



The optokinetic reaction in foveate and afoveate geckos

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Abstract

To investigate determinants of symmetry of the monocular horizontal optokinetic reaction (hOKR) in vertebrates, we performed behavioural studies in diurnal foveate, as well as nocturnal afoveate geckos. During binocular viewing hOKR gain was equal for movement to the left or right, during monocular stimulation, all afoveate geckos (*Lepidodactylus lugubris*, *Gekko gecko*, *Eublepharis macularius*) and the foveate *Lygodactylus* spp. exclusively reacted to temporo-nasal stimulation with stabilising head movements whereas in *Phelsuma madagascariensis* a naso-temporal component of hOKR could be elicited albeit much weaker. Thus, neither the presence of a fovea nor lifestyle seems to be decisive for a symmetrical monocular hOKR.

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1. Introduction

In all vertebrates the optokinetic reaction (OKR) ensures a stable image of the environment on the retina during ego and external motion. During OKR the eyes, head or even the whole body move at nearly the same velocity and in the same direction as the retinal stimulus. If stimulation is long lasting these pursuit movements are interrupted by resetting saccades in the opposite direction. Monocular horizontal OKR (hOKR) varies in different vertebrates: Some species have a largely symmetrical monocular hOKR where motion in temporo-nasal (TN) and naso-temporal (NT) direction elicits largely equal responses, e.g. rainbow trout (Klar & Hoffmann, 2002), chameleon (Gioanni, Bennis, & Sansonetti, 1993; Tauber & Atkin, 1967); ferret (Hein, Courjon, Flandrin, & Arzi, 1990); cat (e.g. Wood, Spear, & Braun, 1973; Distler & Hoffmann, 1992; Markner & Hoffmann, 1985), monkey (Kato, Hasegawa, Igarashi, Koike, & Kawasaki, 1986) and human (e.g. van den Berg & Collewijn, 1988).

In other species, e.g. Butterflyfish (Fritsches & Marshall, 2002), frog (Katte & Hoffmann, 1980; Lazar, 1973), pigeon (Fite, Reiner, & Hunt, 1979), chicken (Wallmann & Velez, 1985; Bonaventure, Kim, Jardon, & Yucel, 1992), rabbit (Collewijn, 1975), rat (Hess, Precht, Reber, & Cazin, 1985) and mouse (Grüsser-Cornehls & Böhm, 1988), monocular hOKR is asymmetrical, i.e. motion in temporo-nasal direction elicits a larger response than in the opposite direction.

Several hypotheses to explain this diversity have been put forward. The “fovea theory” proposed by Tauber and Atkin (1968) proposes that foveate animals perform a symmetrical monocular hOKR. The “decussation theory” proposed by Fukuda and Tokita (1957) suggests the decussation pattern of retinal axons as the key determinant for a symmetrical monocular hOKR: the larger the amount of ipsilaterally projecting retinofugal fibers the more symmetrical the monocular hOKR should be. Other authors tried to correlate different lifestyles with the characteristics of optomotor reflexes (e.g. Dieringer, Reichenberger, & Graf, 1992; Fritsches & Marshall, 2002).

Generally lateral-eyed mammals without a fovea show asymmetric monocular hOKR (e.g. rat, mouse, rabbit)

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whereas frontal-eyed mammals show symmetrical hOKR independent of the presence of a fovea (e.g. ferret, cat, monkey, human).

In all vertebrates tested so far, the neuronal substrate for the hOKR involves pretectal structures and structures of the accessory optic system. In sharks the corpus geniculatum laterale and in rainbow trout the area pretectalis (APT) contain direction-selective neurons, which code for all directions of motion (shark: Masseck & Hoffmann, in press; rainbow trout: Klar & Hoffmann, 2002). Thus in contrast to the decussation theory many fish with their completely crossed optic nerves perform a nearly symmetrical monocular hOKR. In amphibians, reptiles and birds the nucleus lenticularis mesencephali (LM) has been identified as the visuomotor interface for OKR (frog: Fite, 1985; Katte & Hoffmann, 1980; turtle: Fan, Weber, Pickard, Faber, & Ariel, 1995; bird: Fite et al., 1979; Winterson & Brauth, 1985). Neurons in the LM code predominantly for temporo-nasal motion; however also neurons which code for other directions than ipsiversive (i.e. neurons of the left LM code for leftwards movements, whereas neurons of the right LM code for rightward motion) can be found.

In mammals neurons of the nucleus of the optic tract and the dorsal terminal nucleus (NOT-DTN) code for ipsiversive horizontal stimulus movements, whereas neurons in the medial and lateral terminal nucleus (MTN and LTN) code for vertical directions.

Binocular projections from the visual cortex to the NOT-DTN are responsible for a symmetrical monocular hOKR (ferret: Klauer, Sengpiel, & Hoffmann, 1990; cat: Wood et al., 1973) in mammals. As such corticopretectal projections are absent in fish, amphibians, reptiles and birds, the question of the cause for a monocular symmetry in non-mammals arises.

In addition some differences between foveal vision (like prey tracking) and gaze stabilization exist. Diurnal geckos use foveal vision mainly for binocular prey fixation and not for gaze stabilization. They can direct their highly movable eyes forward to reach binocular vision (Röll, 2001). Furthermore foveal tracking can not be performed separately in the two eyes, e.g. chameleons were not able to follow two prey items independently with their two eyes (Kirmse, 1988; Ott, 2001). In contrast hOKR can be executed independently in the two eyes (Kirmse, 1988; Ott, 2001).

A study by Bellintani-Guardia and Ott (2002) revealed that displaced ganglion cells projecting to the nBOR in the foveate chameleon are evenly distributed throughout the entire retina and have no retinotopic organization. As well as in the chameleon in afoveate chicken ganglion cells from the entire retina project to the nBOR (Reiner, Brecha, & Karten, 1979). Thus a foveal involvement in generating OKR or even in a symmetric monocular OKR seems unlikely.

To date the optokinetic system has been studied in only a few reptiles (gecko: Tauber & Atkin, 1968; turtle: Fite et al., 1979; Ariel, 1997; chameleon: Giovanni et al., 1993; Ott, 2001). For our investigation geckos were chosen.

Geckos are small lizards which live in tropical and subtropical regions. Most of them (ca. 75%) are nocturnal. Nocturnal geckos developed from primarily diurnal lizards with pure cone retinæ (Walls, 1934; Walls, 1942). The rod-like photoreceptors of nocturnal geckos are actually modified cones (Tansley, 1964; Röhl, 2000). However, some genera became tertiary diurnal again and transmuted their visual cells back to cones. The retinæ of primarily diurnal lizards are usually characterized by centrally located foveae either convexiculate or more concaviclevate or shallow (Röll, 2001). In geckos, foveae could only be demonstrated in diurnal representatives (Underwood, 1951; Tansley, 1964; Röhl, 2001). Here, foveation reaches its highest development in the genera *Gonatodes*, *Lygodactylus* and *Sphaerodactylus* with concaviclevate foveae, whereas in species of the genus *Phelsuma* the foveae are shallow and less specialized. Eyes of both the strictly nocturnal geckos (e.g. of the genera *Coleonyx*, *Gekko*, *Paroedura*, *Uroplatus*) and the diurno-nocturnal species (e.g. *Lepidodactylus*) completely lack foveae (Röll, 2001; Tansley, 1964; Underwood, 1951). However, nocturnal geckos exploit binocular vision to enhance visual sensitivity (Röll, 2001). Diurnal gekkonid species have retained binocular vision from their nocturnal ancestors and have developed foveae which are consequently located not in the central but in the temporal region of the retina (Röll, 2001). Species of the genus *Lygodactylus* possess a binocular visual field of approximately 30 degrees (unpublished observations).

We measured optokinetic head movements under binocular and monocular conditions in diurnal foveate geckos and nocturnal afoveate geckos to determine if the presence of a fovea is a prerequisite for symmetrical monocular hOKR.

2. Materials and methods

2.1. Animals

Five different gecko genera were studied. Diurnal foveate geckos belonged to the species *Lygodactylus capensis* ($n = 1$), *L. bradfieldi* ($n = 1$), *L. chobienensis* ($n = 1$), *L. arnoulthi* ($n = 2$) (~40–50 mm) and *Phelsuma madagascariensis* ($n = 3$) (25 cm). Nocturnal afoveate species were *Lepidodactylus lugubris* ($n = 5$) (50 mm), *Gekko gekko* ($n = 3$) (35 cm) and *Eublepharis macularius* ($n = 4$) (25–30 cm). All experiments were approved by the local authorities (Regierungspräsidium Arnsberg) and carried out in accordance with the Deutsche Tierschutzgesetz of 12 April 2001, the European Communities Council Directive of 24 November 1986 (S6 609 EEC) and NIH guidelines for care and use of animals for experimental procedures.

All animals were kept in a terrarium at a twelve hour light cycle and fed twice a week with house crickets. Drinking water enriched with calcium, phosphate and vitamins was available ad libitum. All species of *Lygodactylus* and *Lepidodactylus* were housed individually, whereas *Phelsuma*, *Eublepharis* and *Gekko* were kept in groups.

2.2. Optokinetic measurements and analysis

Binocular and monocular measurements were performed using an optokinetic drum covered with a black and white Julesz-random dot pattern and moving in clockwise (CW) and counterclockwise (CCW) direction. Animals were placed in a Petri dish in the center of the optokinetic drum (small geckos: $\phi = 30$ cm, $h = 29$ cm; others: $\phi = 70$ cm,



Fig. 1. Photomicrograph with a superimposed outline of the measured angle α . Black arrow indicates direction of the smooth pursuit movement.

$h = 64$ cm). For *Lepidodactylus lugubris* and *Lygodactylus* spp. stimulus velocities of 20 and 50°/s were used. All other geckos were measured at 20, 30 and 40°/s. For the small geckos each dot of the random dot pattern was $1.9^\circ \times 1.9^\circ$ visual angle, whereas for all other geckos dots had a size of $1.6^\circ \times 1.6^\circ$ visual angle.

For monocular measurements a black cap was reversibly attached on the right or the left eye. Usually the left eye was stimulated during monocular viewing, however the right eye was always monocularly tested for control. Head movements were video taped. One session consisted of a 30–60 s long lasting stimulation, in each session up to 10 consecutive pursuit movements were calculated. For analysis the angle between consecutive head orientations during the pursuit movements was calculated by a frame by frame (frame-rate of the video: 50 Hz) analysis of the video data (Fig. 1). The angle was measured between the start position of the slow phase eye-movement and its end position (before a resetting saccade starts). The gain for each value was calculated as the head pursuit movement angle divided by the duration of movement and stimulus velocity. All in all fifty smooth pursuit head movements of *L. capensis*, *L. bradfieldi*, *L. chobiensis*, *L. arnoulthi* and *L. lugubris* are included in the data analysis, whereas for *P. madagascariensis*, *G. gecko* and *E. macularius* hundred binocular gain values are used to calculate the median. The median of the gains was calculated and plotted in a boxplot diagram. To test for significant differences a *t*-test was used for normally distributed data; otherwise a Mann–Whitney Rank Sum test was used (Sigma-Stat).

3. Results

3.1. Optokinetic measurements

Altogether 12 nocturnal and eight diurnal geckos were measured. All geckos responded to the start of the stimulus with a smooth pursuit movement, independent from binocular or monocular measurements and independent of whether they possess a fovea or not.

3.2. Afoveate animals

3.2.1. *Lepidodactylus lugubris*

The optokinetic reactions were measured in five individuals of the nocturnal afoveate *L. lugubris*. In the binocular condition there was no significant difference between CW and CCW stimulation at 20 or 50°/s ($p = .798$ and $.452$) (Fig. 2A). However, the gain was significantly lower at 50°/s than at 20°/s (20°/s: gain = 1.0; 50°/s: gain = 0.9, $p \leq .003$). In TN direction again at 20°/s the median of the gain was significantly higher than at 50°/s (20°/s:

gain = 1.1; 50°/s: gain = 0.6, $p \leq .001$). During monocular viewing, no OKR could be elicited by stimulation in NT direction (Fig. 2B).

3.2.2. *Eublepharis macularius*

The data of four nocturnal afoveate *E. macularius* are presented in Fig. 2C and D. During binocular stimulation the median of the gain of OKR declined with increasing stimulus velocity (20°/s: CW 0.9; CCW 0.9; 30°/s: CW 0.8, CCW 0.9; 40°/s: CW 0.8, CCW 0.7) (Fig. 2C). Only at the highest stimulus velocity a significant difference in the response to the two stimulus directions ($p = .004$) existed. Gain was generally lower during monocular viewing at TN stimulation as in the binocular condition. At 30 and 40°/s the gain declined significantly (20°/s: 0.7, 30°/s: 0.6, 40°/s: 0.4, $p = .025$) during monocular stimulation. No OKR could be elicited at all in NT direction (Fig. 2D).

3.2.3. *Gekko gecko*

A total of three individuals of the nocturnal afoveate species *G. gecko* was tested. During binocular viewing these animals showed equal OKR in CW and CCW direction at all velocities (Fig. 2E). Again, gain clearly declined with increasing stimulus velocity (20°/s: 0, 8; 30°/s: 0.7; 40°/s: 0, 6). This decrease was stronger than in the other species investigated. Also in this species, monocular gain was lower than binocular gain (20°/s: 0.7; 30°/s: 0.7; 40°/s: 0.5; $p \leq .026$). Monocularly, OKR was asymmetric (Fig. 2F), i.e. no OKR could be elicited by stimulation in the NT direction.

3.3. Foveate animals

3.3.1. *Lygodactylus* spp.

Altogether five individuals of the diurnal foveate genus *Lygodactylus* spp. were analysed. During binocular viewing, the gain was close to one at 20 and 50°/s during CW and CCW stimulation. At 20°/s the response to CCW stimulation was significantly higher ($p < .002$; median of the gain = 1.3). As a gain higher than 1 is physiologically not plausible this result may be due to the fact that the geckos were not fixed, but could freely move inside the petri dish. Therefore the relative distance of the gecko to the drum wall influenced the perceived pattern velocity.

During monocular viewing all individuals of the genus *Lygodactylus* showed a complete loss of OKR in NT direction (Fig. 3B). During NT stimulation the geckos sometimes followed the stimulus by running, but never showed a regular head nystagmus. During the TN stimulation the gain was comparable to the binocular conditions with a median gain of 1 during 20°/s stimulation and a median gain of 0.9 during a stimulation at 50°/s.

3.3.2. *Phelsuma madagascariensis*

The optokinetic reaction was measured also in three diurnal foveate *P. madagascariensis* (Fig. 3C). Binocularly, this species showed a robust bidirectional OKR

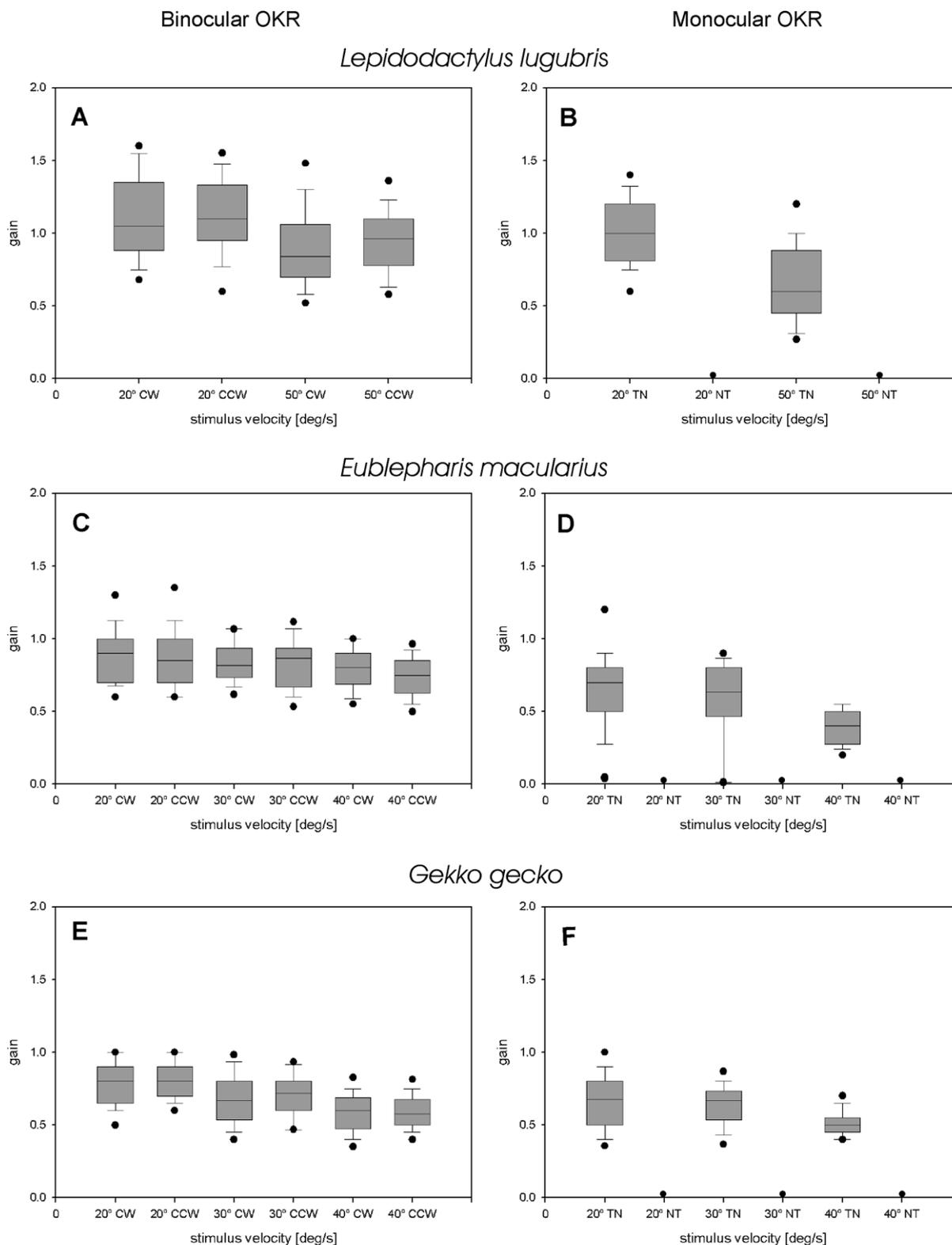


Fig. 2. Boxplot diagrams of binocular and monocular measurements of the gain of OKR in afoveate species. The 5% and 95% percentiles are displayed as dots, boxplots show the range from the 25% percentile to the 75% percentile (A) Binocular condition *L. lugubris*, $n = 50$, (B) Monocular condition *L. lugubris*, $n = 50$, (C) Binocular condition *E. macularius*, $n = 100$, (D) Monocular condition *E. macularius*, $n = 100$, (E) Binocular condition *G. gecko*, $n = 100$, (F) Monocular condition *G. gecko*, $n = 100$. The median and the 5%, 25%, 50%, 75% and 95% percentiles are shown. CW, clockwise stimulation; CCW, counterclockwise stimulation; NT, naso-temporal stimulation; TN, temporo-nasal stimulation.

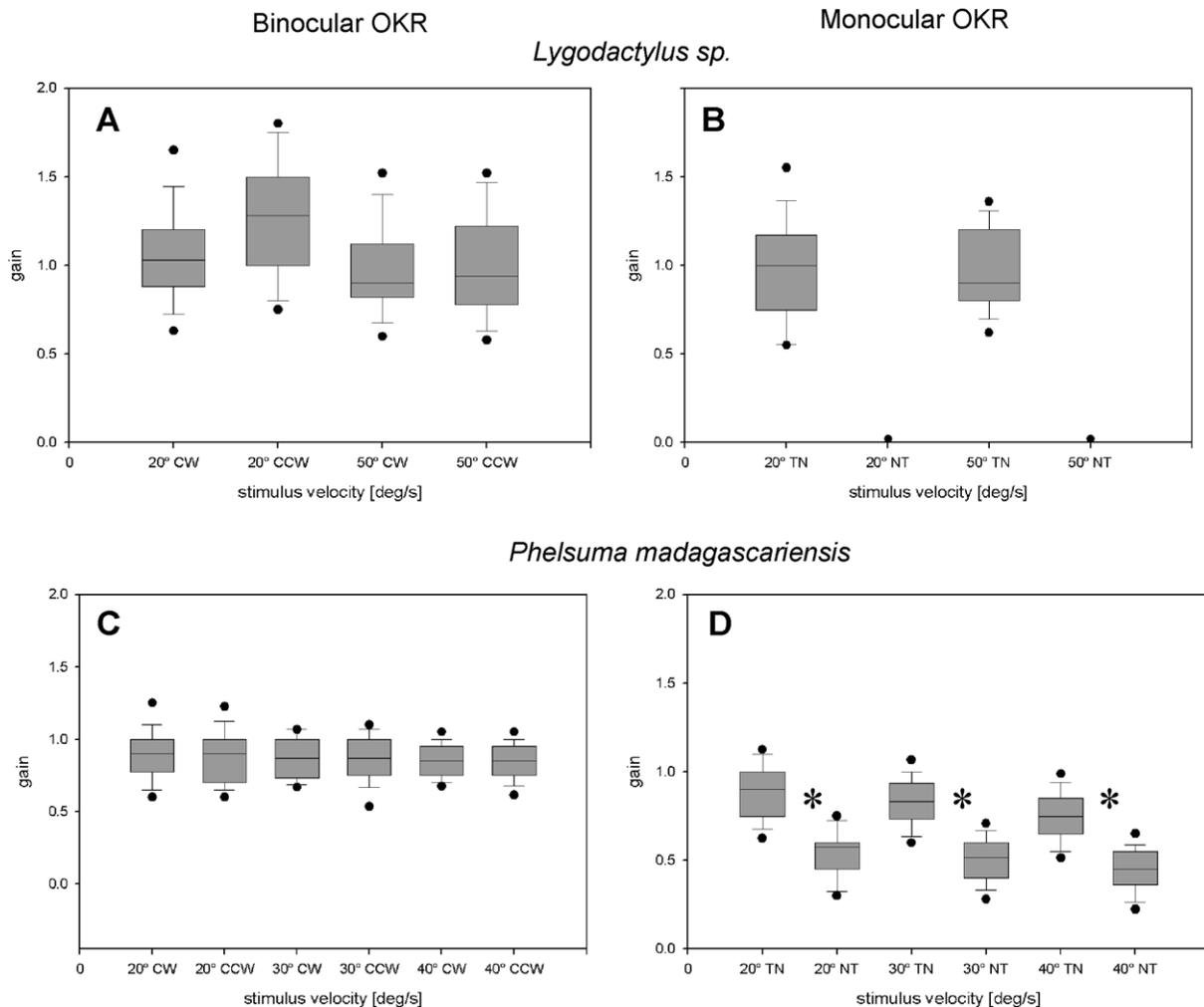


Fig. 3. Boxplot diagrams of binocular and monocular measurements of the gain of OKR in foveate species. (A) Binocular condition *Lygodactylus* spp., $n = 50$. (B) Monocular condition *Lygodactylus* spp., $n = 50$, (C) Binocular condition *P. madagascariensis*, $n = 100$, (D) Monocular condition *P. madagascariensis*, TN: $n = 100$, NT: $n = 30$. Conventions as in Fig. 1. Stars indicate significant differences.

at all velocities (gain at 20°/s. CW 0.9 CCW 0.9; 30°/s CW 0.9, CCW 0.9; 40°/s CW 0.9, CCW 0.8). *P. madagascariensis* was the only species investigated in the present study that showed an optokinetic reaction during monocular stimulation in NT, albeit significantly weaker than in TN direction (20°/s: TN 0.9, NT 0.6, 30°/s, $p \leq .001$ and 40°/s TN 0.8, NT 0.5, $p \leq .001$). A head nystagmus in NT direction could not be elicited in each session thus resulting in fewer measurements in NT than in TN direction. Only in 30% of the sessions during monocular stimulation in NT direction a hOKR could be elicited at all, clearly the NT component is not as reliable as the TN component. Thus gain was calculated only from the periods showing OKR.

Thus summarizing our data we could show that under binocular viewing conditions foveate as well as afoveate geckos show largely symmetrical bidirectional optokinetic reactions in horizontal directions with a gain close to 1. In all but one species (*P. madagascariensis*) gain of hOKR decreases with increasing stimulus velocity over a range of 20 to 50°/s.

Under monocular viewing conditions, two trends were recognizable in our data. Generally, monocular gain in TN direction was lower than binocular gain. A complete loss of head nystagmus in NT direction was observed in all afoveate geckos tested (*L. lugubris*, *G. gecko*, *E. macularius*) as well as in the foveate genus *Lygodactylus*. By contrast, our second foveate species *P. madagascariensis* displayed a clear hOKR in NT direction albeit at significantly lower gain than in TN direction.

4. Discussion

4.1. Optokinetic measurements

Geckos generally stabilize gaze more by head (80%) than by eye movements (Dieringer, Cochran, & Precht, 1983). Therefore in our study we concentrated on head movements. All individuals of all species tested showed a robust hOKR during binocular viewing. Monocularly all individuals were asymmetric in their response, i.e. only TN stimulation reliably elicited hOKR whereas NT stimu-

lation yielded no response at all (*Lygodactylus*, *L. lugubris*, *G. gecko*, *E. macularius*) or a rather weak response in some of the sessions (*P. madagascariensis*). This monocular asymmetry was independent of lifestyle (diurnal vs. nocturnal) or retinal specialisation (foveate vs. afoveate). Especially the findings in the foveate diurnal *Phelsuma* and *Lygodactylus* disagree with earlier results of Tauber and Atkin (1968), who claimed that monocular symmetry is related to foveation. It is unlikely that these different results are caused by the different stimulus parameters used by Tauber and Atkin (vertical black and white grating) and in the present study (Julesz random dot pattern). As hOKR could readily be elicited under binocular viewing conditions. Also, during monocular viewing a rapid switch between NT and TN led to an immediate beginning of an optokinetic response in TN direction whereas in NT direction the hOKR was totally abolished (*Lygodactylus*, *L. lugubris*, *G. gecko*, *E. macularius*) or diminished (*P. madagascariensis*). All tested species could be judged as asymmetric, although *P. madagascariensis* showed a weak NT component. In a second preliminary approach, eye movements were recorded in *P. madagascariensis* and *G. gecko* using electrooculography (EOG). In head restrained animals an optokinetic reaction could only be elicited in about 20% of the sessions. Nevertheless, our data suggest a slight contribution of eye movements to gaze stabilization in geckos. Both species tested showed optokinetic eye movements during binocular and monocular stimulation. Monocular asymmetry persisted in *P. madagascariensis* and *E. macularius* ($p \leq .001$), whereas in binocular measurements no differences for CW and CCW stimulation can be seen.

In lateral eyed animals (like geckos) monocular asymmetry facilitates a suppression of optokinetic drive during forward locomotion, as optic flow during forward locomotion corresponds to stimulation in naso-temporal direction.

4.2. Neuronal substrate

A study by Northcutt and Butler (1974) using a degeneration method and silver staining revealed sparse ipsilateral fiber projections to all main retinorecipient areas in *G. gecko*. In turtle, only an ipsilateral projection to the nucleus posterodorsalis, a retinofugal area, which has no known function in OKN control was revealed using HRP (Fan et al., 1995). Anyway, functionality of ipsilateral fibers for the optokinetic reaction is in question, as at least in frogs an ipsilateral retinal projection does not contribute to it. After sagittal section of the optic chiasm no optokinetic reaction can be elicited (Dieringer & Precht, 1982). Furthermore even *G. gecko* possess ipsilateral retinofugal fibers (Northcutt & Butler, 1974) and is monocularly not able to generate hOKR in NT-direction.

Various electrophysiological and lesion studies suggest that the nucleus lentiformis mesencephali (LM) of tetrapodes other than mammals, the area pretectalis (APT) in trout and the corpus geniculatum laterale in sharks are involved as visuomotor interface in the generation of slow

following eye and head movements during hOKR (shark: Masseck & Hoffmann, in press; trout: Klar & Hoffmann, 2002; frog: Katte & Hoffmann, 1980; Dieringer & Precht, 1982; turtle: Fite et al., 1979; Fan et al., 1995). In frog 15% of the LM neurons code for contraversive motion (i.e.: 15% of the neurons in the right LM code for leftward motion and vice versa for the right LM) (Katte & Hoffmann, 1980). In the mammalian NOT-DTN a strict preference for ipsiversive stimulus movement has been shown in all species investigated so far (e.g. rat: Precht & Strata, 1980; rabbit: Collewijn, 1975; cat: Hoffmann & Schoppmann, 1981; ferret: Klauer et al., 1990; opossum: Volchan et al., 1989; monkey: Hoffmann, Distler, Erikson, & Mader, 1988; Mustari & Fuchs, 1990).

In addition, the nucleus of the basal optic root (nBOR), a major component of the accessory optic system, is involved in gaze stabilization in amphibians, reptiles and birds. Neurons in the nBOR code for all but ipsiversive direction of motion (Dieringer & Precht, 1982; Fan et al., 1995). Together neurons in the LM and nBOR represent all directions of motion. The LM and nBOR are interconnected reciprocally with each other (turtle: Fan et al., 1995). In pigeons electrical stimulation of the LM modulates the firing rate in the nBOR (Nogueira & Britto, 1991) and vice versa. However, the nBOR only modulates hOKR gain and is not responsible for eliciting an horizontal optokinetic reaction (turtle: Fite et al., 1979). An involvement of telencephalic or tectal structures in the optokinetic reaction of non-mammalian vertebrates seems unlikely (Hertzler & Hayes, 1967; Hobbelen & Collewijn, 1971; Lazar, 1973).

Thus, a NT component of monocular hOKR could be generated by a cooperation of the LM and nBOR. Alternatively, even the LM alone could generate a weak NT component, as in pigeons the LM is also activated by NT stimulation (Winterson & Brauth, 1985).

5. Conclusion

Monocular symmetric hOKR in geckos is neither related to retinal specializations nor to lifestyle. So our data do not support the generality of the fovea theory of Tauber and Atkin. The decussation theory can not be verified nor refuted by our data, however it is questionable if sparse ipsilateral fiber connections as described for reptiles could generate a naso-temporal monocular hOKR at all.

Among non-mammalian vertebrates only some fish and reptiles (e.g.: *Chamaeleo melleri*) display a symmetric monocular hOKR, possibly due to a different anatomical organisation (trout: Klar & Hoffmann, 2002, chameleon: Tauber & Atkin, 1967; Gianni et al., 1993).

Further behavioural and electrophysiological experiments are needed to quantify the symmetry of monocular hOKR in various species to clarify interspecies differences of the underlying neuronal circuits.

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