

# The optokinetic reaction in foveate and afoveate geckos

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Received 31 August 2007; received in revised form 1 December 2007

## 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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**Keywords:** Optokinetic reaction; Pretectum; Reptiles; Fovea

## 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 retinae (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 retinae of primarily diurnal lizards are usually characterized by centrally located foveae either convexiculate or more concaviculate 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 concaviculate 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,

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