Prey snapping and visual distance estimation in Texas horned lizards, *Phrynosoma cornutum*

Matthias Ott[1,*], Joachim Ostheim[2] and Wade C. Sherbrooke[3]

[1]*Institute for Anatomy, University of Tübingen, Österbergstrasse 3, 72074 Tübingen, Germany,* [2]*Allgemeine Psychologie, University of Konstanz, Postfach 5560 C36, 78457 Konstanz, Germany* and [3]*Southwestern Research Station, American Museum of Natural History, Portal, AZ 85632, USA*

*Author for correspondence (e-mail: ott@anatu.uni-tuebingen.de)

Summary

Captive Texas horned lizards were high-speed video-taped while feeding on ants in order to study the role of vision in facilitating tongue-protrusion capture of prey. Analysis of tongue movements revealed that prey snapping in these lizards is not a typical fixed-action pattern. By contrast, it is variable in performance and duration. Lizards adjusted head and tongue direction during the strike, within a few milliseconds, in response to movements of the prey. The duration of a typical tongue strike was 100–150 ms. The strike duration was prolonged after ophthalmic lenses were placed in front of one or both eyes. These lenses were used to investigate whether horned lizards use accommodation to judge prey distance. Focal changes of negatively powered ophthalmic lenses (employed monocularly) induced a clear underestimation of prey distance by the lizards, confirming the hypothesized expectation that accommodation is used for depth perception. The effect of the lenses was different in the two animals tested with monocular restriction. This, together with the lack of difference in responses by the lizards when untreated and when both eyes were lens covered (binocular treatment of equal power, –9 D), illustrates that horned lizards also use other visual parameters for depth perception.

Key words: visual depth perception, accommodation, horned lizard, tongue protrusion, fixed-action pattern.

Introduction

The use of a prehensile tongue for capturing prey is a typical feature of all iguanian lizards (Agamidae, Chamaeleonidae and Iguanidae; Schwenk and Throckmorton, 1989). The kinematics of the tongue strike was investigated together with the muscular activity of the hyolingual apparatus in several iguanian species using slow-motion video recording (Herrel et al., 1996; Meyers and Nishikawa, 2000). The present paper investigates aspects of the sensorimotor activity of a prey-snapping lizard, the Texas horned lizard (*Phrynosoma cornutum*). These lizards feed almost exclusively on seed-harvester ants (*Pogonomyrmex* ssp.), which are collected one after the other by quick tongue strikes (Sherbrooke, 2003). A high-speed video camera system was used to evaluate the role of accommodation as a distance cue for prey capture. At first glance, the tongue strikes of Texas horned lizards resembled those of prey-snapping toads. But, distinct from anurans, where the tongue strike is regarded as a classical fixed-action pattern (Curio 1976), we describe in the present paper a remarkable plasticity in the performance of the strike of Texas horned lizards.

The initial goal of the present study, the evaluation of accommodation as a distance cue, was inspired by previous work on chameleons. Although distances to objects can be estimated visually by a number of monocular and binocular cues (Collett and Harkness, 1982; Davies and Green, 1994), it was found that chameleons rely solely on accommodation to judge the distance of prey items (Harkness, 1977; Ott and Schaeffel, 1995). We were interested in finding out whether this mechanism of depth perception is also predominant outside the Chamaeleonidae, in other lizards with different feeding strategies. The question was whether *Phrynosoma* would judge prey distances mainly by accommodation, similar to chameleons, or whether their different prey capture requirements, on the ground and at relatively short distances, would promote the use of other mechanisms of visual distance estimation.

In our experiments, the focal plane of the eye was experimentally shifted by ophthalmic lenses that were placed in front of one or both eyes. Such treatment should result in a systematic error of depth perception corresponding to the power of the ophthalmic lens if accommodation is used to judge distance (Harkness, 1977; Ott et al., 1998). Our results clearly show that (1) accommodation was used by *Phrynosoma* to judge distances but that (2), in contrast to chameleons, accommodation was apparently used in combination with additional cues in determining prey distance, such as binocular

vision and/or a simple trial and error task. This was suggested by the observation that animals with lens treatment showed an increased duration of the tongue strike according to the lizard's unusual ability to adjust the length and direction of the tongue's movement during prey snapping.

Materials and methods

Several *Phrynosoma cornutum* Harlan 1825 were collected in southeastern Arizona (Sherbrooke, 2002) with permits from the Arizona Game and Fish Department. The lizards were shipped to Germany where they were housed in terraria in the laboratory. Lizards were fed local ants and juvenile field crickets (*Gryllus bimaculatus*). Two animals showed excellent responses during the trials and were used for the statistical analysis shown in Figs 3, 4. The other animals were more lethargic and allowed only qualitative observations.

Lizards were allowed to move freely in a glass terrarium (60 cm×30 cm×30 cm) with a sand-covered bottom. Illumination was provided by the fluorescent lights of the laboratory, and heat was supplied by an infrared bulb. Ants were collected into a short plastic tube. The tube was covered by a piece of foam rubber through which a small aperture was left that allowed the ants to crawl out one after the other. The lizards usually captured the ants directly from the foam rubber cover. Prey snapping was recorded with a high-speed video system at 500 frames s^{-1} (Speedcam +500; Weinberger, Dietikon, Switzerland), with two cameras for simultaneous recordings from above and from one side.

To evaluate the use of accommodation as a distance cue, the animals were allowed to catch their prey either under binocular or monocular conditions and with or without ophthalmic lenses. Monocular vision was achieved by placing a small piece of cardboard in front of one eye so that the frontal visual field was occluded. Commercially available contact lenses were used as ophthalmic lenses and placed in front of the eye with the aid of a wire fixed to the cranium by adhesive tape. If accommodation was being used for visual distance estimation, the lizards would be expected to make predictable errors corresponding to the power of the ophthalmic lens. For example, a negatively powered lens increases the focal length of the eye and the lizard has to accommodate more in order to compensate for the lens. Accordingly, the lizard would judge the distance of the prey to be closer than it actually was and the snap would be too short. The opposite would be expected for a lens with positive power. In order to exclude tactile information when the tongue hits the prey, it was initially planned to produce an illusory target by placing prism spectacles in front of the eyes, similar to the study of Harkness (1977) in chameleons. However, we found that spectacles were not useful in *Phrynosoma*, which has a much shorter tongue than the chameleon and, due to the closer distance of its prey, would require high powers of spectacles in order to obtain a reasonable optical displacement of the prey image. Apparently, the thick prism glass excessively distorted the image of the prey, resulting in either no prey-snapping response at all
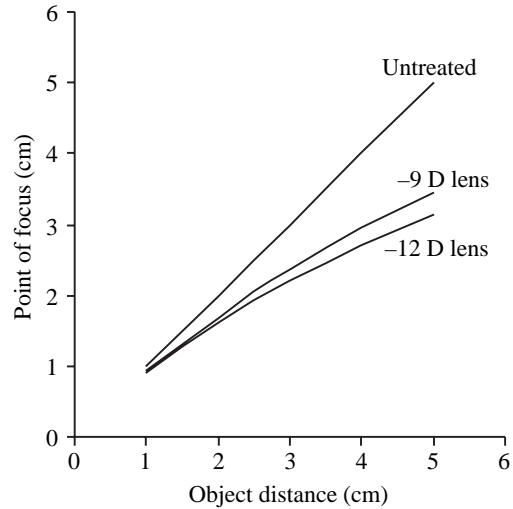

Fig. 1. Within the range of typical prey-attacking distances, the lines show the shift in focal plane (compared with untreated) that is induced by the two negatively powered ophthalmic lenses (–9 D and –12 D) used in the experiments.

or random errors. As an alternative, we restricted our experimental design to lenses of negative power that prevented tactile information because the focal plane was shifted to a point in front of the prey (and not behind, as with positive lenses). The powers must be strong enough to change the focal plane to a measurable extent. The shorter the prey distance, the weaker is the effect of the ophthalmic lens power on the overall accommodation that the animal must exert to bring the prey into focus. Two lens powers were used in the experiments: –9 diopters (–9 D) and –12 D. The changes in focal point of the two lens powers used are shown in Fig. 1. Compared with the untreated line, both lenses induced a substantial shift in focal plane within the typical range of prey-snapping distances (2–5 cm). Stronger lens powers were not used in order to avoid image distortions due to thick lenses. Also, the distance between the ophthalmic lens and the eye cannot be ignored with higher lens powers.

Prey distance was measured as the distance between the tip of the snout and the prey at the time when the tongue had just reached its maximal extension. It was at this time that prey was hit by the tongue tip in untreated lizards. If an animal underestimated the prey distance, its tongue was fully extended before it hit the prey. As a result, the distance between snout tip and prey was longer at the moment of maximal tongue extension than in the untreated lizards. In the experimental procedure, we determined the position of the snout tip when the tongue had reached 75% of its maximal extension. By this time in tongue protrusion, no tactile information was available to the animal, even in those cases where the distance was correctly estimated (Fig. 3A).

We were not able to investigate the refractive state of the eye directly by infrared retinoscopy, as was done in an earlier study of the chameleon (Ott et al., 1998). At ambient light
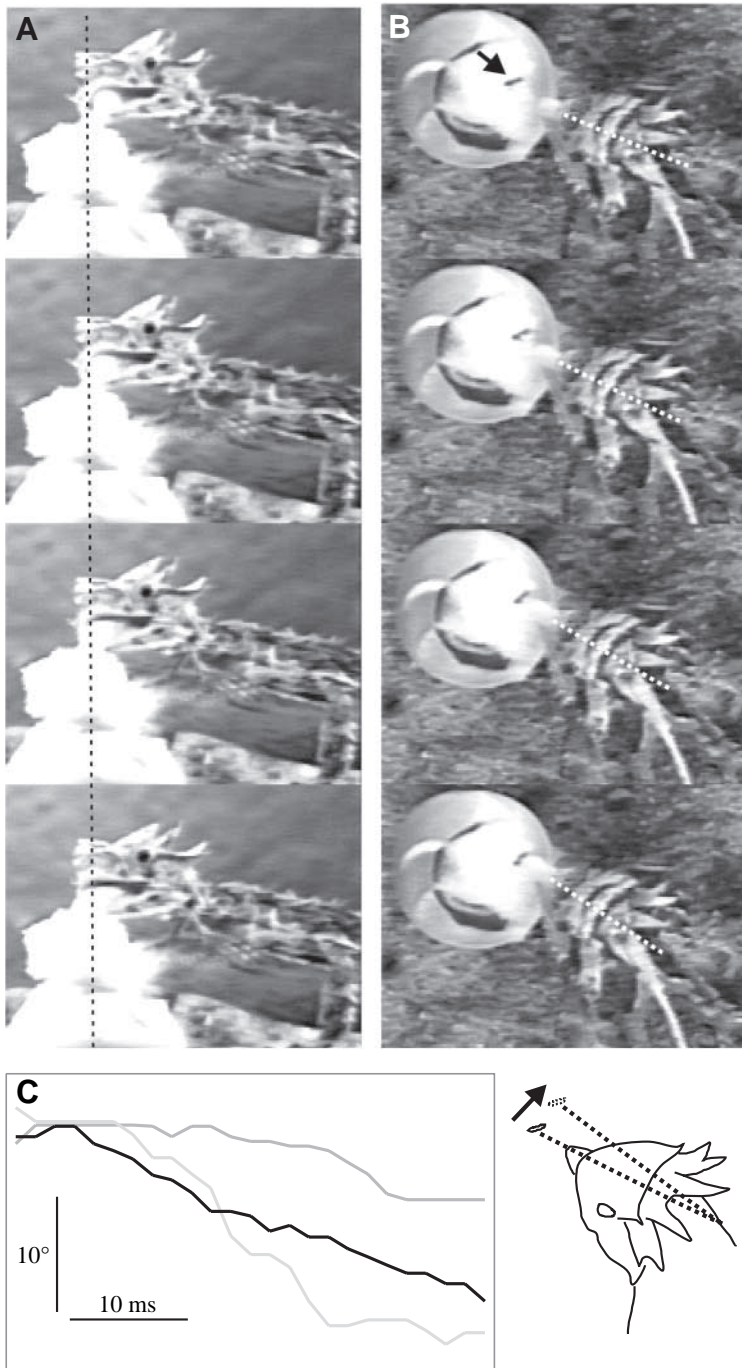
Fig. 2. (A,B) Selected video frames from a feeding sequence for *Phrynosoma cornutum*. Two video cameras were used simultaneously, one from a side view (A) and the other from above (B). As demonstrated by the frames in A, the horned lizard rotated its head to its right to adjust the direction of the tongue strike at the moving ant. The final position of the snout tip is marked by a dotted line. In the same frames recorded from above (B), the ant is marked by an arrow in the first frame. The mediosagittal plane of the lizard is marked by white dotted lines. The resolution of the frames was low due to the high speed of the video camera. (C) The schematic on the right is an outline of the lizard in the first frame in B. It illustrates schematically the turn of the mediosagittal line (dotted black lines) in relation to the movement of the ant. The graph on the left illustrates the angular change of the mediosagittal line for three other prey snaps from two different lizards.

tongue protrusion started while the head was still moving. Both movements ended when the tongue was fully extended and reached the prey with its tip (Figs 2, 3). The first two steps of the prey capture behavior, monocular fixation and quick approach, were often omitted by lizards in our experimental situation when the lizards were already positioned in front of the foam rubber from which ants emerged.

Plasticity of the tongue strike

From inspection of the high-speed video recordings, it became apparent that the horned lizards were able to adjust the trajectory of their tongue during the strike in response to the moving ant (Fig. 2). This seemed to be a prerequisite for a successful strike since quickly running ants often moved several millimeters during the duration of the tongue strike (100–150 ms). The reaction time of the lizard was difficult to determine exactly since the ants were continuously moving and, accordingly, the lizards were constantly adjusting their heads (Fig. 2C). Nevertheless, some video sequences included sudden stops and starts of the ants. From these, we estimated a very short lizard reaction time of 4–6 ms after the ants started to move again. Further measurements with a suitable experimental setup are needed to confirm this estimate. From Fig. 3, it is apparent that during the strike not only was the direction of the head axis to the prey adjusted but also the lizards modified the duration of the tongue strike according to the experimental situation. Fig. 3B shows the change of the protrusion length of the tongue and of the distance of snout to prey with time in an untreated, normal-sighted animal. The protruding tongue reached its final length within 50–80 ms. In Fig. 3C, the same animal is shown but now with a –9 D lens in front of the left eye and an occluder in front of the right eye. Vision was now monocular and the plane of focus shifted. As a consequence, the lizard underestimated the prey distance and did not hit the ant at the expected position. The animal then continued the protrusion of the tongue with lower velocity (visible as a flattening of slopes
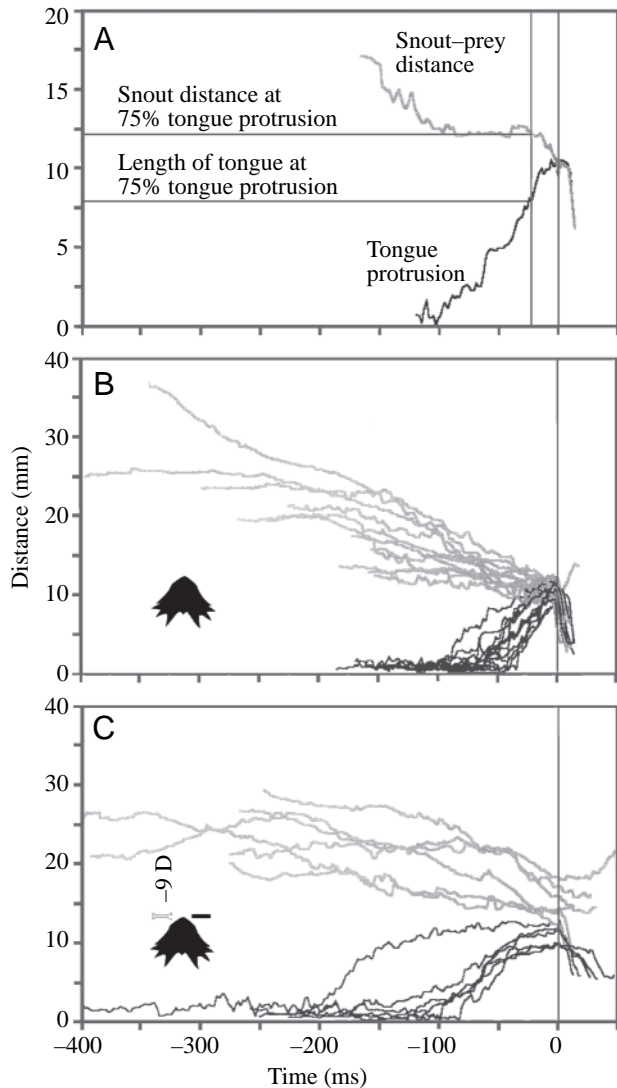
levels required for horned lizard activity, the fundus of the eye did not reflect enough light to allow measurements.

Results
Prey capture behavior

Prey capture consists of four stages: (1) monocular detection of an ant and a head-turn towards the prey, (2) quick approach to the prey up to a distance close enough for the tongue strike, (3) short phase of binocular fixation and (4) the strike, which includes the protrusion of both the head and the tongue. The

Fig. 3. Changes in the length of the protruding tongue (black lines) and the distance of the snout from the prey (gray lines) with time. (A) The method that was used to determine the correctness of the distance estimation in prey-snapping horned lizards before the prey was touched (see text). The distance of the snout from the prey was determined when the tongue had reached 75% of its final extension length. (B) Traces from 11 snaps of one untreated animal. (C) Six traces from the same animal after one eye was covered with a –9 D lens and the other eye occluded. Black silhouettes represent a dorsal view of the horned lizard's cranium, with posteriorly directed horns. The symbols in front of the cranium mean either no treatment (no symbol), occluded eye (black bar) or negatively powered ophthalmic lens (lens symbol with lens power, D=diopters). Note that the snout-to-prey distance (gray line) of the treated animal (C) is usually increased compared with that of the untreated animal (B) and that the duration of the tongue strike is longer. The tongue was usually extended at the same speed in both treatments (similar slopes of tongue protrusion in B and C) but protruded further at lower speed (flattening of slopes) during which the animal moved its head further towards the prey.

different extent (Fig. 4). A lens of –9 D induced a significant underestimation of prey distance in animal 1 but not in animal 2, where the effect of the –9 D lens was apparent but not significant compared with the untreated situation. A significant change in the second animal was only seen with the use of a lens of –12 D. Under binocular conditions (both eyes without lenses or both covered with lenses of similar power), the effect of the lens was reduced and not significant in either animal (Fig. 4).

Discussion

Plasticity and visual control of the snap

Prey snapping as the consummatory act of the prey-catching sequence (orienting, approaching, fixating, snapping) is usually regarded as a stereotyped, ballistic action, at least in salamanders (Roth, 1976) and anurans (Hinsche, 1935; Grobstein et al., 1983; Weerasuriya, 1989). Amphibians usually close their eyes during snapping, thus making visual feedback impossible. Similarly, chameleons move both eyes backward when the tongue is shot at prey (Ott, 2001). But even with visual monitoring, it would be impossible for a chameleon to change the trajectory of its tongue due to the ballistic nature of the tongue shot. The same inability for post-thrust adjustments is seen in anolis lizards that jump to catch their prey (Moermond, 1981). By contrast, horned lizards do not jump, have shorter tongues than chameleons and do not shoot their tongue out of the mouth in the ballistic manner of a chameleon (Sherbrooke, 2003). The body of the tongue in all members of the Iguanidae remains on the entoglossal process during the tongue strike (Meyers and Nishikawa, 2000). The direction of the tongue snap can thus be changed during the strike by turns of the head. To our knowledge, no previous study has reported such a change of tongue trajectory. Perhaps the specialization to feed on fast-moving ants facilitated the ability of quick tongue

of the black curves in Fig. 3C) while the head was still moving further towards the prey.

Effects of ophthalmic lenses

From Fig. 3B,C, it can be seen that the distance of the head to the prey was variable when the animals initiated the snap. During the strike, the head was moved forward up to a position of 10–12 mm away from the ant. This final position was equivalent to the length of the fully protruded tongue, which, at this time, hit the prey in visually untreated lizards. Animals that wore negatively powered ophthalmic lenses usually underestimated the distance towards the prey. The distance of the head to the ant at the reference time of 75% tongue protrusion was then longer than in untreated animals and the lizards had their tongues fully protruded before the prey was hit. Such an underestimation was expected if the animal uses accommodation as a distance cue. Under monocular conditions (frontal field of one eye occluded and the other eye provided with or without a negatively powered lens), the effect of the ophthalmic lens was noticeable in both animals tested but to a
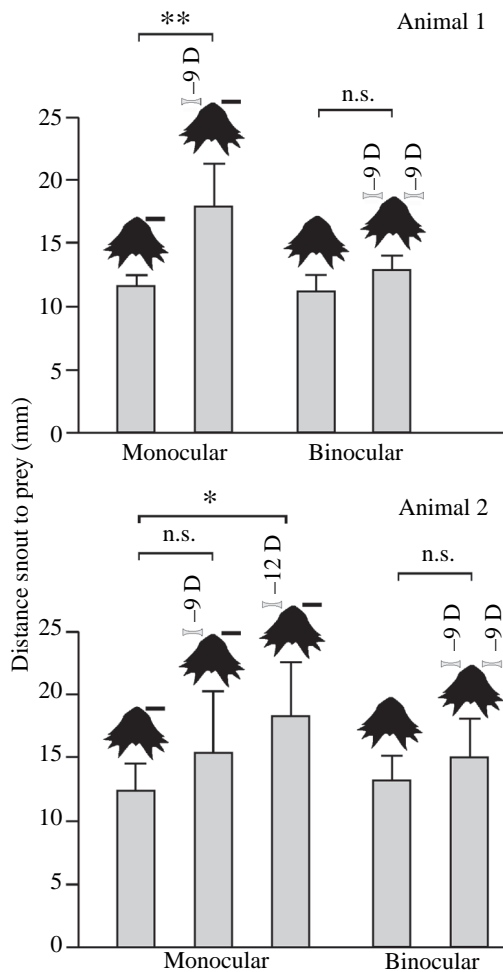
Fig. 4. The histograms summarize the effect of negatively powered ophthalmic lenses on visual perception of depth. Black silhouettes represent a dorsal view of the horned lizard's cranium, with posteriorly directed horns. The symbols in front of the cranium mean either no treatment (no symbol), occluded eye (black bar) or negatively powered ophthalmic lens (lens symbol with lens power, D=diopters). A clear effect of the lens was observed in both animals in monocular trials, where one eye was occluded and the other eye either untreated (control) or covered by a –9 D lens [**$P<0.001$ for animal 1; not significant (n.s.) for animal 2] and –12 D lens (*$P<0.05$ for animal 2). The different effect of the –9 D lens in both lizards indicates the use of additional cues for distance estimation. The effect of the lens was clearly reduced if the animals were allowed to use both eyes for binocular vision. Results are based on an analysis of variance (ANOVA; $F_{3,32}=22$, $P<0.001$ for animal 1; $F_{4,40}=3.54$, $P=0.014$ for animal 2; P-values as mentioned above).

corrections in horned lizards. The estimated reaction time of only a few milliseconds implicates a short visuomotor neuronal pathway, with only a few intervening synapses. Further studies are needed to determine (1) the precise reaction time (as a prerequisite for studies of the underlying neuronal substrate) and (2) whether a visuomotor control of the prey snap is adaptively present in horned lizards or is also found in other closely or distantly related taxa of lizards.

Effect of negatively powered ophthalmic lenses on distance estimation by accommodation

In horned lizards, we observed a clear underestimation of prey distance after the focal plane of one eye had been changed by negative lenses (Figs 3B,C, 4). This was in accordance with the hypothesis that horned lizards use accommodation as a distance cue, similar to the previous report from chameleons (Harkness, 1977; Ott and Schaeffel, 1995). The effect was very clear and significant in both lizards tested even though it was less prominent in the second lizard (Fig. 4). Precision is a prerequisite for the use of accommodation as a distance cue. Precise accommodation requires high visual acuity. Based on the structure of the eye (M.O., personal observation) and the retina (Detwiler and Laurens, 1921) it is apparent that horned lizards have high visual acuity, comparable with that of chameleons (Ott and Schaeffel, 1995). Therefore, the eye of *Phrynosoma* should be capable of detecting small deviations in image focus and, hence, be capable of precise accommodation control. A variance of estimated distance values in each trial might be associated with the tolerance that is caused by the depth of field of the eye. The following calculation, however, shows that the depth of field is very small in the eye of *Phrynosoma* at close distances. It is, therefore, not a major reason for the observed variability of prey-snapping distances. The depth of field can be calculated by the relation: $D=7.03$/spatial frequency $\times$ pupil diameter (Green et al., 1980).

For the eye of *Phrynosoma*, this equation yields a value of 0.31 D for the depth of field [pupil diameter=1.5 mm, as measured in the living eye, and maximal resolved spatial frequency calculated by the equation SF=PND/$\sqrt{3}$ $\times$ photoreceptor-distance $\times$ 57.3 (Reymond, 1985), assuming a receptor spacing of 2 μm (after Detwiler and Laurens, 1921) and a posterior nodal distance (PND) of 0.6 $\times$ axial length (5 mm) of the eye]. With this conservative calculation (it is very likely that the actual resolving power of the eye is higher than estimated), the lizard would have a depth of field of 0.022 mm at a focal distance of 2 cm, 0.06 mm at 3 cm, 0.1 mm at 4 cm and 0.159 mm at 5 cm. These values are low compared with the experimental lens-induced shifts of the focal plane (compare with Fig. 1).

Evidence of additional modes of prey distance estimation

While the lens-induced effect of underestimation was probably similar in both animals, they might have used different strategies to deal with this treatment, including other depth parameters such as motion parallax or inborn or learned knowledge of prey size. For any animal it is advantageous to use more than one visual distance cue and to weigh the information from each cue according to its signal-to-noise ratio, which determines its reliability (Davies and Green, 1994). The kind of parameters that are used is determined by the physical constraints of the visual system of the animal and its environment. For the toad, Collett and Harkness (1982) have estimated that depth perception from disparity cues was 16 times more accurate than distance estimation based on

accommodation. The reverse was calculated by the same authors for the eye of the chameleon, where accommodation was more reliable than stereopsis.

The use of additional binocular cues in *Phrynosoma* was apparent in the binocular trials, where both eyes were covered with lenses of similar power (Fig. 4). In these cases, the underestimation of prey distance nearly disappeared in both lizards tested. It is not clear whether three-dimensional (3-D) vision was involved, since stereopsis is difficult to determine in lower vertebrates that cannot be trained on artificial stimuli containing nothing other than 3-D information. Prisms that alter the direction of gaze while leaving the focus of the eye unaffected have been used to demonstrate the presence of steropsis in toads (Collett, 1977) and to exclude this mechanism for chameleons (Harkness, 1977). As mentioned earlier, we were not able to apply a similar method in horned lizards because high-powered prisms were needed and these distorted the image. Nevertheless, our data clearly demonstrate that horned lizards have the ability to employ multiple systems, including accommodation, in determining prey distances during tongue snapping.

References

Collett, T. S. (1977). Stereopsis in toads. *Nature* **267**, 349-351.

Collett, T. S. and Harkness, L. (1982). Depth vision in animals. In *Analysis of Vertebrate Behaviour* (ed. D. J. Ingle, M. A. Goodale and J. W. Mansfield), pp. 111-176. Boston: MIT Press.

Curio, E. (1976). *The Ethology of Predation.* New York: Springer-Verlag.

Davies, M. N. O. and Green, P. R. (1994). Multiple sources of depth information, an ecological approach. In *Perception and Motor Control in Birds* (ed. M. N. O. Davies and P. R. Green), pp. 339-355. Berlin, Heidelberg, NewYork: Springer.

Detwiler, S. R. and Laurens, H. (1921). Studies on the retina. The structure of the retina of *Phrynosoma cornutum*. *J. Comp. Neurol.* **32**, 347-356.

Green, D. G., Powers, M. K. and Banks, M. S. (1980). Depth of focus, eye size and visual acuity. *Vision Res.* **20**, 827-835.

Grobstein, P., Comer, C. and Kostyk, S. K. (1983). Frog prey capture, between the sensory maps and directed motor output. In *Advances in Vertebrate Neuroethology* (ed. J. P. Ewert, R. R. Capranica and D. J. Ingle), pp. 331-347. New York: Plenum Press.

Harkness, L. (1977). Chameleons use accommodation cues to judge distance. *Nature* **267**, 346-349.

Herrel A., Cleuren, J. and De Free, F. (1996). Kinematics of feeding in the lizard *Agama stellio*. *J. Exp. Biol.* **199**, 1727-1742.

Hinsche, G. (1935). Ein Schnappreflex nach "Nichts" bei Anuren. *Zool. Anz.* **111**, 113-122.

Meyers, J. J. and Nishikawa, K. C. (2000). Comparative study of tongue protrusion in three iguanian lizards, *Sceloporus undulatus*, *Pseudotrapelus siniatus* and *Chamaeleo jacksonii*. *J. Exp. Biol.* **203**, 2833-2849.

Moermond, T. C. (1981). Prey-attack behavior of *Anolis* lizards. *Z. Tierpsychol.* **56**, 128-136.

Ott, M. (2001). Chameleons have independent eye movements but synchronize both eyes during saccadic prey tracking. *Exp. Brain Res.* **139**, 173-179.

Ott, M. and Schaeffel, F. (1995). A negatively powered lens in the chameleon. *Nature* **373**, 692-694.

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

Reymond, L. (1985). Spatial visual acuity of the eagle *Aquila audax*, a behavioural, optical and anatomical investigation. *Vision Res.* **25**, 1477-1491.

Roth, G. (1976). Experimental analysis of the prey catching behavior of *Hydromantes italicus* Dunn (Amphibia, Plethodontidae). *J. Comp. Physiol.* **109**, 47-58.

Sherbrooke, W. C. (2002). Seasonally skewed sex-ratios of road-collected Texas horned lizards (*Phrynosoma cornutum*). *Herpetol. Rev.* **33**, 21-24.

Sherbrooke, W. C. (2003). *Introduction to horned lizards of north America. California Natural History Guides No. 64.* Berkeley: University of California Press.

Schwenk, K. and Throckmorton, G. S. (1989). Functional and evolutional morphology of lingual feeding in squamate reptiles: phylogenetics and kinematics. *J. Zool. Lond.* **219**, 153-175.

Weerasuriya, A. (1989). In search of the motor pattern generator for snapping in toads. In *Visuomotor Coordination, Amphibians, Comparisons and Robots* (ed. J. P. Ewert and M. A. Arbib), pp. 589-614. New York: Plenum Press.