exteroceptive and proprioceptive senses to monitor the environment and their own body movements. The vestibular system in the inner ear perceives linear and angular accelerations. This information enables gaze stabilisation and the creation of a stable, world-bound reference frame for the integration of the information of other senses. During locomotion, both functions are known to be facilitated by head stabilisation in several animals with an erect posture. Animals with a sprawled body posture, however, undergo very large body undulations while running. Using high speed video recordings, we tested whether they nevertheless stabilise their head during running, and how this is influenced by perturbations. We found that running *Acanthodactylus boskianus* lizards strongly stabilise their head yaw rotations when running on a flat, straight runway: the head rotation amplitude is only 4.76 ± 0.99°, while the adjacent trunk part rotates over 27.0 ± 3.8°. Lateral head translations are not stabilised (average amplitude of 7.4 ± 2.0 mm). When the lizards are experimentally perturbed by a large and unexpected lateral substrate movement, lateral translations of both the head and the body decrease (on average by 1.52 ± 0.81 mm). At the same time, the rotations of the head and trunk also decrease (on average by 1.62° ± 7.21°). These results show that head stabilisation intensifies because of the perturbation, which emphasises the importance of vestibular perception and balance in these fast and manoeuvrable animals.

1. Introduction

Animals move about for finding food and mates, escaping predators, migration and foraging. During steady state locomotion, their limbs and body make cyclic movements that are controlled by central pattern generators (Chevallier et al., 2008; Ijspeert, 2008; Lacquaniti et al., 2012; Squire et al., 2013). However, these cyclic patterns are frequently disturbed under natural conditions, especially during terrestrial locomotion (Daley et al., 2006). The terrain can be uneven with varying magnitude and degrees of complexity or inclination, the substrate can move (e.g. rolling or sliding stones or branches, moving sand), or animals can simply misjudge situations; all of which can have a determining influence on prey capture and predator avoidance.

Animals can recover from small perturbations in a passive, mechanical way, comparable to a spinning top that restores balance automatically when gently perturbed (e.g. Jindrich and Full, 2002; Bruijn et al., 2013). Recovery from larger perturbations, however, requires controlled corrective actions, which may, or may not, be reflexive. Such controlled dynamic stability requires monitoring of the environment and of the dynamic status of the system (e.g. Bruijn et al., 2013). Tendon organs, muscle spindles and joint receptors provide proprioceptive information on the positions, movements and dynamics of body parts relative to each other (e.g. Mileusnic and Loeb, 2006; Mileusnic et al., 2006; Latash, 2008). These receptors can therefore detect unforeseen segmental movements that are caused by perturbations. Further, animals rely on exteroception (haptic and vestibular sense and vision) to perceive the environment (Kandel et al., 1991; Nishikawa et al., 2007; Latash, 2008; Squire et al., 2013). The vestibular system, consisting of otolith organs and semi-circular canals in the inner ear, is highly sensitive for linear and angular accelerations of the head, including gravitational acceleration (Rabbitt et al., 2004; Angelaki and Cullen, 2008; Cullen, 2012; Squire et al., 2013). The vestibular system facilitates a stable gaze because perceiving head rotation enables compensatory eye rotations (Angelaki and Cullen, 2008). Vestibular signals integrate immediately and continuously with other exteroceptive information (vision, skin sense, etc.), motor efferent signals

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and, importantly, also with the proprioceptive information coming from the limbs and body segments (i.e. with the internal dynamic status of the body) (Angelaki and Cullen, 2008; Cullen, 2012; Squire et al., 2013). Interestingly, the frames of reference of the vestibular and proprioceptive components may differ drastically. Although initially head centred, the processed vestibular information refers to a world-bound frame (as does the visual information that interacts with the vestibular signals), while proprioception is body centred. Therefore, proper perception of position and motion of body segments relative to the outside world (perception of self-motion) probably requires mapping of these reference frames onto each other (Cohen and Andersen, 2002; Angelaki and Cullen, 2008; Cullen, 2012).

Stabilising head movements while running may facilitate the formation of such a world-bound frame of reference for body orientation (or inertial guidance system) that is based on vestibular information (Pozzo et al., 1990; Dunbar, 2004a). This has experimentally been observed, for instance in running humans and galloping Hanuman langurs and bonnet macaques (Pozzo et al., 1990; Dunbar, 2004b). Interestingly, a stabilised trunk seems to fulfil a similar role at lower velocities during walking, by combining information from the vestibular system and proprioceptors in the neck and trunk (Mergner et al., 1992; Dunbar, 2004a, b). As a result, a stabilised trunk that provides a stable spatial reference frame may enable voluntary head movements (e.g. during sightseeing) without disturbing balance (Dunbar et al., 2008). Further, head stabilisation facilitates a stable gaze, as observed for instance in humans, rhesus monkeys, cynomolgus monkeys and hovering passerine birds (Cromwell et al., 2001a,b; Xiang et al., 2008; Su et al., 2011). Head rotations, which are detected by the vestibular system, can be compensated by eye movements in the opposite direction through the vestibulo-ocular reflex (VOR) (Angelaki and Cullen, 2008). Especially at higher frequencies, the gaze is more optimally stabilised when head movements in space are confined (Cromwell et al., 2001b).

Locomotion in small lizards offers a good model to evaluate head stabilization in case of a strong perturbation. These lizards exhibit highly transient locomotor behaviour, and many species move in a highly dynamical, unsteady manner, realizing very high accelerations (e.g. up to 4.3 g; Curtin et al., 2005). They run in intermitted bursts with high cycling frequencies (e.g. up to 20 Hz; Aerts et al., 2003), which leaves little time for corrective movements within the duration of a single step. They are very manoeuvrable and often live on substrates that are complex in 3 dimensions. Fast feedback is most probably crucial for successful locomotion in these animals. Further, their (relatively) massive trunk and tail (together > 75% of total body mass; Aerts et al., 2003) undergo large undulations in the horizontal plane, due to their sprawled body posture. The undulation of their spine causes their limb girdles to rotate, which contributes significantly to their limb excursion (up to 52% of progression) (Daan and Belterman, 1968; Russell and Bels, 2001; Fischer et al., 2010). Because of the large yaw rotations of the trunk, head stabilisation seems a lot more challenging for these animals. However, head stabilisation is probably all the more important in this situation for gaze stabilisation and the formation of the world-bound frame of reference.

We investigated head stabilisation in *Acanthodactylus boskianus* lizards. This is an agile Mediterranean lacertid species that specialises in running in open, sandy areas (Vanhooydonck and Van Damme, 1999; Curtin et al., 2005; Uzüm et al., 2014). During straight running, we suddenly applied a lateral substrate movement as an unforeseen perturbation. This mimics a fast and unexpected perturbation, such as encountered in nature when a stone or branch stepped upon slides away. We chose a large perturbation amplitude (approximately 25% of the average snout–hip length), so that active stabilisation (rather than passive recovery) from the perturbation was more likely. Because the large body undulations occur in the horizontal plane, we focused on yaw rotations and sideward translations of the head and the trunk. First, we tested whether the amplitude of head rotation was smaller than that of the trunk rotation during straight undisturbed running (the control condition). If true, this would indicate that lizards are capable of head stabilisation, despite their large trunk undulations. Next, we focussed on the perturbed stride to investigate the instantaneous effects of a perturbation on body movements. Fast active reactions upon the perturbation (such as tuning of trunk and head rotations/translations) seem essential in these fast and manoeuvrable animals, e.g. to avoid temporarily blurred vision. Hence, we hypothesise that head stabilisation (rotation/translation) will be maintained when being perturbed. If true, this would again indicate the skill for (and the importance of) head stabilisation in lizards.

2. Materials and methods

2.1. Experimental animals

Four *A. boskianus* individuals were obtained from a commercial dealer (Fantasia Reptiles, Antwerp, Belgium). Body lengths ranged from 6.4 to 7.4 cm (snout–hip length, measured on calibrated video recordings, see Section 2.3). The animals were individually housed in terraria (100 cm x 40 cm x 50 cm) with a sand substrate and rocks that provided shelter and cage enrichment. Two 60-Watt bulbs that were suspended above the terrarium provided light and heat (10 h/d). The lizards were fed crickets (*Acheta domesticus*) twice a week, and drinking water was provided *ad libitum*.

Our experiments were approved by the ethical committee of the University of Antwerp (ECD 2013-76) and were conducted in compliance with the legal requirements.

2.2. Experimental setup

The lizards were easily encouraged to run through an open top corridor by following it with the hand of the experimenter. The walls of this runway (length 2 m, width 0.1 m, height 0.2 m) were made of transparent PMMA (Perspex) and the bottom was covered with smooth cork, which provides good grip to the animals. Halfway along the

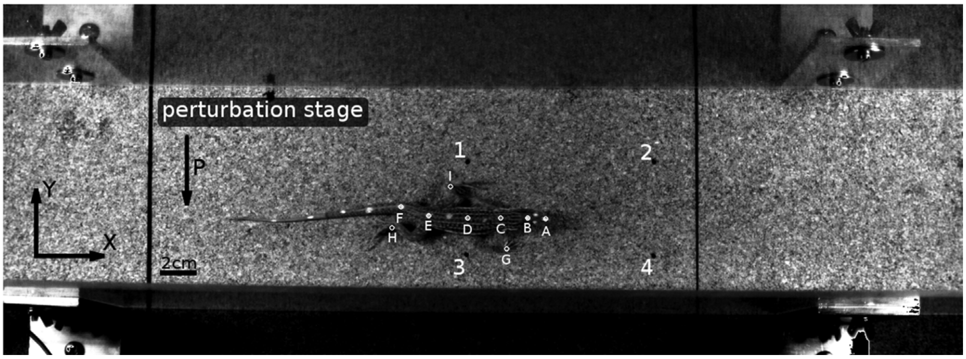

Fig. 1. Recording of an *Acanthodactylus boskianus* lizard running on the perturbation stage. Four black dots (1–4) were used to calibrate the digitisations. The digitised points are indicated by white circles: (A) snout tip, (B) base of the head, (C) shoulder, (D) mid-trunk, (E) hip, (F) tail, (G) right hand, (H) right foot, and (I) left foot. The left hand is not visible on this frame. Arrow P indicates the movement direction of the perturbation stage.