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Research Article

Visual Acuity and Optokinetic Directionality in the Common Chameleon (*Chamaeleo chamaeleon*)

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Abstract

Chameleons (*Chamaeleo* spp.) use vision in prey capture and in predator avoidance. They scan the environment with large amplitude, "independent", eye movements and once a target has been sighted the eyes converge to a binocular fixation. To precisely determine target distance, chameleons uniquely employ accommodation effort of their negatively powered lenses. Our research aimed at determining the visual acuity of the common chameleon, *Chamaeleo chameleon*. Behavioral visual acuity, as determined by optomotor (OMR) and optokinetic (OKR) responses, was ca. 9 cycles pre-degree (CPD) in mature and ca. 5 CPD in newly hatched individuals. Acuity was positively correlated with eye size. Responses to stimulus motion in the temporo- nasal (TN) direction were more pronounced compared with stimulus motion in the naso-temporal direction (NT). Overall the results from OKR were more reliable compared with OMR.

Keywords: *Visual Acuity; Tracking; Chameleons; Naso-Temporal/Tempro- Nasal; Eye Size*

Abbreviations

RE: Right Eye; LE: Left Eye; TN: Temporo-Nasal; NT: Naso-Tempral; OKR: Optokinetic Response; OMR: Optomotor Response; CW: Clockwise; CCW: Counterclockwise; CPD: Cycles Per Degree

Introduction

Visual acuity, the capacity of the visual system to resolve spatial detail [1], is dependent on the optical quality of the eye, on eye size and on receptor density. Because photoreceptor minimal diameter is limited by wavelength, resolution can be improved by increasing the focal length through increased eye size [2]. Acuity can be determined behaviorally by analyzing visually elicited motor reflexes of the eyes and/or of the body. Many animals respond to a moving pattern of alternating, high contrast, bars or spots, by a patterned motion such as the optomotor (OMR) and the optokinetic reflexes (OKR) that pertain respectively to body motion and to eye movements. OMR is observed, for example, when a fish swims in circles in response to a pattern of black and white vertical bars moved horizontally in a circle [3]. In OKR, the eyes follow a moving pattern of high contrast bars or spots with alternating smooth (slow) tracking and fast, saccade-like resetting of the eyes [4-6]. By gradually increasing stimulus frequency (i.e. reducing subtending angle of each bar) a point is reached at which the animal fails to respond, indicating its limit of perception [4]. Because OKR and OMR are innate, robust reflexes they have been widely used to determine visual capacities such as contrast sensitivity [7,8] color discrimination [3,9,10] and visual acuity [11,12] in different species.

While OKR may be observed when stimulus motion is either the temporo-nasal (TN) or in the naso-temporal (NT) direction, the former elicits higher responses compared with the latter [13]. This directional sensitivity may stem from the need to prevent stimulation by translational movements during forward locomotion [14]. OKR sensitivity to rotational movements of head and body in the TN direction can also help in maximizing gaze stabilization [15].

Chameleons (Chamaeleonidae, Reptilia) depend on vision to catch prey and to avoid predators [16]. They are slow moving and regularly scan their environment using large amplitude, disconjugate eye movements [17-20]. In predation, their tongue is struck at speeds of ca. 5 m/s [21] and prey is captured by the tongue tip [22]. Chameleons are unique in their capacity to precisely judge target distance monocularly, using accommodation effort of their negatively powered lens [17,20,21] that enlarges the retinal image. For example, in *Chamaeleo dilepis*, the retinal image is 15% larger compared with that of the chicken (*Gallus gallus domesticus*) for similar axial lengths [23].

Here we aimed to determine (1) the behavioral visual acuity of the common chameleon, (2) the relationships between visual acuity and eye size, (3) differences between OMR and OKR (4) differences in response between in TN and NT stimulus motion.

Methods

We tested common chameleons of two age groups: Mature individuals (ca. 1 year or older) and newly hatched (ca. one month old). We measured external eye diameter using calibrated photographs. External eye diameter (Figure 2) of matures was 10.1 ± 0.6 mm (mean ± SE., N = 12) and 3.3 ± 0.13 mm in the juveniles (N = 10). The experimental apparatus (Figure 1) comprised a rotatable drum, on the inner wall of which a pattern of alternating, high contrast (74%) black and white vertical gratings could be displayed. Drum radius was 68cm for OMR tests, and 46.5 cm or 68 cm for OKR tests. Bar width was 2, 1 or 0.5 mm providing 2.6, 5.2, 10.3 cycles per degree (CPD) for the OMR tests and four different 3, 5.9, 8.3, 11.9 CPD for OKR test. The drum was illuminated from above four light bulbs (Sunlight Compact electronic fluorescent lamp, daylight 2750lm = 225W), providing > 1800 lux (Yokogawa type 3281 light meter). A video camera (Panasonic NV-GS500) perpendicular and above the center of the drum and connected to a Sony monitor (KV-1484MT) provided the on-line imaging and recording of the tested chameleon. Room temperature was kept at 26°C - 28°C.

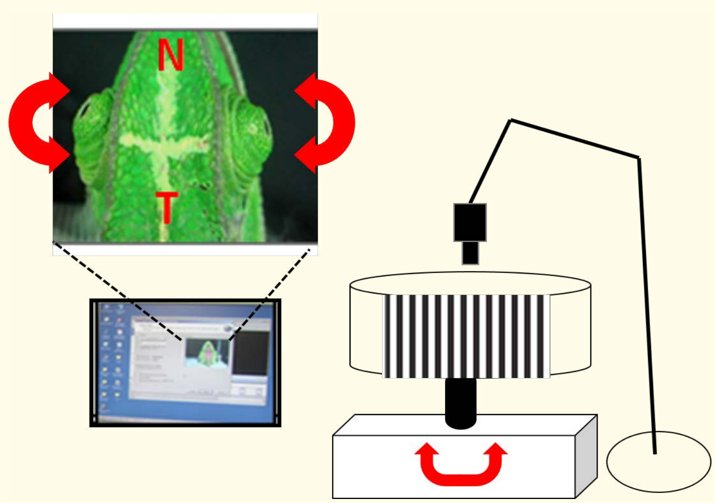

Figure 1: *A schematic of the experimental setup used to test OMR and OKR (not to scale). N= nasal, T= temporal, red arrow - the direction of rotation CW or CCW.*

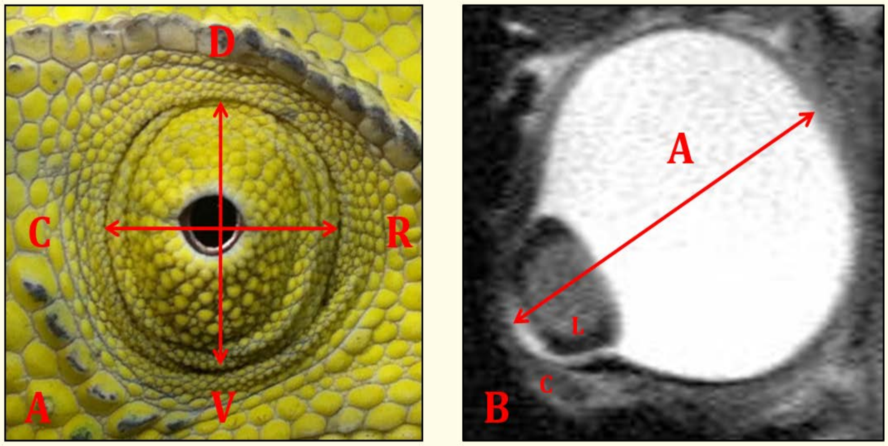

Figure 2: *Eye size measurement (marked with a red arrow). (1) External eye diameter (1), dorsal (D), ventral (V), caudal (C), rostral (R). (2) Coronal image from an MRI scene, showing the axial (A) length of a chameleon eye.*

In OMR tests a chameleon was placed in a circular transparent, stationary arena, 18 cm in diameter, at the center of the drum. The drum was rotated at an angular velocity of 6 °/s, either counter clock wise (CCW) or clock wise (CW) thus exposing each eye of the tested chameleon to either naso-temporal (NT) or tempo-nasal (TN) stimulus motion.

Tests for OMR were performed with newly hatched chameleons only. Each individual (N = 10) was placed in the transparent arena and allowed 30 secs to acclimatize, followed by an initiation of drum rotation. On a given test day, a chameleon was first exposed to gratings of low spatial frequencies, in a given direction of rotation (i.e. CW or CCW), repeated 2 - 3 times followed by exposure to the opposite direction. On the following test day, the procedure was repeated, with gratings of a next high spatial frequency.

We analyzed: (1) Latency from the beginning of rotation of the drum until locomotion is elicited, (2) Distance travelled over a period of 90 seconds, in the direction of drum rotation. Bar subtending angle was calculated for the distance from the wall of the transparent arena to the stimulus. (3) For the OMR an "optomotor gain" was obtained, following the protocol of Krauss and Neumeyer [3]: The inner arena circle was divided into 8 equal sections. We recorded the number of sections the chameleon walked through with (+) or against (-) the direction of drum rotation, over the 90 sec of test duration. The differences over the number of rotations of the drum for the test period were defined as "optomotor gain" which is optimal at a value equal to 1.

In testing for OKR the inner arena was removed and a tested chameleon was restrained in a foam cradle, with its head at the center of the drum. The dorsal edge of each eyelid was marked with a dot of colored nail polish for analysis eye movements. An OKR was recorded if eye motion comprised a slow, smooth following of the target and a subsequent fast saccade, in the opposite direction.

We also tested the OKR when both eyes were open, or under monocular occlusion, tested under a low spatial frequency (0.18 CPD), with 8 mature individuals. In monocular viewing, we restricted vision of one eye using a small medical pad and medical adhesive.

Results

Optomotor response

In response to the motion of the gratings all individuals exhibited an OMR, moving close to and parallel to the wall of the arena **(see supplementary video 1)** and with the direction of rotation.

Supplementary Video 1: *A newly hatched chameleon preforming an Optomotor response.*

Frequently, the tested chameleon halted for a few seconds before resuming its motion, or even turned in the opposite direction for a few seconds before resuming its moving with the direction of rotation. Latency to respond was positively correlated with bar frequency for CW, but not for CCW gratings rotation (Figure 3A, Spearman's rank correlation test, rs = -0.316, p = 0.044). Movement velocity was negatively correlated with bar frequency for CCW, but not for CW gratings rotation (Figure 3B, Spearman's rank correlation test, rs = 0.605., p < 0.001). While individual differences in "optomotor gain" were observed (Figure 4), none reached a gain = 1.

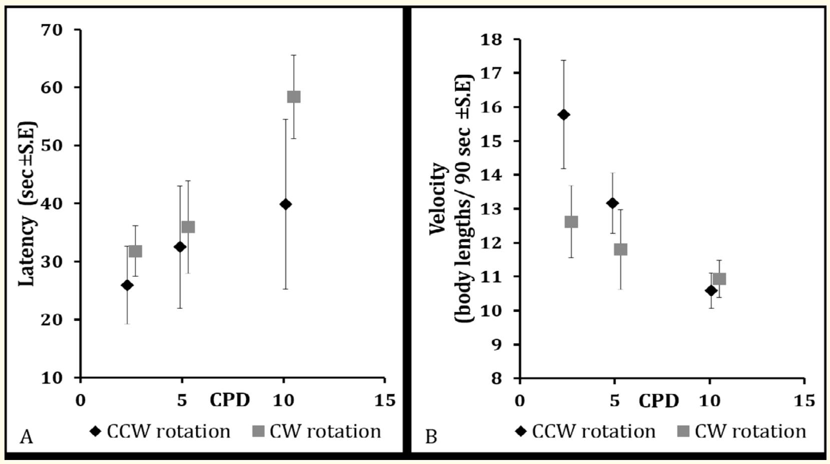

Figure 3: *Optomotor response. (A) Latency to respond and (B) velocity (n = 10).*

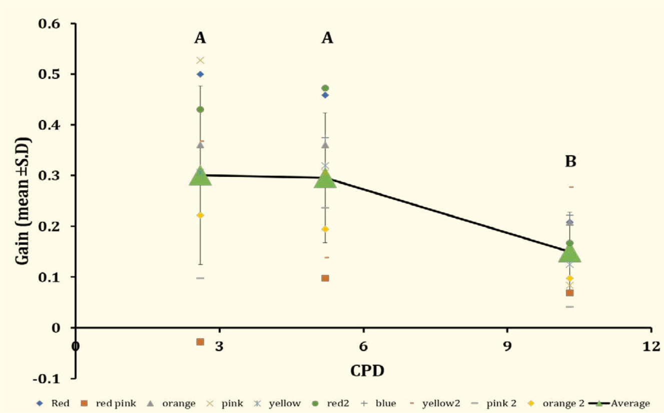

Figure 4: *Optomotor gain of individuals and overall (average, green triangle), under CCW and CW gratings rotation and different gratings frequency.*

Gain under the highest gratings frequency (10.3 CPD) was significantly lower than under the two additional frequencies (2.6, 5.2 CPD; Figure 4, Repeated measures ANOVA, $F_{2, 18} = 7.526$, $p = 0.004$).

Optokinetic response

An OKR was observed in all tests **(see supplementary video 2)**.

Supplementary Video 2: *A chameleon preforming an Optokinetic response.*

The OKR in mature, but not in immature, individuals decreased significantly with increased gratings frequency, up to 8 CPD (Figure 5B, 5D; Repeated measures ANOVA, Right eye; $F_{3, 27} = 42.609$, $p < 0.001$, Left eye; $F_{1.792, 16.131} = 45.674$, $p < 0.001$).

However, at 12 CPD, there was a subsequent increase in OKR frequency, to levels similar to 6 CPD (Post hoc tests with Bonferroni correction Right eye; p = 1, Left eye; p = 1).

This pattern, was observed also in small individuals, but the increase in frequency at 12 CPD was not significant (Figure 5A 3C Right eye; $F_{3, 27} = 7.640$, $p = 0.001$, Left eye; $F_{3, 27} = 5.837$, $p = 0.003$).

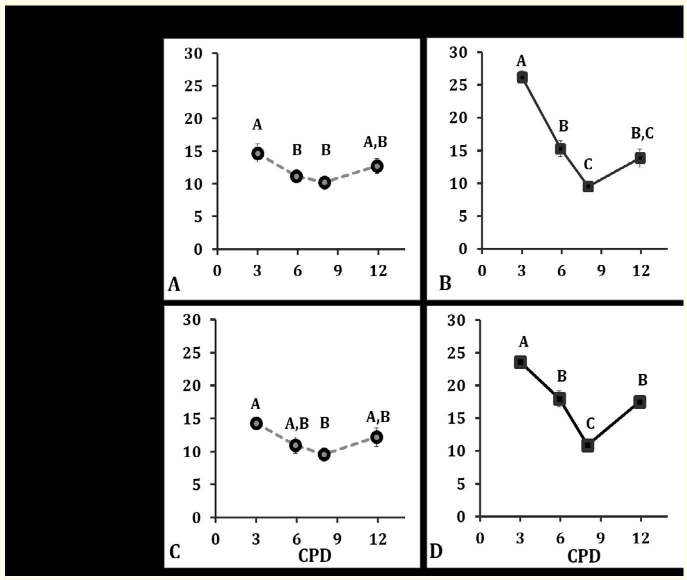

Figure 5: *OKR in relation to gratings spatial frequency and eye size in small (N = 10) and in large (N = 10) individuals.*

Visual Acuity

Vertebrate's posterior nodal point (PND) is calculated as 67% of the eye's axial length [24].

Eye axial lengths, determined from MRI and CT scans (Figure 6) were 9.8 mm in an adult male chameleon (Figure 2) and 3.74mm in a young chameleon providing for respective PNDs of 6.5mm and 2.5 mm.

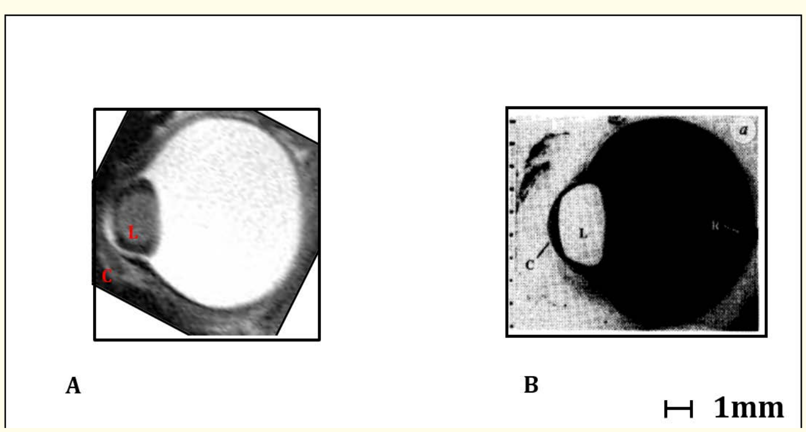

Figure 6: *(A) Eye section of a coronal MRI common chameleon (Chameleo chameleon) eye (UN published) (B) Two-time chameleon (Chameleo dilepis) (Ott and Schaeffel, 1995 [23]). The image shows a structure similarity.*

Visual acuity was calculated using two formulas (New and Bull, 2011) (I) retinal magnification factor (RMF); RMF = 2πPND/360, with an addition of 15% to the RMF due to the negatively powered lens (Figure 6, [23] and (II) Visual acuity= RMFx √D/2 (D is photoreceptor density). In the "horizontal streak" of an adult chameleon there are two areas of maximal ganglion cell density, one of > 13,000 cells/ mm2 and one of >11,000 cells/ mm2 [25]. From these values we calculated the visual acuity of the adult chameleon as 7.4 CPD and of the small individual as 2.5 CPD (using adult photoreceptor density).

Responses to TN and NT stimuli

There was no difference between the eyes (i.e., no lateralization) in the OKR response to either NT or TN stimulus direction (Table 1, Wilcoxon signed-rank test, TN; Z = -0.763, p = 0.445, NT; Z = -0.956, p = 0.339).

TN stimulus motion elicited significantly higher responses compared with the NT stimulus direction for each eye (Table 1, right eye; Z = -3.961, p < 0.001, left eye; Z = -4.010, p < 0.001).

The responses of any given eye under monocular viewing did not differ from its responses under binocular viewing (Table 1, Right eye TN; Z = 0, p = 1, Right eye NT; Z = -0.705, p = 0.481; Left eye TN Z = -1.1335, p = 0.182, Left eye NT Z = -1.612, p = 0.107).

Under binocular and under monocular viewing, the responses to TN stimulus motion were significantly higher than to NT stimulus motion (Table 1; Right eye, TN vs. NT with left eye open; Z = -2.375, P = 0.018; right eye TN vs. NT with left eye occluded; Z = -2.533, P = 0.011; left eye TN vs. NT with right eye open; Z = -2.527, P = 0.012, left eye TN vs. NT with right eye occluded; Z = -2.527, P = 0.012).

Eye motion direction	N	TN	NT	Wilcoxon signed-rank test
LE	22	15.09 ± 0.86	11.05 ± 0.60	p < 0.001
RE	22	14.59 ± 0.72	11.67 ± 0.57	p < 0.001
RE when LE occluded	8	19.62 ± 0.62	12.93 ± 0.80	P = 0.011
RE when both eyes open	8	19.25 ± 0.64	13.62 ± 0.65	P = 0.018
LE when RE occluded	8	18.56 ± 0.76	12.56 ± 0.76	P = 0.012
LE when both eyes open	8	19.56 ± 0.39	13.81 ± 0.85	P = 0.012

Table 1: *OKR (responses/min) under TN or NT gratings directions. LE and RE are the means over all tested chameleons. Bottom lines refer to 8 large individuals, under four conditions (see methods).*

Discussion

Visual Acuity

Studies on visual acuity in reptiles present a range of 4.25 - 6.8 CPD (Loggerhead, *Caretta caretta*, 6.1 CPD, [26]; Midland banded water snake, *Nerodia sipedon pleuralis*, 4.25 CPD, [11]; Red eared slider turtle, *Pseudemys scripta elegans*, 5.6 CPD, [27]; Sleepy lizard, *Tiliqua rugosa*, 6.8 CPD, [28]).

We here tested the chameleon for its behavioral visual acuity limit which was found to be ca 9 CPD in adult chameleons (Figure 5). This value is higher than that found in lizards of similar axial eye size and of higher photoreceptor density e.g., Sleepy lizard (15,500 cells/mm^2, [28], 6.8 CPD). It therefore appears that the chameleons' high visual acuity is mainly due to its negatively powered lens.

We assume that the increases of the OKR under 11.9 CPD (Figure 5) could be explained by the chameleons perceiving optical illusions created by the fine stripe pattern, in which two, or more consecutive relatively narrow stripes appear as a wider stripe. The fine stripe pattern needs to be beyond the threshold of the chameleons' visual acuity level for it to appear as an illusion. Visual illusions are often referred to the difference between image perception and its real geometrical proportions [29,30]. Perception of visual illusions has been documented in insects (honeybees; [31]), birds (barn owl; [32], domestic chicken; [33] and mammals (cat; [34]; monkeys; [35]). The increase of the OKR in 11.9 CPD (Figure 5) could be explained by the chameleons perceiving optical illusions created by the fine stripe pattern, in which two, or more consecutive relatively narrow stripes appear as a wider stripe. The fine stripe pattern needs to be beyond the threshold of the chameleons' visual acuity level for it to appear as an illusion.

Ontogenetic changes in visual acuity

During ontogenesis in vertebrates, the eyes undergo a significant change in size, which in turn, affects their physical properties. A larger eye diameter has a longer focal length and consequently, produces a larger image on the retina [2]. Ontogenetic improvement of visual acuity was found in species of most vertebrate classes. In the Brown-Banded Bamboo Shark (*Chiloscyllium punctatum*), visual resolution improved from 1.47 CPD during embryogenesis to 4.29 CPD in adults (Harahush., *et al*. 2014). In Rhesus monkeys (*Macaca nemestrina*), visual resolutions improve 15-fold during the 30 - 40 postnatal weeks (Kiorpes and Movshon, 1989), and in humans' visual resolutions increase from 5 CPD at 5 months to 40 CPD at 5 years of age (Mayer and Dobson, 1982). We here present the first documentation of the behavioral visual acuity for adult chameleons (ca. 9 CPD) and new hatched chameleon (ca. 5CPD), which is higher than the calculated visual acuity. Thus, chameleon's visual acuity is positively correlated with eye size (Figure 5). Further research is needed due to unknown parameters such as ganglion cells density in juvenile chameleons, corneal refractive power and retinal image magnification for both juveniles and adult chameleons. Yet it is likely that eye size attributes the most to visual acuity differences between adult and newly hatched chameleons.

OMR vs. OKR

The OMR and OKR function to stabilize retinal image and prevent blur [13], and have both been frequently used in vision research: OMR- zebrafish (*Danio rerio*, [36]), goldfish (*Carassius auratus*, [9]), Guppyfish (*Poecilia reticulate*, [37]), Crested Newt (*Triturus cristatus,* [12]), OKR- zebrafish [7], teleost fish [5], white leghorn new domestic chick [8], house mouse (*Mus musculus*, [38]). We found that results obtained from OKR tests were more robust and reliable compared with results from OMR tests. OMR tests were harder to analyze, as (i) individual responses were erratic and in times failed to follow the behavioral paradigm (i.e. moved against bars direction), (ii) measurements of latency and velocity were inconclusive due to the lack of statistical significance (Figure 3) and (iii) large individual differences obscured a conclusive result for "optomotor gain" threshold (Figure 4). One of the main reasons why OMR was less informative in these experiments may stem from the fact that chameleons are "sit and wait" predators, which often keep motionless for long periods of time. Fish however, being generally more mobile, are often used in OMR experiments and yield satisfactory results [3,5,7,9,36,39]. Unlike OMR, the OKR is a less complicated feedback loop with fewer levels of motor control, and so is prone to less "background noises" that may obscure results. It is therefore a better method to evaluate visual acuity in reptiles with large amplitude eye movement such as chameleons.

Oculomotor control

Chameleons use a monocular oculomotor control during spontaneous eye search [20] and in monocular eye tracking [40,41]. Tauber and Atkin [6] presented a disconjugate OKR in the African chameleon, *Chameleo melleri*, in a monocular stimulation, in which the eyes are moving in an uncoordinated manner. We here support their findings and show that chameleons OKR did not differ whether visual input was presented binocularly or monocularly (with one eye occluded, Table 1), this suggests that chameleons have the capacity for monocular oculomotor control during OKR.

TN vs. NT stimulus motion

In most vertebrates with lateral eyes, sensitivity to stimuli in the TN direction is known to be higher, compared with stimuli in the NT. This is true for the teleost fish *Chaetodon rainfordi* [5], the frog *Rana esculenta* [42], some reptiles [43], chickens *G. domesticus* [44], rabbits *Oryctolagus cuniculus* [45] and pigmented rats (DA-HAN, [46]. However, experiments on the African chameleon (*Chameleo melleri*) by Tauber and Atkin (1967) have yielded results with similar response sensitivity in both stimuli directions. Our results here coincide with the situation in most vertebrates that stimulus directionality does affect behavioral responses and seems to contradict Tauber and Atkins' conclusions (Table 1). Although chameleons mainly use a "sit and wait" strategy while avoiding predation on trees and shrubs, they also move forward in order to catch prey and thus having the ability to suppress the OKR by translational movements during forward locomotion and ensure that the prey will be focused on the retina.

Conflict of Interest

None.

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