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Accommodation behaviour during prey capture in the vietnamese leaf turtle (*Geoemyda spengleri*)

Abstract Vietnamese leaf turtles (*Geoemyda spengleri*) were tested for their ability to focus on prey objects at various distances. Accommodation was continuously measured by infrared photoretinoscopy. All animals investigated during this study showed a surprisingly high precision of accommodation over a range of over 30 D. Measured accommodation matched the target distance accurately for distances between 3 and 17 cm. The turtles switched between independent and coupled accommodation in the two eyes. Independent accommodation was observed when the turtles inspected their environment visually without a defined object of interest. Coupled accommodation was only observed during binocular prey fixation. When a turtle aimed at a target, the symmetrical focus of both eyes persisted even if vision was totally blocked in one eye or altered by ophthalmic lenses. This suggests that the eyes were linked by internal neuronal mechanisms. The pupil of the eye responded clearly to changes in ambient light intensity. A strong decrease in pupil size was also observed when the eye was focused on a close target. In this case, the constriction of the pupil probably aids in the deformation of the eye lens during near-accommodation.

Keywords Binocular coupling · Eye · Pupillary reflex · Retinoscope · Stereopsis

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Introduction

Many non-mammalian vertebrates have laterally positioned eyes that move independently from each other (Walls 1942, 1961). Consequently, ocular accommodation is also independent in the two eyes (chicken: Schaeffel et al. 1986; pigeon: Howard and F. Schaeffel, unpublished observations; tuatara: Schmid et al. 1992; snakes: Schaeffel and Mathis 1991). A symmetrical accommodation response, on the other hand, is frequently observed in animals with frontal eyes such as cats, primates (Bishop and Pettigrew 1986) and owls (Schaeffel and Wagner 1992). Usually, these species achieved true three-dimensional vision (stereopsis) during their evolution (Pettigrew and Konishi 1976) suggesting that the coupling of the accommodation response is required for it. Chameleons represent an intermediate state since their usually independently moving eyes are synchronized during prey fixation with respect to both accommodation and saccade generation (Ott et al. 1998; Ott 2001). These lizards accommodate very accurately (Ott and Schaeffel 1995) and use their focusing mechanism to judge the distance of prey objects (Harkness 1977). Chameleons have a number of unusual, highly specialised visual features, including telescopic visual optics, a deep funnel-shaped central fovea and high image resolution (Harkness and Bennett-Clark 1978; Ott et al. 1998). The peculiar precision of accommodation and the ability to switch between coupled and independent accommodation in the two eyes was therefore attributed to several of these special features of the visual system of the chameleon (Pettigrew et al. 1999).

In the present study, we measured the accommodative response in prey catching Vietnamese leaf turtles, *Geoemyda spengleri*. We found remarkable similarities to the visual system of chameleons. The turtles showed a similar switch between independent and strictly coupled accommodation in the two eyes. The accommodation response had a large range and the amplitude was very precise; the required and measured accommodation did

not differ significantly at any distance tested. Since the eye of *G. spengleri* is apparently not different to that of other turtles, it lacks all the special properties of the chameleon eye. The present results suggest that a precise focus response and the ability to switch to binocular coupling is not restricted to chameleons and not necessarily correlated with their unique visual adaptations.

Material and methods

Animals

Wild caught Vietnamese leaf turtles of both sexes were obtained from a commercial dealer and were housed in a large moist terrarium under artificial light. They were fed with various insects and new-born mice.

Accommodation measurements

Accommodation was measured by infrared (IR) photoretinoscopy. Turtles were placed in a cardboard box which was slightly larger than their carapace. A small hole in the box allowed the turtles to move their heads towards the outside where a bait was offered as a focus stimulus. The distance between the prey and the eye of the turtle was monitored by a video camera which was mounted above the animal. The background luminance was kept low (30–50 lx) in order to improve the signal to noise ratio of the refraction measurements. Accommodation was recorded with the aid of an infrared retinoscope (hand-made) attached to the lens (Zeiss $F = 85$ mm $f/1.4$) of an infrared sensitive video camera (Canon CI-20PR). IR light reflected by the ocular fundus caused a reflex pattern visible in the pupil. The slope of this brightness profile as measured in the individual video frames could be converted into refraction. The technique of infrared photoretinoscopy and the analysis of the data was the same as described in a related paper (Henze et al. 2004) and previous studies (Schaeffel et al. 1994; Ott et al. 1998).

For calibration of the refraction technique, we put ophthalmic lenses in front of the eye close to the cornea and correlated the power of the lenses with the brightness profile of the fundus reflex (Fig. 1; for calibration technique see also Schaeffel et al. 1994). In order to avoid spontaneous accommodation during the calibration procedure we covered the eye with a filter (Kodak Wratten 87C) which did not permit the animal to see, but transmitted IR light for measurement. The data remained uncorrected for the distance between the front lens and the principal planes of the eye. Experiments with chickens under similar conditions have shown that this creates no significant error (Schaeffel et al. 1994). Seven turtles were used for the calibration measurements (Fig. 1). In all animals, the data fitted well to a linear regression line ($R^2 = 0.91–0.99$). The slopes were in a range between 0.13 and 0.21 and intersected the ordinate between 0.33 and 1. Brightness profiles measured during the following experiments were converted into refractions individually from the equation of these regression lines (refraction $= y - c/m$, where $y =$ slope of the brightness profile in the pupil, $c =$ intersection of the regression line with the ordinate, and $m =$ slope of the regression line). The hyperopic offset caused by the thickness of the retina which separates the photoreceptor layer from the reflecting vitreal surface (Glickstein and Millodot 1970) was eliminated from the calculation of the refractive state due to the direct calibration. All measurements were made at a distance of 70 cm from the eye. During the experiments the animals were videotaped constantly. For analysis, a selection from the recordings was digitised and read frame by frame into a computer via a video board (Matrox Meteor-II). A program written by F. Schaeffel automatically determined the slope of the intensity profile by linear regression across the vertical meridian of the pupil. We then converted the result into a refractive value as described above.
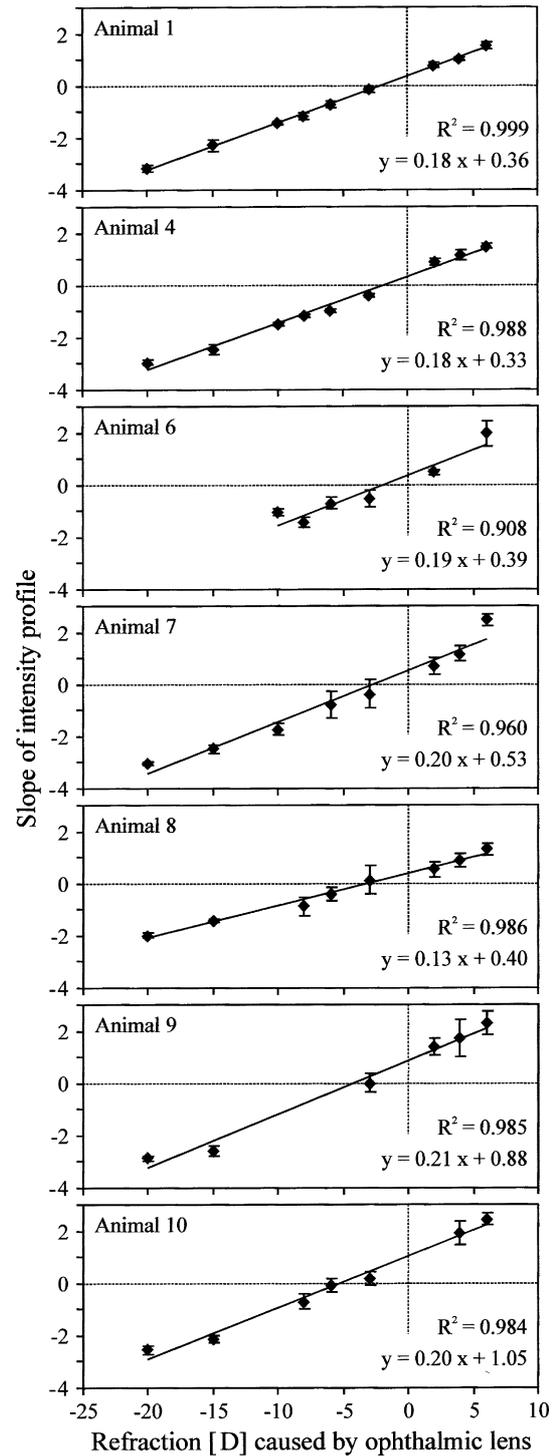

Fig. 1 Calibration of the photorefraction technique. For each individual, the intensity profile in the pupil was correlated with the refractive state of the eye by placing ophthalmic lenses of known power close to the cornea. The slope of the brightness gradient (an average of several measurements; $n > 6$) is plotted against refraction. Error bars represent standard deviations. The calibration curve was determined by linear regression. Its equation and the square of the correlation coefficient (R^2) are given in the lower right corner of each diagram

Results

Range and precision of accommodation

The dynamics of accommodation is shown for one animal in Fig. 2. Prey was presented at various distances. In all cases, the absolute value of measured refraction in
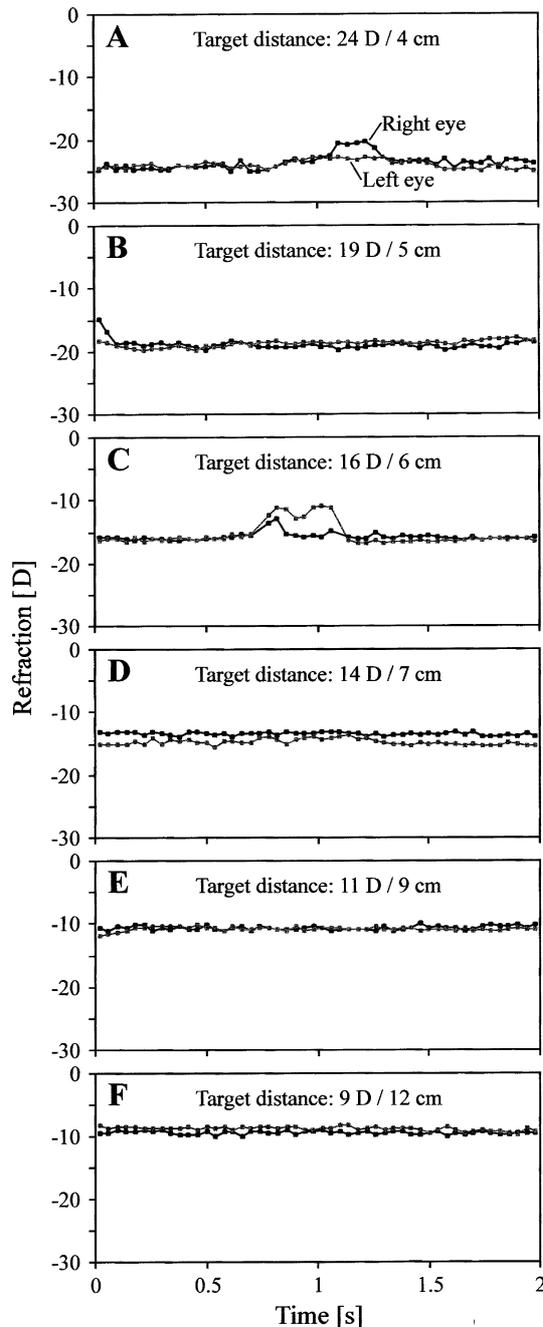

Fig. 2 Time-course of refraction in one individual (animal 9) while focussing on a prey target presented at different distances (A–F). *Black dots*: right eye, *grey dots*: left eye. The absolute value of refraction matched the distance between the prey and the eyes (given in dioptres) accurately indicating that the turtle accommodated precisely

both eyes was similar to the distance of the prey expressed in dioptres [D = 1/distance of prey (m)]. During the fixation of near targets the turtles sometimes relaxed their accommodation tonus and showed short sections of under-accommodation in one or both eyes (Fig. 2A and C). Figure 3 gives the mean values of the measured accommodation (y-axis) for prey distances (x-axis) between 6 and 31 D (equivalent to 17 and 3 cm). At all distances tested the average accommodation response did not deviate significantly from the straight line of $x = y$, which marks the accommodative level required for accurate focus [average square deviation (s^2) of measured from required values: animal 4: $s^2 = 0.15$ D^2, animal 7: $s^2 = 0.04$ D^2; animal 9: $s^2 = 0.05$ D^2]. This shows that the ocular focus of the eye was very precise over a large range of target distances. Resting turtles that did not focus on a presented prey item were often hyperopic by 10 or even 20 D. With these hyperopic values included, we observed a total accommodation range of about 55 D. The speed of accommodation was impressively large. Based on occasional jumps during continuous accommodation we estimated an average speed of 55 D s^{-1} with maximal values of 120 D s^{-1} (for comparison: maximal speed of human accommodation is 33 D s^{-1} in children and 18 D s^{-1} in adults; Schaeffel et al. 1993).

Switch between independent and coupled accommodation

Leaf turtles usually move their eyes independently from each other (Rudloff 1990). During visual prey fixation, however, we observed that both eyes converged to achieve binocular fixation of the prey. This was quite similar to the behaviour of the chameleon. However, we found an interesting difference in that the turtles apparently lacked saccadic eye movements. Accommodation was also always independent in the two eyes if no prey item was in sight. After a prey target was presented, the turtles usually focussed with one eye first and, shortly thereafter, with the other eye (Fig. 4). This resulted in a symmetrical refraction in the two eyes during binocular prey fixation (Fig. 2). At the end of a binocular fixation sequence, the two eyes relaxed often also one after the other (Fig. 5). In a subsequent set of experiments we tested whether the symmetry of accommodation was achieved independently in the two eyes or by internal neuronal coupling. One eye was covered by an infrared light transmitting filter (Kodak Wratten 87C) which permitted measurements but blocked vision. We found that the refraction was still symmetrical in the two eyes (Fig. 6A). This strongly supported the hypothesis that the accommodation of the two eyes was coupled by an internal neuronal mechanism. We then replaced the IR light-transmitting filter by an ophthalmic lens (Fig. 6B). Now, both eyes could see the prey but the plane of focus was artificially altered in one eye with respect to the other. If accommodation was firmly
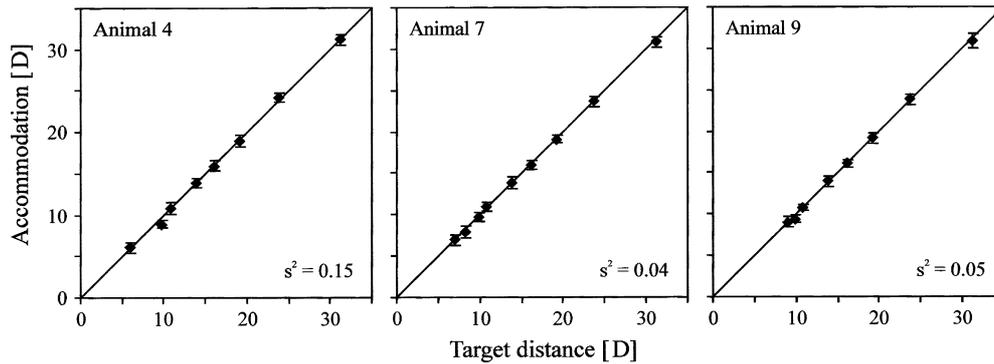
Fig. 3 Accommodative stimulus/response function for three individuals. Accommodation (y) is plotted versus target distance (x), both stated in dioptres. Values were averaged from numerous measurements ($n > 10$) recorded during the presentation of a prey target. Distinct pauses in fixation were not evaluated. Error bars represent standard deviations. Accurate focus is achieved if the amount of accommodation matches the target distance ($x = y$). The average square deviation (s^2) from this ideal correlation was very small for the prey distances investigated (6–31 D, corresponding to distances between 17 and 3 cm) demonstrating a precise focus over a large range of dioptres

linked in the two eyes, the refraction of the covered eye should differ from the uncovered one by the power of the ophthalmic lens. This was confirmed by quantitative measurements of the refractive values in the two eyes. Figure 7A shows that the refraction of the covered (left) eye differed from the uncovered (right) eye by 6 D. This difference was equivalent to the power of the front lens. The same is seen in Fig. 7B and C. These traces also include changes of accommodation that are interesting with respect to the nature of binocular accommodation coupling. In Fig. 7B, the target was correctly focussed first by the uncovered eye while the covered one was under-accommodated by 6 D. The two eyes then changed their focus simultaneously. The covered eye was now in correct focus. To achieve this correct focus, the left eye (covered with −6-D lens) has to accommodate 6 D more than normal in order to eliminate the added lens power. This increase of accommodation can be seen in the (still coupled) uncovered eye which was now 6 D over-accommodated with respect to the prey distance (the retinoscope measures the actual refraction of both the dioptric apparatus of the eye and the ophthalmic lens. Symmetrical accommodation is present if the refractions of the two eyes differ from each other by 6 D). Figure 7C shows similar changes of accommodation in the covered and uncovered eye. In the second half of the sequence, however, the two eyes changed their focus not simultaneously but subsequently one after the

Fig. 4A–D Infrared video frames showing two specimens of *Geoemyda spengleri* together with a prey target (mealworm presented in a clamp; visible in the lower part of the pictures). The animals were placed in a cardboard box with a hole just big enough to let their head but not the carapace pass through. **A, C** Uncoupled accommodation was observed during independent fixation movements of the two eyes. Opposite gradients of the IR light reflexes in the pupils indicated large differences of refractive power. **B, D** Coupled accommodation: identical intensity profiles of the IR light reflexes in both eyes during binocular prey fixation
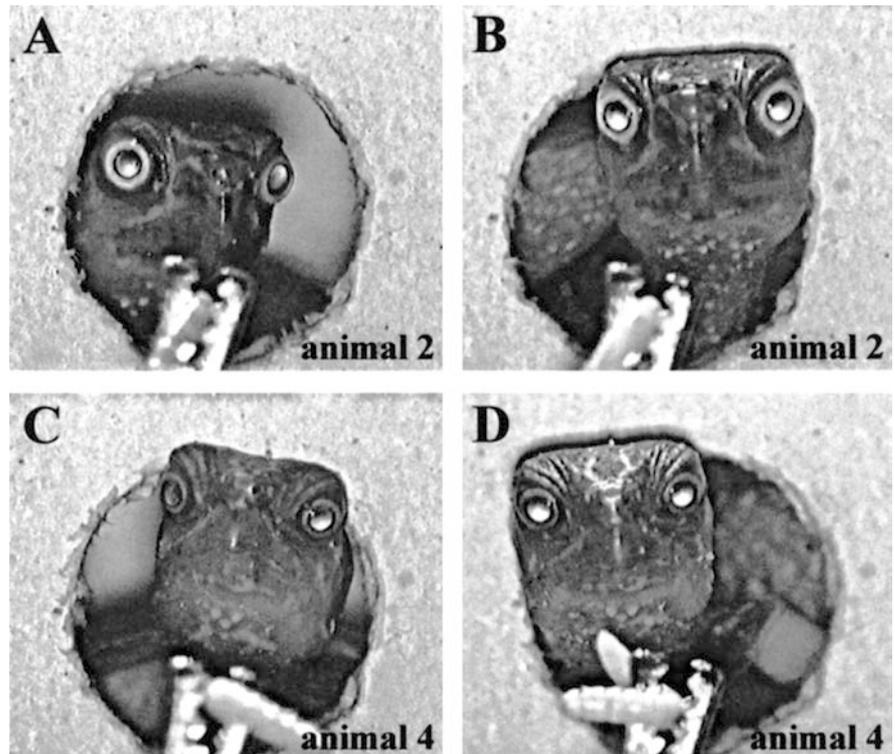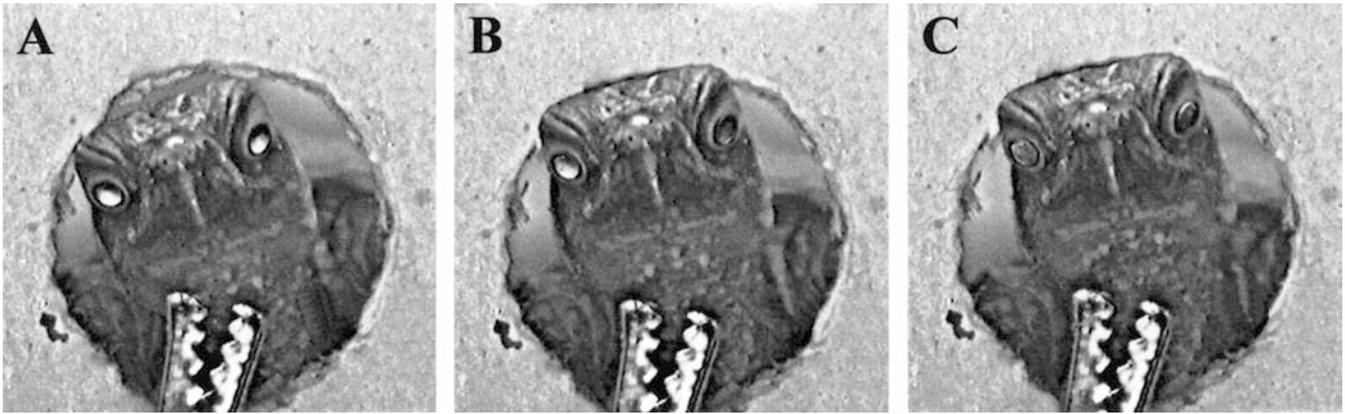
Fig. 5A–C A sequence of infrared video frames at the end of binocular focus: the prey has just dropped from the clamp. Note that the symmetrical focus in both eyes (**A**) is lost when the accommodation tonus relaxes (**B**). In the end both eyes are far-accommodated. They are not focused on the same distance, though, as indicated by a slight difference of the intensity profiles in the pupils (**C**)

other. The left eye retained its original refractive state until it converged its accommodation tonus to the new level of the right eye. In addition to this uncoupled mode of focal changes, it is also apparent from Fig. 7C that a previous state of accommodation is stored by the neural template. The right eye was defocused with respect to the target distance at the beginning of the sequence. After a short time with correct focus it returned to the same inappropriate state of focus again. A similar phenomenon is seen for the left eye at the end of the same sequence and was observed frequently also in other trials that have not been included into the figures.

Change of pupil size with accommodation

In addition to accommodation, we also monitored the pupil size during visual prey fixation under bright and dim light conditions. We found that the diameter of the pupil was affected both by the ambient light level and by accommodation. Figure 8 shows that, in the non-accommodating eye, the pupil reacts to an increase in ambient light intensity with a decrease in size. A pupillary constriction was also observed during near-accommodation (target distance < 2 cm). In this case, the size of the constricted pupil did not differ in both light conditions. The pupillary responses were generally independent in the two eyes as illustrated in Fig. 9.

Discussion

Precise focus control in an afoveate species

In this paper, we report that Vietnamese leaf turtles focused precisely over a large dioptric range. A similar precision of the accommodation response was previously found in chameleons that use ocular focus as a
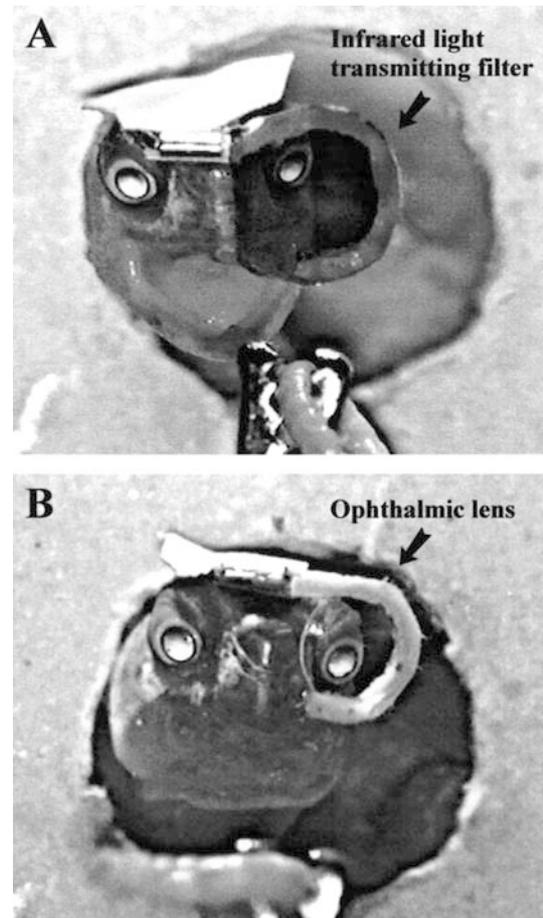

Fig. 6 A An IR light-transmitting filter placed in front of one eye of a Vietnamese leaf turtle (animal 9). Vision is blocked in the occluded eye but the reflex of the IR light from the retinoscope is still visible. Despite the monocular deprivation, both eyes are focused on the target (note the similar light gradients in the pupils). **B** Ophthalmic lens of −6 D placed in front of one eye of the same individual. To test whether accommodation is also linked together during binocular prey fixation if both eyes get visual input, one eye was covered with a lens that shifted the plane of focus. For results see Fig. 7

distance cue during prey capture (Harkness 1977; Ott and Schaeffel 1995). For the chameleon eye, Harkness and Bennett-Clark (1978) proposed that the deep, funnel-shaped convexiclivate fovea in the central fundus
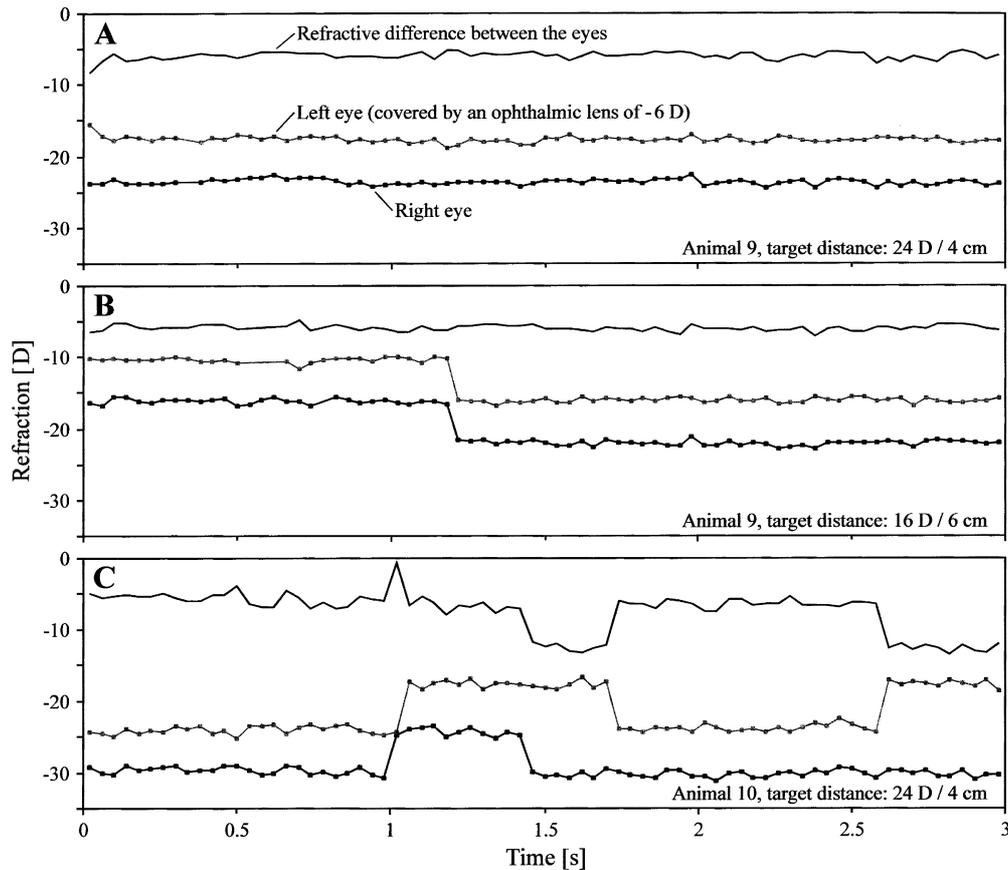
Fig. 7A–C Time-course of refraction in Vietnamese leaf turtles wearing an ophthalmic lens of −6 D in front of their left eye. **A** Animal 9, target distance 24 D/4 cm; **B** animal 9, target distance 16 D/6 cm; **C** animal 10, target distance 24 D/4 cm. Note that the retinoscopic measures represent the total refraction and, therefore, include the power of the ophthalmic lens in the left eye. The turtles were focusing on a prey target presented at different distances. *Black dots*: right eye, *grey dots*: left eye, *smooth black line*: difference between the refractive values of the two eyes. Usually, the refractive state measured in the lens-covered eye is about 6 D more hyperopic than the one determined in the other eye. Hence, both eyes actually accommodate by the same amount which provides evidence for an internal coupling. If both eyes were focusing independently from each other on the same target, the measured refractions would be similar. Occasionally, the animals showed non-symmetrical accommodation, which was apparent by the different refractions in the two eyes

served as a focus detector because it distorted the image in such a way that the focus error was enhanced and more easily detected. In a study of the eyes of raptors Snyder and Miller (1978) argued that the spherical bottom of the convexiclivate fovea acted as a negative lens which, due to a telephoto effect, created a 1.45-fold larger foveal image. This, in turn, should improve the detection of focus errors. A similar effect, unique to the chameleon, is created by the negative lens power of these lizards (Ott and Schaeffel 1995). Combined with a cornea of high refractive power, the negatively powered lens of the chameleon creates a telephoto system that enlarges the retinal image as a whole. The significance of this effect was studied in various vertebrate eyes scaled

to the same axial length. The relative size of the retinal image was largest in the eye of the chameleon. As a general trend, species with high visual acuity had greater retinal image sizes which were achieved by an increase of corneal relative to lens power (Ott and Schaeffel 1995).

An anatomical investigation of the retina (Henze et al. 2004) revealed that the retina of *G. spengleri* has a horizontal visual streak of enhanced ganglion cell density but not a central fovea. Visual resolution is unknown for *G. spengleri* but the investigation of red-eared sliders (*Pseudemys scripta elegans*) revealed values of up to 10 cycles/deg (Northmore and Granda 1991) which is considerably lower than visual acuity in humans (53–60 cycles/deg; Williams 1988). For the chameleon, no direct data exists about visual resolution but anatomical investigation showed that, in addition to a higher image magnification, there is a closer spacing of photoreceptors than in the central human retina (Püter 1912, cited by Franz 1934). While the anatomical resolving power of *Pseudemys* is generally lower, it is even more reduced in *Geoemyda* since the maximal density of retinal ganglion cells is considerably lower than in Pseudemys (Henze et al. 2004). The lack of ocular specializations that improve visual acuity in a species with high accommodative precision indirectly questions the significance of high image resolution or a specially shaped convexiclivate fovea for accurate focus control. Taken together, the evidence suggests that precise accommodation does not require high visual acuity. A similar
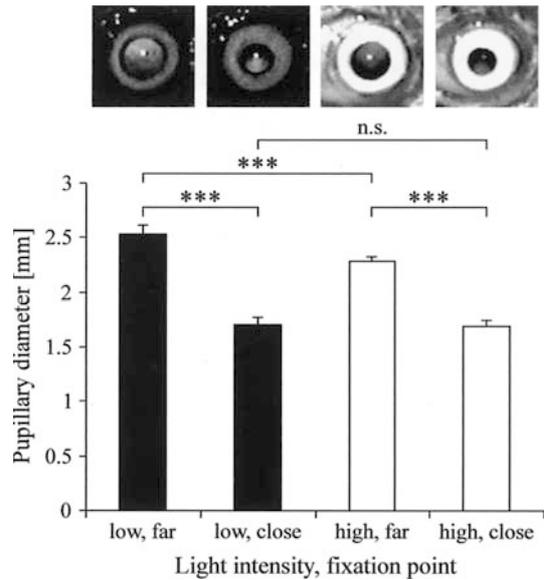
Fig. 8 Pupillary response to light and accommodation in *G. spengleri*. Images on the *top* show the pupil of a Vietnamese leaf turtle (animal 1) under different conditions (from left to right): (1) low light intensity and far-accommodation, (2) low light intensity and near-accommodation, (3) high light intensity and far-accommodation, (4) high light intensity and near-accommodation. Averaged measures of pupillary diameter from seven animals in the respective situation are presented in the graph below. Error bars indicate standard deviations. An increase in ambient illumination did not influence the pupil size in the near-accommodated eye ($P > 0.9$, n.s.). During far-accommodation, however, it induced a highly significant decrease in the diameter of the pupil (***$P < 0.001$). A similar, highly significant pupillary constriction was observed when the turtle changed fixation from far to near, no matter whether illumination was high or low (in both cases ***$P < 0.001$). Results are based on an ANOVA ($F_{(3,24)} = 341$, $P < 0.001$) and post hoc paired *t*-tests with Bonferroni correction (P values as mentioned above)
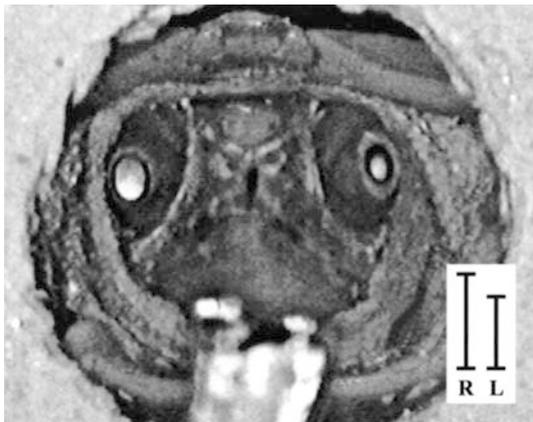

Fig. 9 IR video frame showing the lack of consensual pupillary response in *G. spengleri* (animal 8). For better comparison, the inset gives the maximum diameter of both pupils (*R* right, *L* left; both with respect to the animal) in a twofold higher scale

conclusion exists for the visual control of axial eye growth. Schaeffel and Diether (1999) found that em-metropization occurred even from very poor images

with low spatial frequency content and image contrast. At present, it is not known which cue the visual system uses for accommodation control. Various possibilities have been discussed (see Kruger et al. 1997 for references). Recent studies of human accommodation strongly suggest that longitudinal chromatic aberration is used as a major cue (Kruger et al. 1997; Kröger and Binder 2000). In addition, Seidemann and Schaeffel (2002) found that chickens responded with an immediate accommodative shift when the ambient illumination was changed from red to blue light. The finding that the focusing system is colour sensitive implies that it should benefit from a higher diversification of spectrally sensitive cones. Tetrachromatic vision is common among birds and reptiles and was proved to be present in chameleons (Bowmaker et al. 2000) as well as in turtles (*Pseudemys scripta elegans*; see also Ventura et al. 2001 for further references). Additional studies are needed to elucidate the role of longitudinal chromatic aberration for the accommodation system of reptiles.

Coupling of accommodation

Both eyes are highly moveable in *G. spengleri* and achieve a large binocular overlap in the visual field during prey fixation (Rudloff 1990). In this study, we found that accommodation was normally independent in the two eyes but was locked together when the animal focussed on a bait. The same observations were previously made in chameleons (Ott et al. 1998). In both species, the coupling of the accommodation feedback loop is mediated by internal neuronal circuits since even monocular deprivation did not affect symmetrical refractions. The only sauropsids in which accommodation was found to be always symmetrically in the two eyes were barn owls (Schaeffel and Wagner 1992). Owls have very restricted eye movements (Steinbach and Money 1973) and it is possible that the neural circuitry was fixed in a mode of binocular coupling once both eyes had lost their mobility and were locked in the frontal position. Moreover, these birds achieved true three-dimensional vision (stereopsis) during their evolution (Pettigrew and Konishi 1976). In chameleons, binocular coupling also affects the neural control of eye movements since saccades were synchronized during prey fixation but otherwise independent from each other (Ott 2001). Behavioural and search coil studies, however, showed that stereopsis or even triangulation is unlikely to be present in chameleons (Harkness 1977; Kirmse et al. 1994; Ott et al. 1998). For turtles, no data exist about stereoscopic vision or other types of binocular interaction. In a behavioural situation not related to prey fixation, Ariel (1990) found that the optokinetic nystagmus (OKN) of the eyes was unyoked. This was also observed in the OKN of chameleons (Kirmse 1988). The situation in Vietnamese leaf turtles and chameleons which switch to a symmetrical focus during prey fixation probably represents an intermediate state between

monocular and fused binocular vision. As a first advantage prior to stereopsis, parallel binocular processing improves visual acuity since the signal-to-noise ratio is reduced by the factor of $\sqrt{2}$ (Campbell and Green 1965).

Pupillary response to light and accommodation

Both bright light and near-accommodation induced a pupillary constriction in *G. spengleri*. The response to light was for a long time denied for turtles (Walls 1942; Duke-Elder 1958) but was later shown to be present in red-eared sliders (Granda et al. 1995). In *G. spengleri*, the constriction of the pupil was apparently maximal during accommodation at targets closer than 2 cm below which no further decrease in pupil size was observed under brighter ambient illumination. A constriction of the pupil with accommodation was described as pupillary near response in humans (Semmlow and Stark 1973) as well as in chameleons (Ott et al. 1998). In some turtle species, a high degree of accommodation is achieved by squeezing the soft lens through the pupil aperture (Fritzberg 1912; Walls 1942; Duke-Elder 1958). A constriction of the pupil might, therefore, be a consequence of this special mechanism of accommodation.

References

Ariel M (1990) Independent eye movements in the turtle. Vis Neurosci 5:29–41

Bishop PO, Pettigrew JD (1986) Neural mechanisms of binocular vision. Vision Res 26:1587–600

Bowmaker JK, Loew ER, Ott M (2000) Porphyrins and rhodopsins in chameleons, *Chamaeleo dilepis* and *Furcifer lateralis*. IOVS 41: B275

Campbell FW, Green DG (1965) Monocular versus binocular visual acuity. Nature 208:228–229

Duke-Elder S (1958) System of ophthalmology. I. The eye in evolution. Kimpton, London, pp 353–395

Franz V (1934) Vergleichende Anatomie des Wirbeltierauges. In: Bolk L, Göppert E, Kallius E, Lubosch W (eds) Handbuch der vergleichenden Anatomie der Wirbeltiere Bd. 2, Urban und Schwarzenberg, Berlin

Fritzberg W (1912) Beiträge zur Kenntnis des Akkommodationsapparates bei Reptilien. Arch Vergl Ophthalmol 3:292–322

Glickstein M, Millodot M (1970) Retinoscopy and eye size. Science 168:605–606

Granda AM, Dearworth JR, Kittila CA, Boyd WD (1995) The pupillary response to light in the turtle. Vis Neurosci 12:1127–1133

Harkness L (1977) Chameleons use accommodation cues to judge distance. Nature 267:346–349

Harkness L, Bennett-Clark HC (1978) The deep fovea as a focus indicator. Nature 272:814–816

Henze M, Schaeffel F, Ott M (2004) Variations in the off-axis refractive state in the eye of the Vietnamese leaf turtle (*Geoemyda spengleri*). J Comp Physiol A

Kirmse W (1988) Foveal and ambient visuomotor control in chameleons (Squamata) – experimental results and comparative review. Zool Jb Physiol 92:341–350

Kirmse W, Kirmse R, Milev E (1994) Visuomotor operation in transition from object fixation to prey shooting in chameleons. Biol Cybern 71:209–214

Kröger RH, Binder S (2000) Use of paper selectively absorbing long wavelengths to reduce the impact of educational near work on human refractive development. British J Ophthalmology 84:890–893

Kruger PB, Mathews S, Katz M, Aggarwala KR, Nowbotsing S (1997) Accommodation without feedback suggests directional signals specify ocular focus. Vision Res 37:2511–2526

Ott M (2001) Chameleons have independent eye movements but synchronise both eyes during saccadic prey tracking. Exp Brain Res 139:173–179

Ott M, Schaeffel F (1995) A negatively powered lens in the chameleon. Nature (Lond) 373:692–694

Ott M, Schaeffel F, Kirmse W (1998) Binocular vision and accommodation in prey-catching chameleons. J Comp Physiol A 182:319–330

Northmore DPM, Granda AM (1991) Refractive state, contrast sensitivity, and resolution in the freshwater turtle, *Pseudemys scripta* elegance, determined by visual evoked potentials. Vis Neurosci 7:619–625

Pettigrew JD, Konishi M (1976) Neurons selective for orientation and binocular disparity in the visual wulst of the barn owl (*Tyto alba*). Science 193:675–678

Pettigrew JD, Collin SP, Ott M (1999) Convergence of specialised behaviour, eye movements and visual optics in the sandlance (Teleostei) and the chameleon (Reptilia). Curr Biol 9:421–424

Rudloff HW (1990) Schildkröten. Urania, Leipzig

Schaeffel F, Diether S (1999) The growing eye: an autofocus system that works on very poor images. Vision Res 39:1585–1589

Schaeffel F, Mathis U (1991) Underwater vision in semi-aquatic European snakes. Naturwissenschaften 78:373–375

Schaeffel F, Wagner H (1992) Barn owls have symmetrical accommodation in both eyes, but independent pupillary responses to light. Vision Res 32:1149–1155

Schaeffel F, Howland HC, Farkas L (1986) Natural accommodation in the growing chicken. Vision Res 26:1977–1993

Schaeffel F, Wilhelm H, Zrenner E (1993) Inter-individual variability in the dynamics of natural accommodation in humans: relation to age and refractive errors. J Physiol (Lond) 461:301–320

Schaeffel F, Hagel G, Eikermann J, Collett T (1994) Lower field myopia and astigmatism in amphibians and chickens. J Opt Soc Am A 11:487–495

Schmid KL, Howland HC, Howland MJ (1992) Focusing and accommodation in tuatara (*Sphenodon punctatus*). J Comp Physiol A 170:263–266

Seidemann A, Schaeffel F (2002) Effects of longitudinal chromatic aberration on accommodation and emmetropization. Vision Res 42:2409–2417

Semmlow J, Stark L (1973) Pupil movements to light and accommodative stimulation: a comparative study. Vision Res 13:1087–1100

Snyder AW, Miller WH (1978) Telephoto lens system of falconiform eyes. Nature 275:127–129

Steinbach MJ, Money KE (1973) Eye movements of the owl. Vision Res 13:889–891

Ventura DF, Zana Y, De Souza JM, Devoe RD (2001) Ultraviolet colour opponency in the turtle retina. J Exp Biol 204:2527–2534

Walls GL (1942) The vertebrate eye and its adaptive radiation. Hafner, New York

Walls GL (1961) The evolutionary history of eye movements. Vision Res 2:69–80

Williams DR (1988) Topography of the foveal cone mosaic in the living human eye. Vision Res 88:433–439