



Contents lists available at ScienceDirect

Seminars in Cell & Developmental Biology

journal homepage: www.elsevier.com/locate/semcdb

Vision in chameleons—A model for non-mammalian vertebrates

Hadas Ketter-Katz^{a,b,1}, Tidhar Lev-Ari^{c,1}, Gadi Katzir^{d,*}^a Goldschleger Eye Institute, Sheba Medical Center, Tel-Hashomer, 52621, Israel^b Sackler Faculty of Medicine, Tel-Aviv University, Tel-Aviv, 69978, Israel^c Biomedical Engineering, Georgia Institute of Technology and Emory University, Atlanta, GA, 30332, USA^d Department of Evolutionary and Environmental Biology, University of Haifa, 199 Aba Khoushy Ave., Mount Carmel, Haifa, 3498838, Israel

ARTICLE INFO

Keywords:

Animal model
Chameleon
Vision
Visually-guided behaviour
Eye
Lateralisation
Binocular independence
Conjugate
Threat avoidance
Predatory strikes

ABSTRACT

Chameleons (Chamaeleonidae, Reptilia) are known for their extreme sensory and motor adaptations to arboreal life and insectivory. They show most distinct sequences of visuo-motor patterns in threat avoidance and in predation with prey capture being performed by tongue strikes that are unparalleled in vertebrates. Optical adaptations result in retinal image enlargement and the unique capacity to determine target distance by accommodation cues. Ocular adaptations result in complex eye movements that are *context dependent*, not independent, as observed in threat avoidance and predation. In predation, evidence from the chameleons' capacity to track multiple targets support the view that their eyes are under individual controls. Eye movements and body movements are lateralised, with lateralisation being a function of many factors at the population, individual, and specific-situation levels. Chameleons are considered a potentially important model for vision in non-mammalian vertebrates. They provide exceptional behavioural tools for studying eye movements as well as information gathering and analysis. They open the field of lateralisation, decision making, and context dependence. Finally, chameleons allow a deeper examination of the relationships between their unique visuo-motor capacities and the central nervous system of reptiles and ectotherms, in general, as compared with mammals.

1. Introduction

Chameleons (Reptilia, Iguania, Chamaeleonidae) are arboreal lizards that inhabit forests, savannahs, and steppes. The evolutionary origins of chameleons are African, yet their current centre of speciation is Madagascar, with approximately one half of the 200 odd chameleon species inhabiting this island [1]. Chameleons prey predominately on insects and display extreme morphological, behavioural, and neural adaptations to both arboreality and insectivory. These adaptations are expressed in body form, motion, body colouration, and sensory systems. Of the sensory modalities, vision plays the major role in chameleons' guidance of motion, foraging, prey detection and capture, anti-predator behaviour, and communication [1].

A chameleon moving slowly through the vegetation, keeps its body bilaterally compressed and its legs close to the body, while grasping the branches with its syndactylous toes and its long prehensile tail. The chameleon's eyes scan the environment continuously with large amplitude eye movements that may span ca. 180° horizontally and ca. 90°

vertically [2–4]. The eyes are extremely large, protrude from their sockets and are completely covered by skin, with only a frontal aperture for the pupil visible.

If a chameleon detects a potential threat (e.g., a predator or a large moving object) it freezes. If the threat approaches, it swings its body so as to keep to the side of the branch distal to the threat. The motion is smooth and the branch acts as a visual obstacle between the chameleon and the threat. Throughout, the chameleon keeps sight of the threat with one or with both eyes, while its body surface, exposed to the threat, is reduced by the motion so that only a thin strip of the ventrum is mostly visible (Fig. 1A, Supplementary movie #1). If the threat continues to move, the chameleon also moves, keeping its relative position to the threat unchanged. If the threat approach is fast, the chameleon drops to the ground and attempts to escape by running [5]. In contrast, if a chameleon detects a prey (e.g., an insect), it responds very differently. First, it fixates on the prey with one eye, then it swings its head in the direction of the prey and fixates on the prey with the contralateral eye as well. If the insect moves, the chameleon tracks it

Abbreviations: CNS, Central Nervous System; OT, Optic Tectum; OMR, Optomotor Response; OKR, Optokinetic Response; CPD, Cycles per Degree; TN, Temporal to Nasal; NT, Nasal to Temporal; IP, Initial Protrusion

* Corresponding author at: University of Haifa, 199 Aba Khoushy Ave., Mount Carmel, Haifa, 3498838, Israel.

E-mail address: katgad@gmail.com (G. Katzir).

¹ Equal contribution.

<https://doi.org/10.1016/j.semcdb.2020.05.009>

Received 28 February 2020; Received in revised form 12 May 2020; Accepted 12 May 2020

1084-9521/© 2020 Elsevier Ltd. All rights reserved.

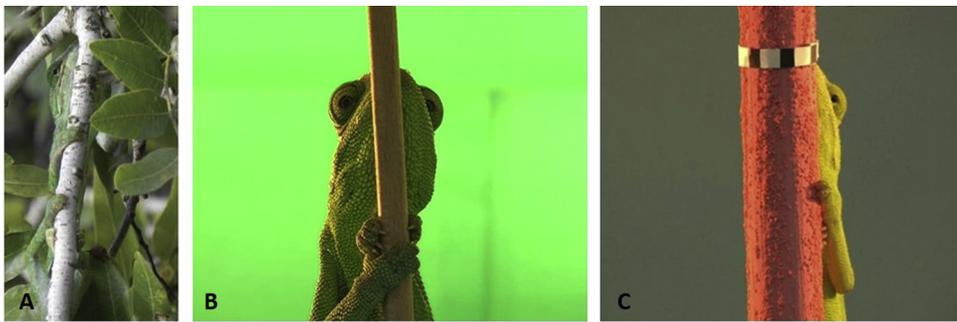


Fig. 1. Threat-avoidance response: a chameleon, *C. chameleon*, (A) on a branch (B) on a wide pole (C) on a narrow pole, (side views). The chameleon keeps to the distal side of the perch/pole, with its ventrum in the direction of the threat, while viewing the threat monocularly or binocularly (Lustig, et al. 2012, PlosOne; Lev Ari, et al. 2016; Journal of Comparative Physiology; With permission).

with head motion. Its tongue gradually protrudes between the mandibles (initial intrusion, IP) and suddenly strikes at the insect, engulfing it by the glove-like tongue-pad and drawing it to the mouth (Supplementary movie #2) [6]. If the insect withdraws from the chameleon, even by a few cm, the tongue is drawn back to the mouth and the hunt may cease.

Chameleons' capacities for extreme colour changes are one of their best known trademarks [7]. It has been demonstrated recently that in chameleons (the Panther chameleon as a model) rapid changes in colour (hue) occur by active tuning of the photonic response of a lattice of small guanine nanocrystals in S-iridophores. The organization of iridophores into superposed layers, constitutes an evolutionary novelty that allows some species to combine efficient camouflage with spectacular display [8].

Chameleons provide several examples of unique behavioural patterns and optical/anatomical structures related to eye and head movements, visual optics, and the unique relationships between the visual system, and the tongue system [6]. The threat avoidance and the predatory behaviour described are both distinct, visually based, and comprise visual target detection, recognition, and subsequent motor responses. Both threat avoidance and predatory tongue strikes are observed in chameleons immediately after hatching and thus may be regarded as innate, with 'threat' and 'prey' acting as 'releasers' [9].

Here, we discuss unique aspects of vision, optics and lateralization (asymmetry at the functional/behavioural levels) in chameleons. We bring evidence that eye movements are 'context dependent' and advocate the use of chameleons as a model for vision in non-mammalian vertebrates, complementary to currently used vertebrate models [10,11].

2. The retina and visual pathways

The retina of chameleons is complex and, in certain aspects, comparable to mammals' [12,13]. It contains no rods and comprises double cones (max 555–610 nm) and four spectrally distinct classes of single cones (max 555–610, 480–505, 440–450, and 375–385 nm), all containing oil droplets [14–23]. The isodensity lines for all retinal cells (ganglion, glial, and displaced amacrine cells) are concentric at the periphery and become horizontal at the centre, thus forming a 'visual streak'. Within the streak, there are two foveae, pit like structures with the highest ganglion densities (Fig. 2) [12], one of which is deep and convexiculate [3,24]. Displaced ganglion cells are found distributed throughout the retina with a slightly lower density in the vicinity of the foveae and the retinal margin (Fig. 3) [25].

The total number of ganglia in chameleons is ca. 320,000 [12] and the total number of fibres in the optic nerves is ca. 405,000 [26]. Chameleons' foveal photoreceptor density is ca. 760,000/mm² [27], a value that may be somewhat overestimated [3], and is the highest reported for lizards (e.g., ca. 76,000 photoreceptors/mm² in the sleepy lizard) [28]. This density is higher than in humans (98,000–324,000/mm²), [29,30] and similar to birds (in Sparrows, it is ca., 400,000/mm² and in Hawks, regarded as having an exceptionally high acuity, it

is ca. 10⁶ photoreceptors/mm² [31]).

In the chameleon, one fovea peaks at ca. 13,000 ganglions/mm² and the other at ca. 11,000 ganglions/mm² (Fig. 2). These densities are somewhat lower than in the sleepy lizards' (15,500 ganglions/mm² [32]).

The ratio of cone to ganglion density is a central component in determining visual acuity, and it is commonly accepted that the lower the ratio – the higher the acuity. For example, the ratio is ca. 1:1 in Wagtails (ca.120,000/mm²) [33], 2.6:1 in Pigeons [34], 3.4:1–5.9:1 in Red-tailed hawks, Goshawks, Blue jays and Least terns [34], ca. 5:1 in the Sleepy lizard, and ca. 5:1 in humans [35]. It is therefore most surprising that the ratio is ca. 58:1 in chameleons (assuming the values in the literature are valid). From this ratio, one expects chameleons to have a low visual acuity, yet this is not the case (see 2.1 below). This opens exciting questions: (i) Is the high ratio related to improved motion-detection at the retinal level? (ii) Are the ganglions similar in their function? (iii) Are there unique patterns of photoreceptor/ganglion connectivity? (iv) How is information modulated at the retinal level? We hope that future research will elucidate these questions.

As in other reptiles, the chameleons' retina projects to the diencephalon and the midbrain via the optic nerves. The nerves undergo complete decussation at the optic chiasma [36,37] and terminate in the optic tectum (OT) and nuclei in the hypothalamus, thalamus, pretectum, and tegmentum [38]. Complete decussation is observed also in birds and in other ectotherms (fish, amphibians). In vertebrates that lack cortex (e.g., fish, reptiles), the OT is the centre of visual information processing and is in charge of localisation and identification of prey, avoidance, obstacle detection, and optomotor behaviour. The midbrain tegmentum is involved in the integration of these functions and their translation into motor behaviour patterns [39]. In ectotherms, inter-hemispheric connections, via commissures, are sparse while in mammals they are substantial, dominated by the *corpus callosum* [36,40–42]. The visual system of chameleons exhibits several features unique to the group, including lack of ipsilateral retinofugal projections, an additional hypothalamic visual centre, and a *nucleus opticus tegmenti* that is exceptionally large, compared with other lizards [13,26,37,38,43]. In mammals, the optic nerves undergo partial decussation at the chiasm level [44], so that a proportion of the fibres projects to the contralateral hemisphere and the rest to the ipsilateral hemisphere.

2.1. Visual acuity

Behavioural visual acuity of the chameleon (*C. chameleon*) was tested, using optomotor (OMR) and optokinetic (OKR) responses [45]. OMR relies on the bodily tracking of a moving high contrast grating, while OKR relies on smooth slow eye movements that match the gratings speed and fast counter motions in the opposite direction (saccades [46], Supplementary movie #3). Chameleons were tested in a rotating drum, with gratings of differing frequencies (range 2.6–10.3 cycles per degree, CPD, for OMR and 3–11.9 CPD for OKR). The drum was illuminated from above with four fluorescent light bulbs (225 W),

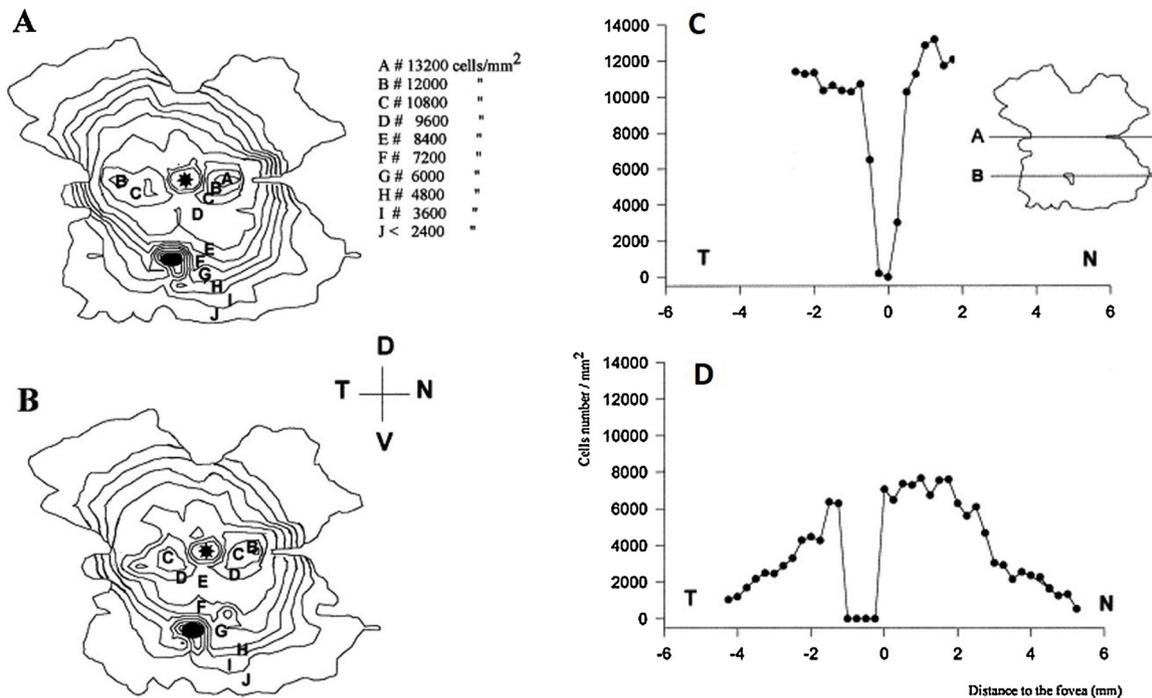


Fig. 2. Maps of the distribution of ganglion cells in the chameleon retina. The black point represents the optic disc. (A) Isodensity of all cells (ganglion cells, glial cells, and displaced amacrine cells) sampled every 250 μm over the retinal surface. In the central retina, the outlines became increasingly horizontal forming the visual streak. (B) The distribution of presumed ganglion cells showing two peak densities in the central retina N: Nasal; T: temporal; D: dorsal; V: ventral; *Central fovea. (C) Density of neurons in the ganglion cell layer plotted at the central visual streak and (D) through the optic disc according to naso-temporal axis (from Hassni et al. 1997; With permission).

providing ca. 1800 lx. In each test, stimuli were initiated with a low frequency and gradually increased until response ceased. Visual acuity was positively correlated with eye size: ca. 9 CPD for mature individuals with eye diameter of 10.1 ± 0.6 mm and 5 CPD in newly hatched individuals, with eye diameter of 3.3 ± 0.13 mm (mean \pm SE, N = 12 and 10, respectively). The visual acuity of mature chameleons was higher than in other reptiles (Loggerhead, *Caretta caretta*, 6.1 CPD [47]; Midland banded water snake, *Nerodia sipedon*, 4.25 CPD [48]; Red eared slider turtle, *Pseudemys scripta*, 5.6 CPD [49]; and Sleepy lizard, *Tiliqua rugosa*, 6.8 CPD [50]).

The OKR responses to stimulus motion in the temporal-to-nasal (TN) direction were more pronounced compared with stimulus motion in the nasal-to-temporal (NT). Tauber & Atkin (1968), reported equal sensitivity to both stimulus directions in the African chameleon (*Chameleo melleri*) [51]. A higher sensitivity to TN direction was found in teleost fish (*Chaetodon rainfordi*) [44], other reptiles [51], chickens (*Gallus domesticus*) [53], and rabbits (*Oryctolagus cuniculus*) [54]. Chameleons use a sit-and-wait strategy, and once a prey is detected, the chameleon moves forward toward it and thus OKR suppression by translational movements ensures that the image of the prey is focused on the retina.

3. Predatory strikes: prey distance & visual-optics

Once prey has been detected, discriminated, and approached, a chameleon uses a tongue strike to capture it. Visually-guided predatory strikes are observed among both invertebrates and vertebrates. Typically, such strikes are rapid and ballistic, i.e., once a strike has begun no corrections are made. Predatory strikes are performed by the entire body (e.g., Sandlance, *Linnichthyes fasciatus* [55]), appendages (e.g., Mantis shrimp, *Lysiosquillina maculata* [56]), neck (e.g., Egret, *Egretta* spp. [57]), or tongue (e.g., Salamander, *Hydromantes italicus* [39]). Because predatory strikes are fast and ballistic, the distance to the target needs to be determined a priori. This distance is dictated by reachability. For example, in the Praying mantis, strike distance is

dictated by the length of the predatory forelegs that, in turn, are age related. Predatory strikes in different species have been the subject of numerous experimental studies of visual perception and visuo-motor control. This is due to the high probability of eliciting a response, low variance in the motor patterns involved, and the capacity of manipulating features such as stimulus motion, distance, size, contrast, etc.

Animals employ different means to judge distance, based on monocular and/or binocular cues (Monocular: motion parallax, retinal image size, texture, perspective. Binocular: retinal image disparity, convergence angle). How precise are the predatory strikes of chameleons and what are the cues used to estimate distance? The capacity of chameleons to precisely estimate prey distance was first established by Harkness (1977), using Jackson's chameleons (*Chamaeleo jacksoni*) [3]. This species has three rostral 'horns' that may be used to hold optical elements (prisms, lenses) in front of the eyes. Thus, the chameleon's line of sight, when taking aim, ran through these elements and could be manipulated. By using prisms, the prey's apparent image could be displaced horizontally, so that the tongue tip did not encounter the real prey. By using positive or negative lenses the apparent image of the prey was displaced to being closer or farther, respectively. Using this ingenious system, it was demonstrated that the tongue is struck to the precise distance of the prey. From overshooting or undershooting of the chameleons' tongue as a function of lens sign and power, it was concluded that distance information is obtained from the accommodation effort [3,58]. This is a unique manner of distance estimation and is currently known only in the Sandlance, a small fish that performs fast strikes at its prey, and shares many optical, visual and behavioural features with Chameleons (Table 1) [55]. In using accommodation cues to determine distance, error detection improves as a function of angular resolution. Indeed, to achieve maximal performance, chameleons have exceptionally well-developed foveae with an extremely high photoreceptor density [3]. An additional factor is depth of field, the narrower it is, the more sensitive it is. Harkness provided an f - number of 5 for Jackson's chameleons and noted that pupil diameter changes very little

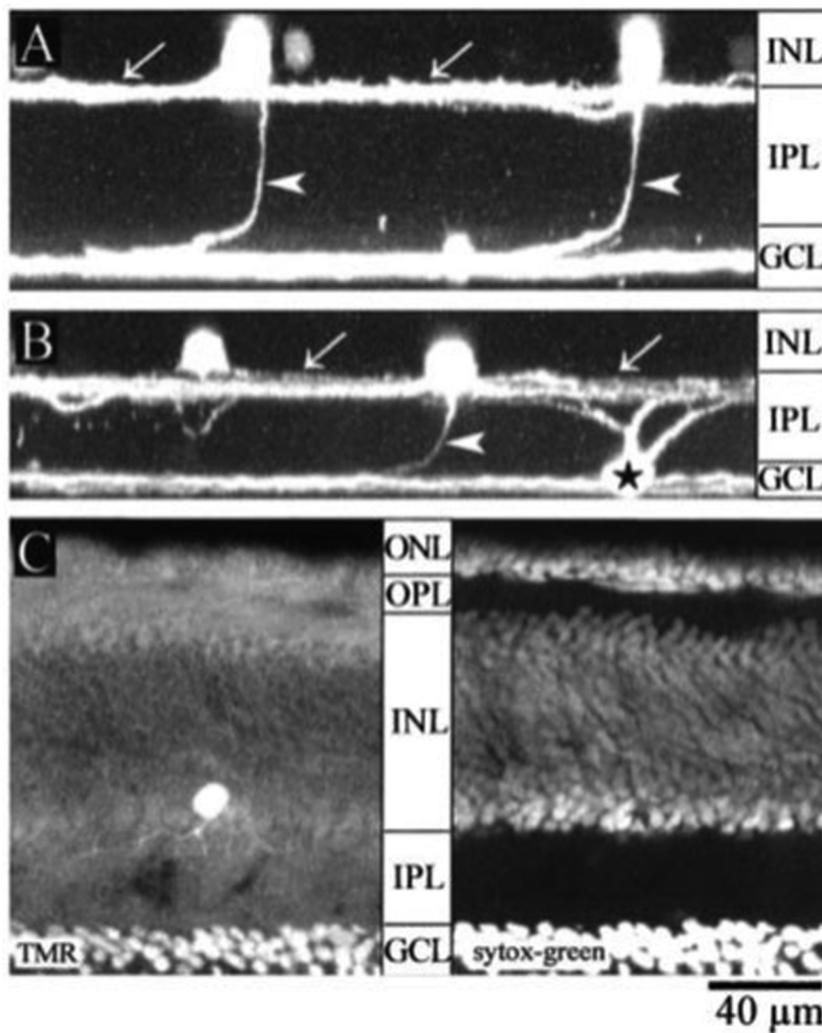


Fig. 3. A–C Radial sections of retinas showing the location of retrogradely labelled displaced ganglion cells. (A) Section of the central retina (B) peripheral area. Arrows indicate the monostratified dendritic fields of displaced ganglion cells at the outer margin of the inner plexiform layer (IPL). Arrowheads show the axons. The star indicates a labelled cell with an orthotopic location in the ganglion cell layer. Note that the first-order dendrites of the orthotopic cell join the dendritic layer of displaced cells. Cross-section of the retina with a retrogradely labelled displaced ganglion cell (left) and the same slice by a Sytox green neutral cell staining to visualise the cell layers (right). INL Inner nuclear layer, GCL ganglion cell layer, ONL outer nuclear layer, OPL outer plexiform layer, TMR tetramethylrhodamine-labelled dextran amine (from Bellintani Guardia and Ott 2002; With permission).

Table 1

Features enhanced in, or unique to, chameleons vision and visually-guided behaviour.

- Camouflage of body and eye, with crystal based integumental colour changes^a
- Rapid, accurate prey capture strikes
- Specialised, hyoid based, feeding apparatus, with tongue strikes reaching extreme velocities and distances
- Extreme ocular mobility
- Between eyes switching of movements
- Crystalline lens with greatly reduced refractive power,^a to the point of negative power – resulting in large retinal image magnification
- Monocular range – finding (accommodation cues)
- Deep convexiculate fovea, with a high foveal photoreceptor density
- Marked separation between the nodal point of the eye and the axis of rotation^a and a monocular movement parallax possible without eye translation^a
- Lateralisation of eye use and body motion
- Visuo-motor patterns are context dependent
- Capacity for monocular tracking of separate targets

^a Not known in other lizards. Based in part on [55].

[3]. However, in the Flap necked chameleon (*Chameleo dilepis*), Ott et al., showed a clear pupillary near response with diameter (ca. 2.2 mm) decreasing with increased accommodation and with an f-number of ca. 3.3 (posterior nodal distance of 7.26 mm) [58].

Accurate focusing requires a large image on the retina. Ott and Schaeffel (1995) demonstrated that the magnification factor in chameleons is ca.15 % higher than in other vertebrates' eyes, scaled to the same size [58]. This is achieved by yet another unique optical design of

the lens and the cornea. The chameleons' crystalline lens has a negative refractive power and thus enlarges the image [46,55,58,59]. The lens is almost flat-faced, or slightly biconvex with, most probably, an unconventional internal refractive structure [46]. Yet, the only other known eye of a similar design is that of the abovementioned Sandlance.

The important role of image formation by the lens is accompanied by a no lesser unique contribution by the cornea. In terrestrial vertebrates, the cornea bears the greater burden of refraction, being the interface between two media (air and water) that differ in their refractive indices. Corneal accommodation is well established in birds. In chameleons, the cornea plays a role in accommodation, a feature unknown in any other squamates (i.e., lizards and snakes). The evolutionary trend observed in terrestrial vertebrates, of an increase corneal power and a decrease in lens power, has culminated in chameleons to a state of a reversal of the sign of the power of the lens and with the cornea now taking on the major role in accommodation.

Increasing the contribution of the cornea to the total refractive power of the eye results in shifting the eye's nodal point forward, to a position frontal to the eye's centre of rotation (the nodal point is the point within the eye through which rays pass without being bent by the lens). This increases the magnification of the retinal image and well separates the nodal point from the axis of rotation of the eye. This is a completely novel design principle that has been described to date only in chameleons and, yet again, in the Sandlance. Moreover, the above design results in the capacity to obtain monocular (motion) parallax cues from eye rotation, without the translation of the animal (when the eye moves, objects at different distances move across the retina at

slightly different speeds, providing a monocular cue for depth discrimination) [60]. This provides the chameleon with the potential capacity to locate prey and disambiguate it from the background, without moving the head or body, an advantage to the stealth, frequently sit-and-wait predatory manner of chameleons.

Along with the aforementioned visual and optical aspects, the processes of accommodation and binocular convergence in the predatory behaviour of chameleons have been studied [24,61]. Accommodation rate (ca. 60 D/sec), amplitude (ca. 45 D, 45 % of the total refractive power of the eye), and precision were found to be superior to other terrestrial vertebrates. Moreover, accommodation was either coupled or uncoupled between the eyes. Coupled accommodation occurred only immediately before tongue strike. Uncoupled accommodation occurred in two situations: (i) During scanning for prey, with one eye accommodated and the contralateral eye remaining in a hyperopic, resting refractive state and with inter-ocular attention switched at ca. 1 Hz; and (ii) During initial distance estimation [61]. Eye direction in a coupled convergence was variable to the state that it could serve to improve precision, but not for matching of corresponding points on the retina, the basic requirement for stereopsis.

3.1. The chameleon's tongue

A central component under the chameleon's strict visual control is its tongue, the individual's unique prey catching mechanism. Once a chameleon has visually detected prey, it moves so as to bring its head and eyes to a position ensuring the execution of the final, explosive, tongue strike (Supplementary movie #2). Tongue strike is most sensitive to distance information and the pre-strike stage of initial protrusion occurs only if prey is at the appropriate distance. If it withdraws, even by a few cm, the tongue is immediately retracted and the eyes switch to visual scanning.

While the use of the tongue to capture prey is common among Iguanian lizards, chameleons are outstanding in their tongue's muscular construction, supportive structures, and performance (Fig. 4). Tongue projection is powered by muscle activity and by elastic recoil, providing peak mass-specific power output that is 2–3 times that achieved by muscle alone. In a strike, the tongue length increases by > 600 % of the resting state, projected distance reaches > 2.15 snout-vent body length of the individual, with maximal acceleration of ca. 490 m s^{-2} and a maximum velocity of ca. 5.8 m s^{-1} . Chameleons can capture large prey (lizards, birds) due to a novel prey prehension mechanism with a suction component and the high viscosity (ca. $\times 400$ times that of human saliva) of the mucus produced at the chameleon's tongue pad [62–64].

4. Threat avoidance: lateralisation and context dependence

The threat avoidance response, described earlier, raises important questions: How precise is the avoidance motion? How fast is it? What are the effects of monocular and binocular viewing of the threat? How well is the body concealed? Is the hiding motion lateralised? Is eye use lateralised (i.e., side dependent/asymmetric at the functional/behavioural levels)? To answer but a few of these, researchers manipulated the direction of an approaching threat (i.e., clockwise or anti-clockwise), the viewing of the threat (i.e., monocular or binocular), and the eye context (role, i.e., leading or following; Fig. 5) [65]. Binocular or monocular viewing was obtained by controlling pole diameter relative to the chameleon's head width. If the pole was wide, only monocular viewing was possible, whereas if the pole was narrow, both monocular and binocular viewing were possible (Fig. 1B, C). Eye use, determined by the duration spent by each eye in viewing the threat and by the frequencies of eye gaze shifts fits three patterns. Under binocular viewing, two of the patterns were side dependent (lateralised) and context dependent, whereas under monocular viewing, no lateralisation was observed (Supplementary Fig. 1) [65].

The abdomen area exposed in the direction of the threat rapidly decreases until only a very narrow strip is visible (Fig. 6). To investigate whether body exposure during threat avoidance is lateralised, changes in ventral surface exposure, in relation to threat approach direction and to viewing (monocular/binocular) were studied [66]. The findings showed that the experimental population comprised a left-biased subgroup and a right-biased subgroup. The left-biased subgroup exhibited a higher decrease in body surface exposure to left approaching threat, weak lateralisation of body exposure under binocular viewing and no lateralisation under monocular viewing. The right-biased subgroup exhibited a greater reduction in body surface exposure to right approaching threat, with strong lateralisation under both monocular and binocular threat viewing (Supplementary movie #4) [67].

Threat avoidance response allowed the investigation of lateralisation of both eye use and simultaneous body motion. The results showed that in the left-biased subgroup, eye use was not lateralised, whereas in the right-biased subgroup, eye use was lateralised under binocular, but not monocular viewing. Overall, the right-biased sub-group determined the lateralisation of the entire group [66].

To explore whether chameleons show lateralisation of eye use and body motion in performing other tasks, chameleons were required to make a left or a right detour of an obstacle in a Y-maze, in order to reach prey. The results showed that eye use was lateralised, with significantly longer durations of viewing the target with the right eye,

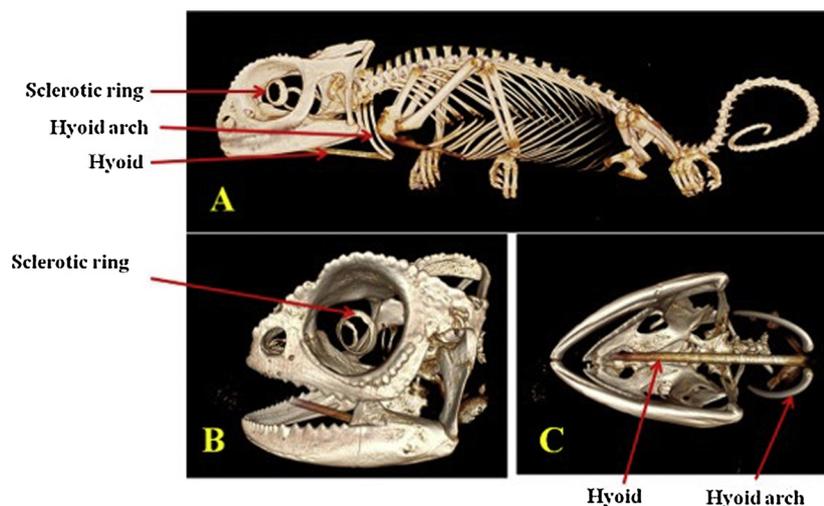


Fig. 4. An MRI of a chameleon (*C. chameleon*) portraying the relative size of the head, the eye orbits and the hyoid apparatus. Courtesy Dr. Inbal Biton and Prof. Alon Harmelin.

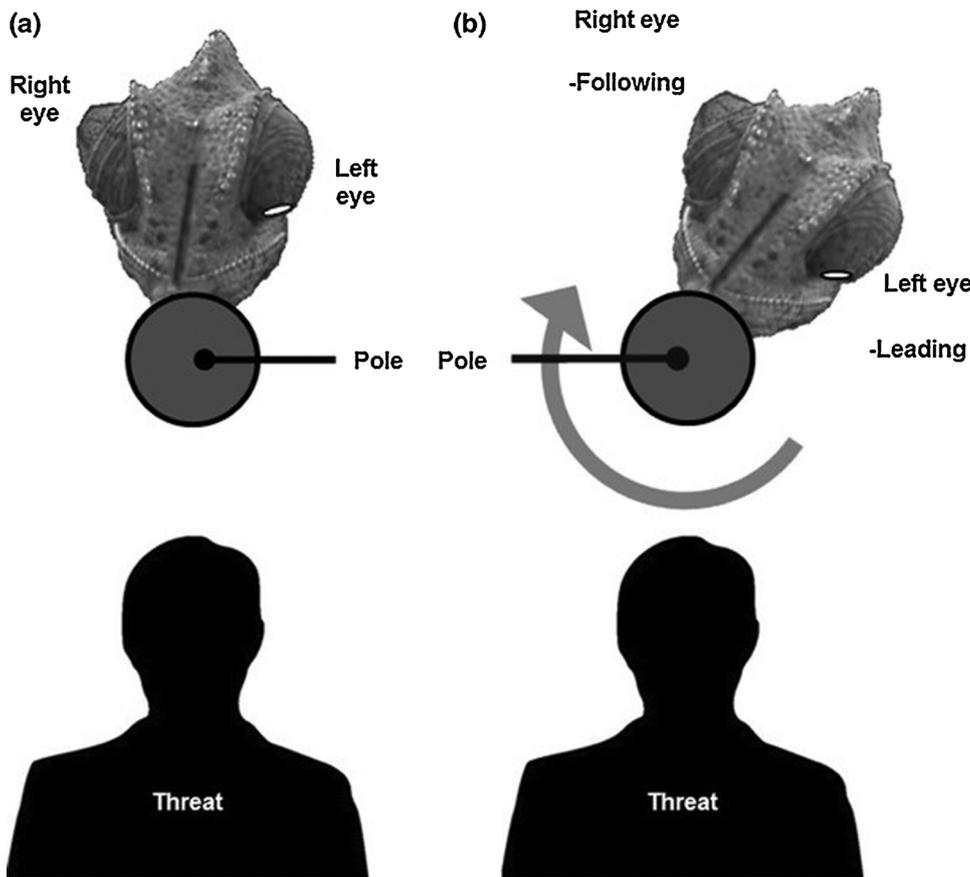


Fig. 5. A scheme of the experimental setup (from overhead) with the chameleon on the vertical pole and the threat (the experimenter or a threatening object). (A) The chameleon is positioned opposite (ca. 180°) the threat, as an initial state, or following position correction with eyes (RE right eye; LE left eye) equidistant from the threat. (B) The relative positions of the chameleon and the threat change by pole rotation, so that one eye (assuming the role of the “Leading Eye”) draws closer to the threat, while the opposite eye (assuming the role of the “Following Eye”) draws away. If the direction of the pole rotation is reversed, the eyes reverse their roles (Lustig, et al. 2012a, *Animal Cognition*, Lustig, et al. 2012b, *PlosOne*; With permission).

compared with the left eye. During left, but not during right side detours, the durations of viewing the target with the right eye were significantly longer than the durations with the left eye [68].

5. Precision of tracking

Animals frequently perform tracking behaviour, such as simultaneous tracking of predators and prey. To avoid image blur during tracking, as in other types of motion, animals keep the image as stable as possible on the retina, using eye, head, and body motion [69,70]. For example, a locust (*Locusta migratoria*) perched on a stem withdraws from an approaching predator by moving to the opposite side of the stem. The locust also withdraws from dark, looming, stimuli. Stimuli that change slow or fast respectively induce slow (< 300°/s) or fast (> 860°/s) hiding movements, with latencies of 0.2–1.2 s. These results may indicate that the locust hiding behaviour is a specific goal-directed type of optomotor behaviour and thus may serve as an image stabilizer [71].

Chameleons perform avoidance responses from hatching (Fig. 7, Supplementary movie #5). How precise is body rotation in avoidance? What are the patterns of body and eye movements? [72]. Avoidance behaviour was tested as described earlier. The chameleons rotated smoothly so that the angle their body formed with the threat was positively and significantly correlated with threat angular position, at angular velocities of up to, and exceeding, 85°/s (Fig. 8A). These rotation values were as accurate, and faster, than the reported tracking by spitting cobras (*Naja nigricollis*) [71,73,74]. The avoidance pattern of the chameleons resembled motion camouflage strategy of dragonflies in which the ‘shadower’ (the dragonfly), imitates the trajectory of a fixed object on the retina of the ‘shadower’ (the prey) [75,76].

A most important aspect was that eye movements were *context-dependent*. In rotation, the leading eye continuously fixated on the threat while the following eye continuously scanned the surroundings

(Fig. 8B). The following eye counter-rotated (see time period between 0 and 640 ms, Fig. 8B), as in smooth tracking, to compensate for the head rotation followed by a saccadic gaze change in the opposite direction, then the leading eye (optomotor response) jumped to follow the threat. This resembles the frequent switching from one mode (smooth or saccade) to another, observed in stomatopod eye-movement [77].

6. Visual tracking of multiple targets

Among vertebrates, marked differences are found in aspects such as the position of the eyes in the skull, eye movements, visual fields, and the underlying neural structures of the visual system. In primates and cats, for example, the eyes are frontal with a high degree of visual fields overlap. However, in most non-mammalian vertebrates (i.e., fish, amphibians, reptiles, and birds) the eyes are laterally placed and show a low degree of visual fields overlap, or no overlap at all [78]. Furthermore, vertebrates vary considerably in their eye movement patterns. Eye movements may be conjugate, with both eyes moving synchronously in the same direction, or disconjugate, with the eyes moving in different directions, asynchronously or synchronously [52]. In primates, eye movements are conjugate with precise alignment of a target on the two foveas, whereas in fish and in birds, eye movements are mostly disconjugate [52]. Such differences raise the question of the ocular control systems that potentially govern monocularly, binocularly and the switch from one to the other (von Helmholtz, 1896 cited in [24,55,60]). Studies of non-mammalian vertebrates suggest that the basic organisation of the oculomotor control system is monocular, with separate motor commands for each eye [24,79–81].

6.1. Are eye movements of chameleons truly ‘independent’?

Eye movements in chameleons are mostly referred to as asynchronous, independent, uncoupled or disconjugate

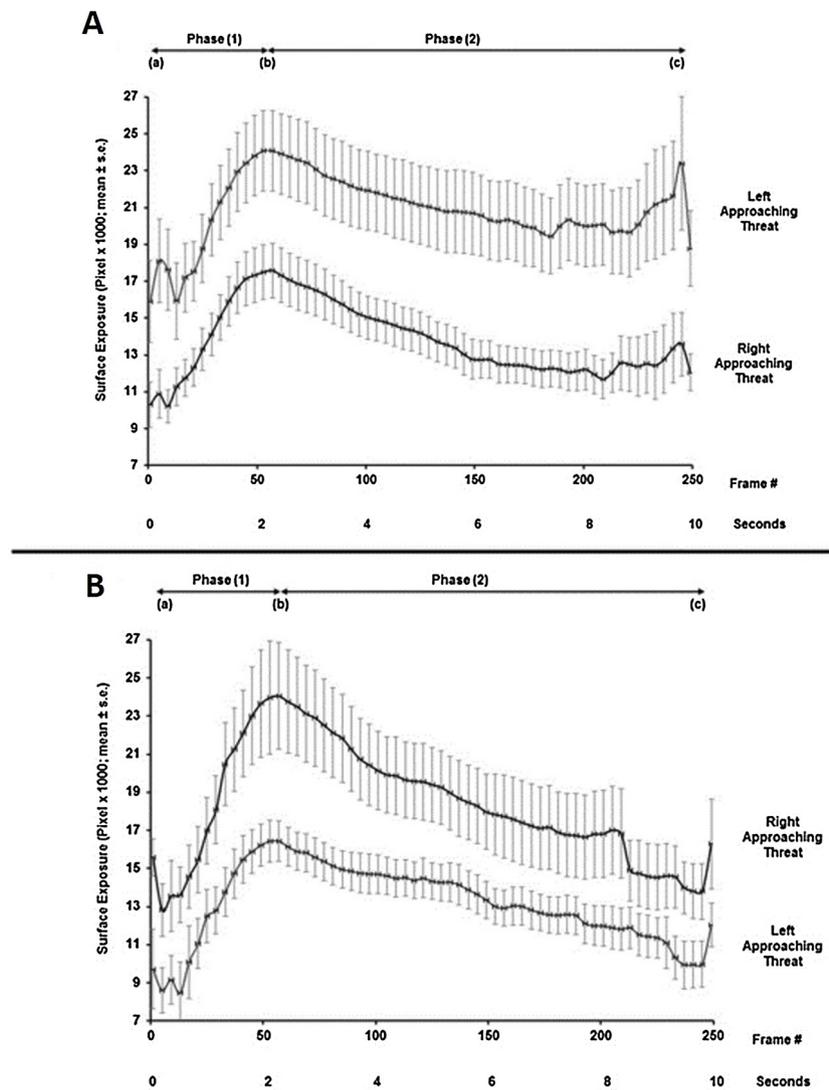


Fig. 6. Avoidance response patterns of the two side-biased groups on a narrow pole. Shown are ventral surface exposure (mean \pm SE) on narrow poles in response to right- or left-approaching threats in chameleons of the right-biased group (A, $N = 14$) and of the left-biased group (B, $N = 10$). Exposure readings are at 200-ms intervals, (a) at the onset of pole rotation, (b) at the end of pole rotation, and (c) at the end of the test (Lustig, et al. 2012, PlosOne; With permission).

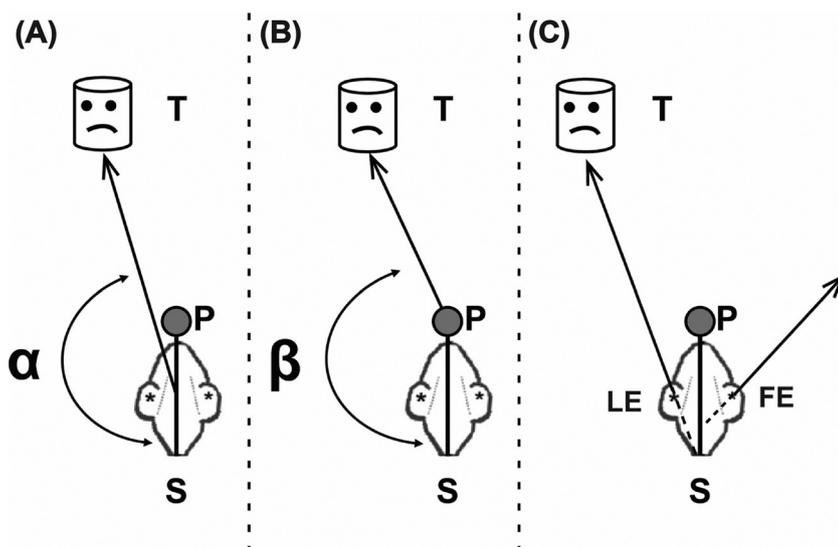


Fig. 7. (A-C), Angular positions of the tested chameleon and the threat (schematic overhead view, threat moving counter-clockwise). (P) - pole. (A) Angle α between the sagittal plane (S) of the chameleon's head and the center of the threat (T). (B) Angle β , between the sagittal plane of the chameleon's head and the line connecting the center of the threat and the center of the pole. (C) An instant during which gaze directed by the left eye (the "leading eye", LE) is on threat and the right eye (the "following eye", FE) - off threat. (D) An overhead view of a just hatched chameleon. Gaze directions: yellow - line of sight of leading eye; red - line of sight of following eye; black - direction of threat. Time - 680 msec from onset of exposure, at angular velocity of $45^\circ/\text{sec}$ (Lev Ari, et al. 2016, Journal of Comparative Physiology; With permission).

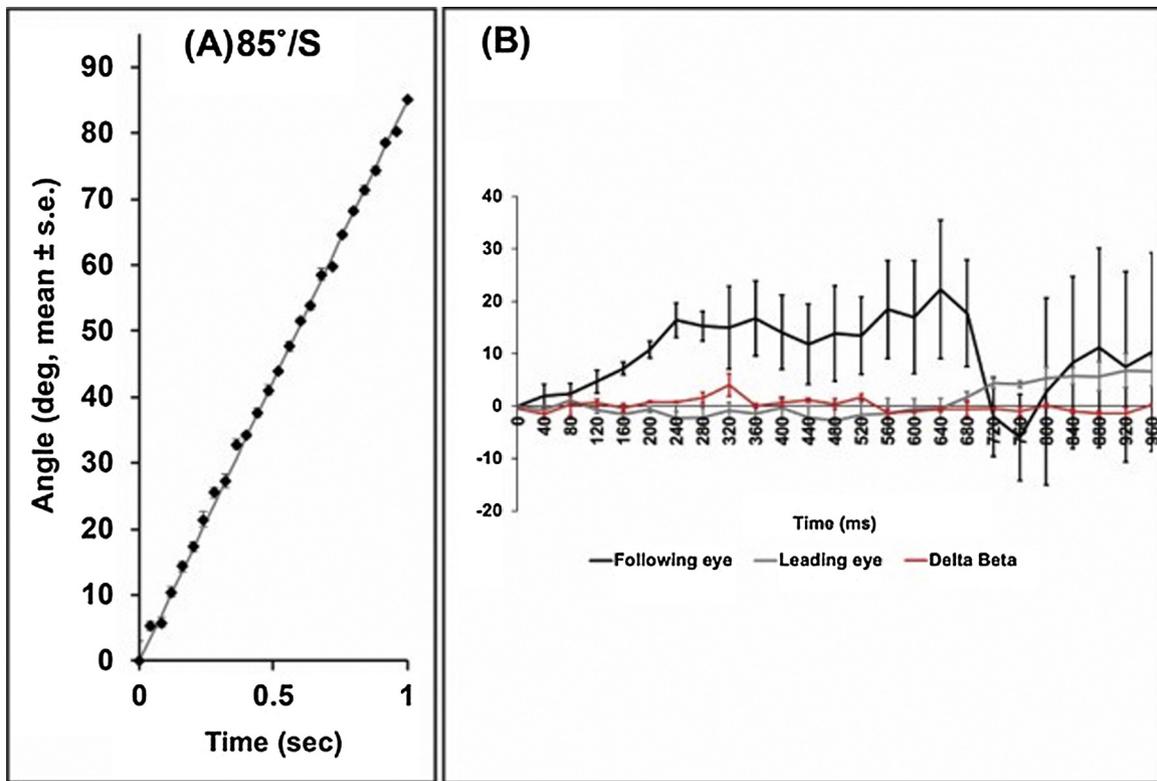


Fig. 8. (A) Avoidance quality: The change in head angle relative to the threat, for threat angular velocity of $85^\circ/\text{s}$ (25 frames, $N = 10$ individuals). Hatched diagonal line - threat position; solid diamonds - $\Delta\beta$. (B) Eye direction and change in angle β ($\Delta\beta$) over three angular velocities (means). The eye patterns are of a smooth phase, with a brief, sharp change of direction at 640 msec (smooth and saccade, Lev Ari, et al. 2016, Journal of Comparative Physiology; With permission).

[2,3,24,51,55,58,82–87], implying an independent motor control for each eye. Similar to other animals with laterally placed eyes and disjunct eye movements, chameleons can simultaneously view two disparate parts of the visual sphere. Each viewed space may contain a moving target that is available only to the respective eye and, if small, may require precise monocular tracking and the need for divided attention. However, knowledge on the capacity among vertebrates to perform simultaneous monocular tracking is lacking.

Von Helmholtz (1896, cited in [24,55,60]) and, more recently, Ott (2001) proposed the operation of two independent premotor neuronal circuits for the left and right eye saccadic motor control [24]. The neuronal coupling of these premotor circuits during eye-head coordination results in binocular coupling in prey tracking. It is possible to learn about the interplay between the command units from the observed switching between coupled and uncoupled saccadic eye movements. Comparable switching between eyes in saccades has been described in the sandlance [55].

How can monocular control of eye movements at the behavioural level be demonstrated? One possibility is to simultaneously present the eyes each with a single, small moving target and determine their capacity to track the targets. Ketter-Katz et al., (2015) used chameleons, *C. chameleon*, as animal models in an attempt to answer this question [88]. Kirmse (1988) tested the ability of chameleons to simultaneously and monocularly track two prey targets moving in opposite directions concluding that chameleons are unable to perform the task [52]. Rather, their gaze alternates, so that when one eye tracks a target, the contralateral eye is idle [79]. In contrast to the above study, Ketter-Katz and colleagues [88] employed the chameleon's distinct pre-capture binocular fixation [2,3,24,83] as a well-defined starting point, to ensure that both eyes were gazing at, and thus were attentive to, the same target at the very onset of each test. It was predicted that the subsequent tracking of the targets would require precise eye motion (e.g., smooth tracking) and division of attention [89].

Can chameleons visually track two targets, simultaneously and monocularly? What are the coarse and fine patterns of the eye movements involved? Do the eyes differ? Chameleons were trained to respond to a digital prey, a small (13×7 mm) black rectangle with two ventral jittering appendages, on a white background [88]. The tested chameleon could approach the screen on a horizontal pole, perpendicular to the screen, and attempt to strike at the target. A positive response comprised the natural predatory sequence: Approaching the target, viewing the target binocularly and performing an IP (Fig. 9A, Supplementary movie #6) [2,24]. At the instant of IP, the target split into two separate targets, identical to the original yet moving horizontally in opposite directions. In response to a single digital, moving target, the eyes converged and remained at an unchanged angle in their orbits while tracking with head movements (Fig. 9C), as towards natural prey [24]. When the target splits into two, the convergent, binocular gaze immediately ceased, and eye direction diverged with each eye tracking the target on its side, leading to an increase in inter-ocular gaze angle (Figs. 9B, D, 10). At a given point, one eye abruptly stopped tracking its target and rapidly converged onto the target on the contralateral side, leading to binocular convergence and IP (Supplementary movie #7). The eyes were consequently termed 'converging eye' and 'tracking eye'. At a finer level, two patterns of gaze shifts were observed, one comprising sequences with minor and one with pronounced gaze shifts. The patterns, respectively termed 'steady' and 'steps' (Fig. 11), share in common aspects of smooth and saccadic tracking [60]. The tracking eye differed from the converging eye in their motion patterns. For example, in the converging eye, the durations of steady events were significantly longer than steps and the frequencies of steady events were lower, compared with the tracking eye (Fig. 12).

A graphic model for context dependence of eye movements in the chameleon (Fig. 13) depicts the chameleon's capacity to switch between different patterns of eye movement, under differing target conditions: (i) While scanning the environment without a specific target,

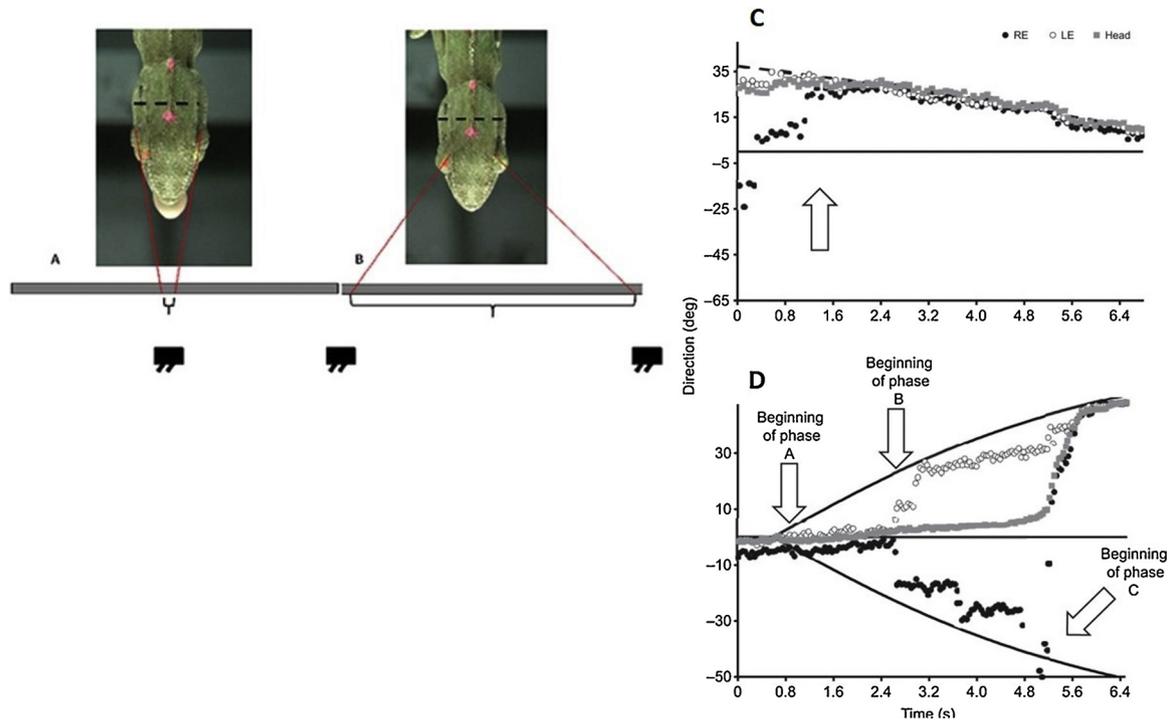


Fig. 9. Eye vergence movements for a single target and for two targets. (A) Eye convergence on a single target. (B) Eye divergence on two targets moving in opposite directions. Red lines- gaze axes; Horizontal hatched bars - head width; Horizontal solid bars - distance between intersection points of the gaze axes (extrapolated) on the screen. An example of the “prey” target is provided beneath each figure. (C) The direction of gaze in a single target test. The instant of eye convergence is depicted by the arrow and is followed by binocular tracking. (D) The direction of gaze in a single diverging target test. Phase A – Begins at the instant of target divergence. Phase B – Begins at the instant of eye divergence. Phase C – Begins at the instant of eye convergence (here the right eye converged towards the left eye). Y axis: origin (0 deg) is the center of screen; positive values – left side, negative values – right side of the screen; hatched lines – target direction; RE – right eye; LE – left eye. (C) A sequence of frames (from left to right, at 160 ms intervals) from a test on diverging targets (DTT). Gaze direction is depicted by the lines running from each eyeball to the screen (S). Initial eye convergence (far left) is followed by gaze divergence (two central frames) and a final convergence (far right, Ketter Katz, et al. 2015, Journal of Experimental Biology; With permission).

chameleons show disconjugate eye movements with large amplitude saccades performed in one eye while the other is unmoving [24,65,86]; (ii) When fixating on a single moving target, the eyes converge binocularly and move in a coordinated manner at the gross level, yet show disconjugate steady and step patterns at the fine level [88]; (iii) When faced with two targets moving in opposite directions, each eye fixates on one target monocularly. The eyes move in a conjugate manner at the gross level and show disconjugate patterns at the fine level. The

frequency and duration of fine eye movements show a high coordination between the two eyes [88]; and (iv) When faced with a moving threat, the body co-rotates with the threat while one eye fixates on the threat (leading eye) and the contralateral eye scans the environment (following eye) [72]. This is yet another support to the notion that eye movements are *context* dependent rather than *side* dependent (Figs. 12 and 13).

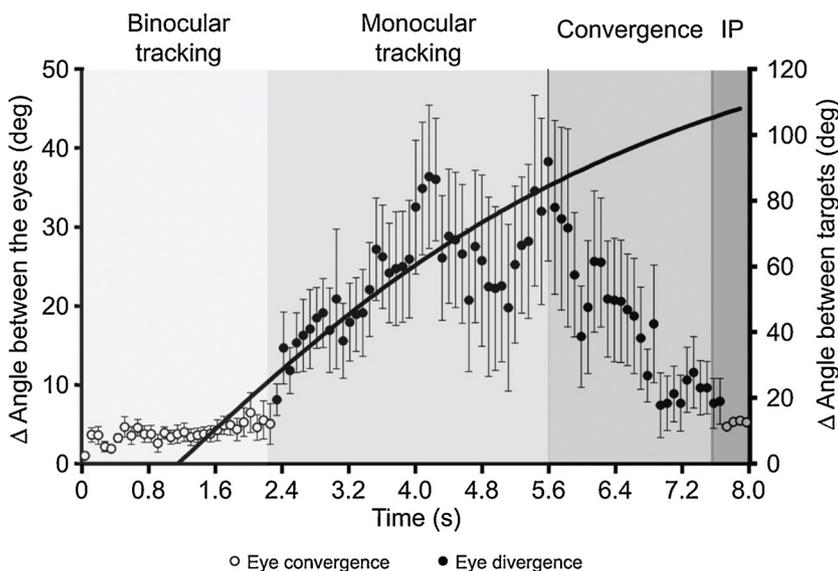


Fig. 10. Eye vergence as a function of angular difference between targets. The figure depicts the absolute magnitude of divergence of the targets (hatched line) and the absolute magnitude of vergence between the eyes (open circles- convergence, solid circles- divergence). Binocular tracking – the period before eye divergence. Monocular tracking – the period from the onset of eye divergence to the onset of eye convergence. Convergence – the period from the beginning of eye convergence until its conclusion. IP – tongue initial protrusion toward one of the targets. Given are mean of means \pm s.e., $n = 7$, 1–4 repetitions per individual (Ketter Katz, et al. 2015, Journal of Experimental Biology; With permission).

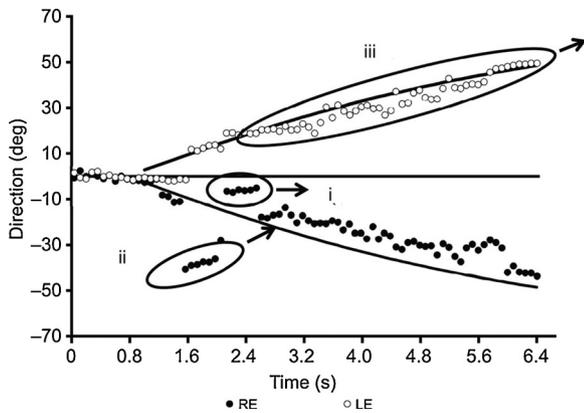


Fig. 11. Shifts in gaze direction. An example of shifts in gaze direction in a DTT. (i) “Unshifted” – the overall direction of gaze does not change, (ii) “Shifting away” – the overall direction of gaze shifts in the direction opposite to that of target motion, (iii) “Shifting with” – the overall direction of gaze shifts in the direction of target motion (Ketter Katz, et al. 2015, Journal of experimental biology).

7. Chameleons as an animal model in vertebrate vision research

Research in different fields portrays chameleons as an important animal model of vision in non-mammalian vertebrates. Why study these exotic reptiles as an animal model? George Mallory, the legendary mountaineer, was once asked: ‘Sir, why did you climb the Everest?’ ‘Because it’s there’ was his reply. Sheer inquisitiveness, the driving force of science, is sufficient. The need to know how other vertebrates are built and how they function, is enough to embark on their study.

Chameleons evolved an array of unique features of colour, shape, motor, and sensory-visual structures and functions related to their ecology. One obvious scientific benefit of the ‘It is unique - study it!’ approach is the probability to encounter novel phenomena and mechanisms that evolved under unstudied selection pressures. One can safely assume that some of the more influential studies of vision in chameleons had begun with this approach that subsequently yielded a rich mine of phenomena and principles. One such case is the study of chameleons’ optics (Table 1).

Visual adaptations of chameleons to arboreal habitats pertain mainly to colour production, changes and perception (not discussed in the present paper). These include a unique integumental colour producing mechanism, and a complex retinal colour perception system. Visual adaptations to insectivory are expressed in eye optics [58,59], eye movements [2,51,82,83,86,87], visual/behavioural processes [3,24,61], and visuo-motor predatory tongue strikes [59]. Optics of

chameleons’ eyes are especially interesting, as they combine an accommodating cornea and a negatively powered lens that overall produce a ‘telephoto eye’. Eye movements of chameleons are extensive and complex. They are not independent [65–67,72,88] but context dependent, well controlled, with each eye potentially operating separately or jointly, with a capacity for inter-ocular switching [55].

The above features enable a thorough examination of ocular performance, to much higher levels than can be achieved with other reptiles, ectotherms or vertebrates in general. Through studying eye movements in chameleons, one can achieve deeper insights into monocular/binocular information processing, attention (through accommodation), and control.

The motion patterns of the eyes and the body, both under threat and in predation, are lateralised. Moreover, lateralisation is context dependent, affected by variety of factors and their interactions. These include origin (left lateralised / right lateralised sub-populations), viewing conditions (monocular / binocular) and derived context (following vs. leading, tracking vs. converging) [12,14,38]. This is a new way of looking at decision making dynamics [90] and raises important questions as to the functional aspects of dynamics of lateralisation in visuo-motor patterns.

A most important aspect to consider relates to the central nervous system (CNS). The CNS of chameleons is anatomically and physiologically similar to other ectotherms, in general, and to reptiles in particular. It differs from the CNS of mammals in many ways. One such feature is the full decussation of the optic nerve at the optic chiasma. This implies that virtually all information from a given eye is first transferred and analysed in the contralateral brain. The evolution of decussation is an open issue. Larsson (2011) presented an ‘eye forelimb’ hypothesis that ‘alteration in the optic chiasma influence the length of neural pathways that transmit visual information...to nuclei involved in forelimb coordination’ [37,91,92]. Chameleons, with their unique visual system and ocular capacities are the prime group to experimentally address such questions.

While chameleons are ‘exotic’, they may well be the better animal model for answering questions such as: What determines laterality at a given task? What drives decisions? What drives context dependency? How does attention affect decisions? [93,94]. It will be of interest to study such questions in chameleons using electrophysiological methods such as single cell analysis methods. These could shed light on questions such as: What are the patterns of activity of the optic tecta in response to monocular and to binocular stimuli? What are the levels of connection between hemispheres and visual areas? What are the patterns of tectal excitation related to lateralization? One may consider cell-level decision making of motion and in the Archerfish (*Toxotes* spp.; [95]) as models for future chameleon investigations. Archerfish shoot water jets to down aerial insects. The fish needs to calculate rapidly where the

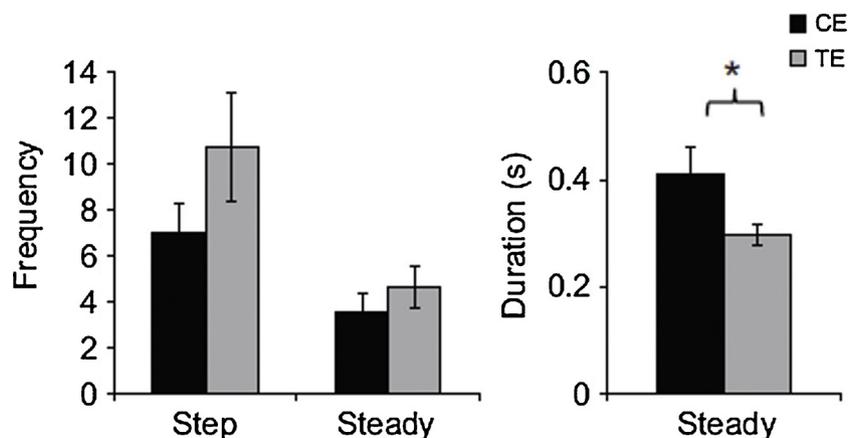


Fig. 12. Fine patterns of eye motion according to eye role. The figure showing differences between the converging eye (CE) and the tracking eye (TE) in the frequency of ‘step’ and ‘steady’ and in the duration of ‘steady’ (Ketter Katz, et al. 2015, Journal of Experimental Biology; With permission).

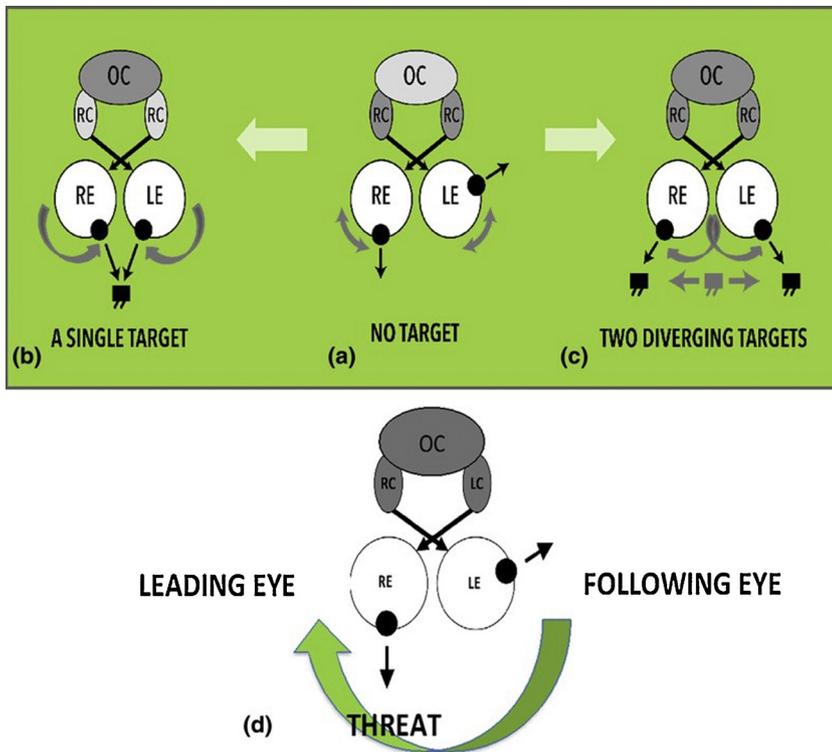


Fig. 13. A model for context dependence of eye movements in the chameleon. (A) Scanning the environment with no specific target, (B) Fixating on a single moving target, (C) Two targets moving in opposite directions, (D) A moving threat. RE right eye, LE left eye, RC right eye motor control, LC left eye motor control, OC overall motor control; solid rectangle, prey. Low and high levels of activation of the motor controls are depicted by light and dark gray, respectively; gray arrows indicate eye movements, black arrows indicate gaze direction (Lev Ari, et al. 2016, *Journal of Comparative Physiology*; With permission).

insect will fall onto the water surface, and reach that point ahead of nearby conspecifics. The decisions as to the fish motion are based on rapid retinal computations performed by populations of directionally selective ganglion cells (see also decision making at the cellular level in Zebrafish) [96].

8. Conclusions

Chameleons (Reptilia, Chamaeleonidae) have evolved an array of extreme morphological, optical, motor and visual-motor adaptations related to their arboreal living and unique prey capture. Most of these adaptations are shared by no other, or very few vertebrates. Chameleons can therefore serve as the most suitable animal models in vision research in aspects such as lateralisation, ocular movements, binocularity, decision making, context dependence, and related topics.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Yossi Baydach for initiating the field observations on chameleons and for making us fall in love with these 'friends from outer space', to Dr. Avichai Lustig, for his major contributions to the research, to Dr. Inbal Biton and Prof. Alon Harmelin for all their support and the use of the MRI system, to Nina Dinov and the staff of the Oranim Campus (University of Haifa) for all their help over the years. The chameleon research was supported by ISF grant to GK.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.semcd.2020.05.009>.

References

- [1] K.A. Tolley, M. Menegon, *Evolution and biogeography of chameleons*, Biol. Chameleons, Univ of California Press, 2013, pp. 131–151.
- [2] M. Flanders, Visually guided head movement in the African chameleon, *Vision Res.* 25 (1985) 935–942.
- [3] L. Harkness, Chameleons use accommodation cues to judge distance, *Nature.* 267 (1977) 346–349.
- [4] D. Souto, D. Kerzel, Dynamics of attention during the initiation of smooth pursuit eye movements, *J. Vis.* 8 (2008) 1–16.
- [5] M. Cuadrado, J. Martián, P. Loápez, Camouflage and escape decisions in the common chameleon *Chamaeleo chamaeleo*, *Biol. J. Linn. Soc. Lond.* 72 (2001) 547–554.
- [6] T.E. Higham, C.V. Anderson, *Function and adaptation of chameleons*, Biol. Chameleons, Univ of California Press, 2013, pp. 63–68.
- [7] D. Stuart-Fox, *Chameleon behavior and color change*, Biol. Chameleons, Univ of California Press, 2013, pp. 115–131.
- [8] J. Teyssier, S.V. Saenko, D. Van Der Marel, M.C. Milinkovitch, Photonic crystals cause active colour change in chameleons, *Nat. Commun.* 6 (2015).
- [9] N. Tinbergen, *The Study of Instinct*, Clarendon Press/Oxford University Press, New York, NY, US, 1951.
- [10] S.C. Neuhauss, Zebrafish vision: structure and function of the zebrafish visual system, *Fish Physiol. Biochem.* 29 (2010) 81–122.
- [11] J. Wittbrodt, A. Shima, M. Schartl, *Medaka - A model organism from the Far East*, *Nat. Rev. Genet.* 3 (2002) 53–64.
- [12] M. El Hassni, S. Ba M'hamed, J. Repé Rant, M. Bennis, Quantitative and topographical study of retinal ganglion cells in the Chameleon (*Chamaeleo chamaeleo*), *Brain Res. Bull.* 44 (1997) 621–625.
- [13] M. Bennis, R.S. Molday, C. Versaux-Botteri, J. Repérant, J.C. Jeanny, D.S. McDevitt, Rhodopsin-like immunoreactivity in the "all cone" retina of the chameleon (*Chamaeleo chamaeleo*), *Exp. Eye Res.* 80 (2005) 623–627.
- [14] J.K. Bowmaker, E.R. Loew, M. Ott, The cone photoreceptors and visual pigments of chameleons, *J. Comp. Physiol. A* 191 (2005) 925–932.
- [15] D.M. Hunt, S.E. Wilkie, J.K. Bowmaker, S. Poopalasundaram, Vision in the ultraviolet, *Cell. Mol. Life Sci.* 58 (2001) 1583–1598.
- [16] D. Stuart-Fox, A. Mousallil, Camouflage, communication and thermoregulation: lessons from colour changing organisms, *Philos. Trans. R. Soc. B Biol. Sci.* 364 (2009) 463–470.
- [17] J.K. Bowmaker, Evolution of colour vision in vertebrates, *Eye.* 12 (1998) 541–547.
- [18] N.S. Hart, The visual ecology of avian photoreceptors, *Prog. Retin. Eye Res.* 20 (2001) 675–703.
- [19] M.W. Wright, J.K. Bowmaker, Retinal photoreceptors of paleognathous birds: The ostrich (*Struthio camelus*) and rhea (*Rhea americana*), *Vision Res.* 41 (2001) 1–12.
- [20] E.R. Loew, L.J. Fleishman, R.G. Foster, I. Provencio, Visual pigments and oil droplets in diurnal lizards, *J. Exp. Biol.* 205 (2002).
- [21] E. Loew, L.J. Fleishman, M. Bowman, D. Saunders, W.E. Miller, M.J. Rury, E.R. Loew, The visual ecology of Puerto Rican anoline lizards: habitat light and spectral sensitivity, *Artic. J. Comp. Physiol.* 181 (1997) 446–460.
- [22] M. Persons, L. Fleishman, M. Frye, Sensory response patterns and the evolution of signal design in anoline lizards Predation risk View project Multisensory integration

- View project, *Artic. J. Comp. Physiol.* 184 (1999) 585–607.
- [23] N.S. Hart, Variations in cone photoreceptor abundance and the visual ecology of birds, *J. Comp. Physiol. A* 187 (2001) 685–697.
- [24] M. Ott, Chameleons have independent eye movements but synchronise both eyes during saccadic prey tracking, *Exp. Brain Res.* 139 (2001) 173–179.
- [25] B. Bellintani-Guardia, M. Ott, Displaced retinal ganglion cells project to the accessory optic system in the chameleon (*Chamaeleo calytratus*), *Exp. Brain Res.* 145 (2002) 56–63, <https://doi.org/10.1007/s00221-002-1091-z>.
- [26] M. Bennis, M. El Hassni, J.-P. Rio, D. Lecren, J. Repérant, W. Roger, A quantitative ultrastructural study of the optic nerve of the Chameleon, *Brain Behav. Evol.* 58 (2001) 49–60.
- [27] G.L. Walls, *The Vertebrate Eye and its Adaptative Radiation*, Cranbook Inst. Sci, MI, 1942.
- [28] S.T.D. New, J.M. Hemmi, G.D. Kerr, C.M. Bull, Ocular anatomy and retinal photoreceptors in a skink, the sleepy lizard (*Tiliqua rugosa*), *Anat. Rec.* 295 (2012) 1727–1735.
- [29] C.A. Curcio, K.R. Sloan, R.E. Kalina, A.E. Hendrickson, Human photoreceptor topography, *J. Comp. Neurol.* 292 (1990) 497–523.
- [30] B.L. Finlay, E.C.S. Franco, E.S. Yamada, J.C. Crowley, M. Parsons, J.A.P.C. Muniz, L.C.L. Silveira, Number and topography of cones, rods and optic nerve axons in New and Old World primates, *Vis. Neurosci.* 25 (2008) 289–299.
- [31] S.W. L, D.H. Robert, Fox, Falcon visual acuity, *AAAS* 192 (1976) 263–265.
- [32] S.T.D. New, C.M. Bull, Retinal ganglion cell topography and visual acuity of the sleepy lizard (*Tiliqua rugosa*), *J. Comp. Physiol. A Neuroethol. Sensory Neural Behav. Physiol.* 197 (2011) 703–709.
- [33] R.J.G. Kare M.R, *Avian physiology, Sense Organs*, Springer, Berlin, Heidelberg, 1976, pp. 29–52.
- [34] A. Querubin, R.L. Hie, J.M. Provis, K.M. Bumsted O'Brien, Photoreceptor and ganglion cell topographies correlate with information convergence and high acuity regions in the adult pigeon (*Columba livia*) retina, *J. Comp. Neurol.* 517 (2009) 711–722.
- [35] C.A. Curcio, K.A. Allen, Topography of ganglion cells in human retina, *J. Comp. Neurol.* 300 (1990) 5–25.
- [36] T. Shimizu, T. Patton, A.B. Butler, Evolution of the visual system in reptiles and birds, *Sea* 161 (2009) 5–24.
- [37] M.L. Larsson, Binocular vision, the optic chiasm, and their associations with vertebrate motor behavior, *Front. Ecol. Evol.* 3 (2015).
- [38] M. Bennis, J. Repérant, J.P. Rio, R. Ward, An experimental re-evaluation of the primary visual system of the European chameleon, *Chamaeleo chamaeleo*, *Brain. Behav. Evol.* 43 (1994) 173–188.
- [39] U. an der Heiden, G. Roth, Mathematical model and simulation of retina and tectum opticum of lower vertebrates, *Acta Biotheor.* 36 (1987) 179–212.
- [40] F. Goldby, H.J. Gamble, The reptilian cerebral hemispheres, *Biol. Rev.* 32 (1957) 383–420.
- [41] W.M. Shanklin, The central nervous system of *Chamaeleo vulgaris*, *Acta Zool.* 11 (1930) 425–490.
- [42] E.I. Knudsen, Neural circuits that mediate selective attention: a comparative perspective, *Trends Neurosci.* 41 (2018) 789–805.
- [43] M. Bennis, J. Reperant, R. Ward, M. Wasowicz, Topography of the NADPH-dia-phorase system in the chameleon brain, *J. Hirnforsch.* 37 (1996) 281–288.
- [44] R.W. Guillery, Anatomical evidence concerning the role of the thalamus in cortico-cortical communication: a brief review, *J. Anat.* 187 (1995) 583–592.
- [45] T. Lev-Ari, H. Ketter Katz, A. Lustig, G. Katzir, H.K. Katz, Visual acuity and opto-kinetic directionality in the Common chameleon (*Chamaeleo chamaeleo*), *EC Ophthalmol.* 6 (2017) 145–154.
- [46] M. Land, J. Layne, The visual control of behaviour in fiddler crabs, *J. Comp. Physiol. A* 177 (1995) 91–103.
- [47] S. Bartol, J.A. Musick, A.L. Ochs, Visual acuity thresholds of juvenile loggerhead sea turtles (*Caretta caretta*): an electrophysiological approach, *J. Comp. Physiol. A* 187 (2002) 953–960.
- [48] R.A. Baker, T.J. Gawne, M.S. Loop, S. Pullman, Visual acuity of the midland banded water snake estimated from evoked telencephalic potentials, *J. Comp. Physiol. A* 193 (2007) 865–870.
- [49] D.P.M. Northmore, A.M. Granda, Ocular dimensions and schematic eyes of fresh-water and sea turtles, *Vis. Neurosci.* 7 (1991) 627–635.
- [50] S.T.D. New, C.M. Bull, Retinal ganglion cell topography and visual acuity of the sleepy lizard (*Tiliqua rugosa*), *J. Comp. Physiol. A* 197 (2011) 703–709.
- [51] E.S. Tauber, A. Atkin, Optomotor responses to monocular stimulation: relation to visual system organization, *Science* 80- (160) (1968) 1365–1367.
- [52] K.A. Fritsches, N.J. Marshall, Independent and conjugate optokinetic in fish, *J. Exp. Biol.* 205 (2002) 1241–1252.
- [53] J. Wallman, J. Velez, Directional asymmetries of optokinetic nystagmus: developmental changes and relation to the accessory optic system and to the vestibular system, *J. Neurosci.* 5 (1985) 317–329.
- [54] H. Collewijn, Direction-selective units in the rabbit's nucleus of the optic tract, *Brain Res.* 100 (1975) 489–508.
- [55] J.D. Pettigrew, S.P. Collin, M. Ott, Convergence of specialised behaviour, eye movements and visual optics in the sandlance (Teleostei) and the chameleon (Reptilia), *Curr. Biol.* 9 (1999) 421–424.
- [56] M.S. DeVries, E.A.K. Murphy, S.N. Patek, Strike mechanics of an ambush predator: the spearing mantis shrimp, *J. Exp. Biol.* 215 (2012) 4374–4384.
- [57] G. Katzir, N. Intrator, Striking of underwater prey by a reef heron, *Egretta gularis schistacea*, *J. Comp. Physiol. A* 160 (1987) 517–523.
- [58] M. Ott, F. Schaeffel, A negatively powered lens in the chameleon, *Nature* 373 (1995) 692–694.
- [59] J.D. Pettigrew, S.P. Collin, J.D. Penigrew, Terrestrial optics in an aquatic eye: the sandlance, *Limnichthyes fasciatus* (Creediidae, Teleostei), *J. Comp. Physiol. A* 177 (1995) 397–408.
- [60] M.F. Land, Visual optics: the sandlance eye breaks all the rules, *Curr. Biol.* 9 (1999) 286–288.
- [61] M. Ott, F. Schaeffel, W. Kirmse, Binocular vision and accommodation in prey-catching chameleons, *J. Comp. Physiol. A* 182 (1998) 319–330.
- [62] F. Brau, D. Lanterbecq, L.N. Zghikh, V. Bels, P. Damman, Dynamics of prey prehension by chameleons through viscous adhesion, *Nat. Phys.* 12 (2016) 931–935.
- [63] P.C.W. Wright, D.M. Kraklau, A.F. Bennett, Kinematics of tongue projection in *Chamaeleo oustaleti*, *J. Exp. Biol.* 159 (1991) 109–133.
- [64] A. Herrel, Mechanics of prey prehension in chameleons, *J. Exp. Biol.* 203 (2000) 3255–3263.
- [65] A. Lustig, H. Ketter-Katz, G. Katzir, Threat perception in the chameleon (*Chamaeleo chamaeleo*): evidence for lateralized eye use, *Anim. Cogn.* 15 (2012) 609–621.
- [66] A. Lustig, H. Ketter-Katz, G. Katzir, Relating lateralization of eye use to body motion in the avoidance behavior of the Chameleon (*Chamaeleo chamaeleo*), *PLoS One* 8 (2013).
- [67] A. Lustig, H. Ketter-Katz, G. Katzir, Visually guided avoidance in the chameleon (*Chamaeleo chamaeleo*): response patterns and lateralization, *PLoS One* 7 (2012).
- [68] A. Lustig, H. Ketter-Katz, G. Katzir, Lateralization of visually guided detour behaviour in the common chameleon, *Chamaeleo chamaeleo*, a reptile with highly independent eye movements, *Behav. Processes* 100 (2013) 110–115.
- [69] J. Wallman, J. Letelier, H.P. Zeigler, H.J. Bischof (Eds.), *Vision, Brain and Behavior in Birds*, MIT Press, Mass, 1993, pp. 245–264.
- [70] M.F. Land, Eye movements of vertebrates and their relation to eye form and function, *J. Comp. Physiol. A* 201 (2014) 195–214.
- [71] B. Hassenstein, R. Hustert, Hiding responses of locusts to approaching objects, *J. Exp. Biol.* 202 (1999) 1701–1710.
- [72] T. Lev-Ari, A. Lustig, H. Ketter-Katz, Y. Baydach, G. Katzir, Avoidance of a moving threat in the common chameleon (*Chamaeleo chamaeleo*): rapid tracking by body motion and eye use, *J. Comp. Physiol. A* 202 (2016) 567–576.
- [73] G. Westhoff, M. Boetig, H. Bleckmann, B.A. Young, Target tracking during venom “spitting” by cobras, *J. Exp. Biol.* 213 (2010) 1797–1802.
- [74] S. Sponberg, J.P. Dyhr, R.W. Hall, T.L. Daniel, Luminance-dependent visual processing enables moth flight in low light, *Science* 80- (348) (2015) 1245–1248.
- [75] M.V. Srinivasan, M. Davey, Strategies for active camouflage of motion, *Ser. B Biol. Sci.* 259 (1995) 19–25.
- [76] A. Mizutani, J.S. Chahl, M.V. Srinivasan, Insect behaviour motion camouflage in dragonflies, *Nature* 423 (2003) 604.
- [77] N.J. Marshall, M.F. Land, T.W. Cronin, Shrimps that pay attention: saccadic eye movements in stomatopod crustaceans, *Philos. Trans. Biol. Sci.* 369 (2014) 20130042.
- [78] G. Jeffery, L. Erskine, Variations in the architecture and development of the vertebrate optic chiasm, *Prog. Retin. Eye Res.* 4 (2005) 721–775.
- [79] W. Kirmse, Foveal and ambient visuomotor control in chameleons (Squamata). Experimental results and comparative review, *Zool. Jahrbücher. Abteilung Für Allg. Zool. Und Physiol. Der Tiere.* 92 (1988) 341–350.
- [80] J. Wallman, J.D. Pettigrews, Conjugate and disjunctive saccades in two avian species with contrasting oculomotor strategies, *Journal Neurosci.* 5 (1985) 1418–1428.
- [81] G.L. Walls, The evolutionary history of eye movements, *Vision Res.* 2 (1962) 69–80.
- [82] J.W.B. Mates, Eye movements of African chameleons: spontaneous saccade timing, *Science* (80-) 199 (1978) 1087–1089.
- [83] M. Flanders, Head movement co-ordination in the African chameleon, *Neuroscience* 24 (1988) 511–517.
- [84] M. Ott, F. Schaeffel, W. Kirmse, Binocular vision and accommodation in prey-catching chameleons, *J. Comp. Physiol. A* 182 (1998) 319–330.
- [85] P.S. Sándor, M.A. Frens, V. Henn, Chameleon eye position obeys Listing's law, *Vision Res.* 41 (2001) 2245–2251.
- [86] M.A. Frens, A.D. Van Beuzekom, P.S. Sándor, V. Henn, Binocular coupling in chameleon saccade generation, *Biol. Cybern.* 78 (1998) 57–61.
- [87] W. Kirmse, R. Kirmse, E. Milev, Visuomotor operation in transition from object fixation to prey shooting in chameleons, *Biol. Cybern.* 3 (1994) 209–214.
- [88] H.K. Katz, A. Lustig, T. Lev-Ari, Y. Nov, E. Rivlin, G. Katzir, Eye movements in chameleons are not truly independent - Evidence from simultaneous monocular tracking of two targets, *J. Exp. Biol.* 218 (2015) 2097–2105.
- [89] R. Dukas, A.C. Kamil, Limited attention: the constraint underlying search image, *Behav. Ecol.* 12 (2001) 192–199.
- [90] Q. Lin, J. Manley, M. Helmreich, F. Schlumm, J.M. Li, D.N. Robson, F. Engert, A. Schier, T. Nöbauer, A. Vaziri, Cerebellar neurodynamics predict decision timing and outcome on the single-trial level, *Cell.* 180 (2020) 536–551 e17.
- [91] M. Larsson, Binocular vision and ipsilateral retinal projections in relation to eye and forelimb coordination, *Brain Behav. Evol.* 77 (2011) 219–230.
- [92] M. Larsson, The optic chiasm: a turning point in the evolution of eye/hand co-ordination, *Front. Zool.* 10 (2013) 41.
- [93] M. Roussigné, P. Blader, S.W. Wilson, Breaking symmetry: the zebrafish as a model for understanding left-right asymmetry in the developing brain, *Dev. Neurobiol.* 72 (2012) 269–281.
- [94] J.M. Fadool, J.E. Dowling, Zebrafish: a model system for the study of eye genetics, *Prog. Retin. Eye Res.* 27 (2008) 89–110.
- [95] V. Tsvilling, O. Donchin, M. Shamir, R. Segev, Archer fish fast hunting maneuver may be guided by directionally selective retinal ganglion cells, *Eur. J. Neurosci.* 35 (2012) 436–444.
- [96] Q. Lin, J. Manley, M. Helmreich, A. Schier, T. No, Q. Lin, J. Manley, M. Helmreich, F. Schlumm, J.M. Li, D.N. Robson, Cerebellar neurodynamics predict decision timing and outcome on the single-trial level, *Cell* 180 (2020) 536–551.