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RESEARCH ARTICLE

Eye movements in chameleons are not truly independent – evidence from simultaneous monocular tracking of two targets

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ABSTRACT

Chameleons perform large-amplitude eye movements that are frequently referred to as independent, or disconjugate. When prey (an insect) is detected, the chameleon's eyes converge to view it binocularly and 'lock' in their sockets so that subsequent visual tracking is by head movements. However, the extent of the eyes' independence is unclear. For example, can a chameleon visually track two small targets simultaneously and monocularly, i.e. one with each eye? This is of special interest because eye movements in ectotherms and birds are frequently independent, with optic nerves that are fully decussated and intertectal connections that are not as developed as in mammals. Here, we demonstrate that chameleons presented with two small targets moving in opposite directions can perform simultaneous, smooth, monocular, visual tracking. To our knowledge, this is the first demonstration of such a capacity. The fine patterns of the eye movements in monocular tracking were composed of alternating, longer, 'smooth' phases and abrupt 'step' events, similar to smooth pursuits and saccades. Monocular tracking differed significantly from binocular tracking with respect to both 'smooth' phases and 'step' events. We suggest that in chameleons, eye movements are not simply 'independent'. Rather, at the gross level, eye movements are (i) disconjugate during scanning, (ii) conjugate during binocular tracking and (iii) disconjugate, but coordinated, during monocular tracking. At the fine level, eye movements are disconjugate in all cases. These results support the view that in vertebrates, basic monocular control is under a higher level of regulation that dictates the eyes' level of coordination according to context.

KEY WORDS: *Chamaeleo chamaeleon*, Independent eye movement, Visual tracking, Monocularity, Binocularity, Gaze divergence, Oculomotor control

INTRODUCTION

Vertebrates commonly attempt to keep a visual image stable on the retina, so as to obtain maximum resolution and minimize motion blur. To stabilize the image, movements of the eyes, head or body are employed. Such movements are frequently composed of slow, smooth components and abrupt fast components (saccades). These are used synergistically, to optimize the tracking of moving targets in a trade-off between velocity and position (Ben-Simon et al., 2012; Land, 1999; Lisberger et al., 1987; Martinez-Conde and Macknik, 2008; Souto and Kerzel, 2008; Tychsen and Lisberger, 1986). Saccades generally eliminate large errors when the target is far from the area of high acuity, such as the area centralis (Land, 1999).

Vertebrate classes differ markedly in central aspects of the visual system such as the position of the eyes in the skull, eye size, the presence of an area of high visual acuity (fovea) and the extent of the visual fields. These and other parameters, together with eye movements, determine the manner in which, and extent to which, the visual sphere is sampled. For example, compared with primates, fish, reptiles and birds mostly have laterally placed eyes with eye movements that produce transient binocular overlap that is not extensive.

Eye movements in vertebrates vary considerably in their spatio-temporal patterns. Eye movements may be conjugate – where the two eyes move synchronously in the same direction – or disconjugate – where they move in different directions (Fritsches and Marshall, 2002). In primates, eye movements are conjugate, resulting in the precise alignment of targets on the two foveas, whereas in fish and birds, eye movements are frequently disconjugate. Such differences raise central questions as to the ocular control systems that might govern monocularity, binocularity and the switch from one to the other (von Helmholtz, 1896, cited in Pettigrew et al., 1999 and Ott, 2001). Studies of non-mammalian vertebrates (fish, amphibians, reptiles and birds) suggest that the basic organization of the oculomotor control system is monocular, with separate motor commands to each eye (Kirmse, 1988; Wallman and Pettigrew, 1985; Walls, 1962). A frequently cited example is that of chameleons (Reptilia), in which eye movements are referred to as being 'asynchronous', 'independent' or 'disconjugate' (Flanders, 1985, 1988; Harkness, 1977; Ott, 2001; Ott et al., 1998; Sándor et al., 2001), thus implying an independent motor control for each eye (Mates, 1978; Ott, 2001).

Chameleons are arboreal lizards that depend exclusively on vision to catch prey (insects). They regularly scan the environment using large-amplitude movements, ca. 180 deg horizontally and ca. 90 deg vertically (Sándor et al., 2001). Once prey has been detected, the eyes converge to view it binocularly (Bellintani-Guardia and Ott, 2002; Haker et al., 2003; Harkness, 1977). This is followed by an initial protrusion (IP) of the tongue and the subsequent projection phase (Flanders, 1985), during which the tongue strikes (Harkness, 1977; Ott et al., 1998). Flanders (1985, 1988) demonstrated that the pursuit of a moving prey is performed by head movements while the eyes are kept 'locked' in their orbits.

Similar to other animals with laterally placed eyes and disconjugate eye movements, chameleons can simultaneously view two disparate parts of the visual sphere. Each viewed space may contain a moving target that is available only to the respective eye and, if small, may require precise monocular tracking. To the best of our knowledge, there is no information on the capacity among vertebrates to perform simultaneous monocular tracking. This capacity would obviously

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List of abbreviations	
CE	converging eye
DTT	diverging target test
IP	initial protrusion
STT	single target test
TE	tracking eye

require precision at the oculomotor control level and the need for 'divided attention'. These issues are also of special interest because ectotherms (fish, amphibians and reptiles) and birds differ from mammals in important aspects of their underlying neural structures. The optic nerves in mammals undergo partial decussation at the optic chiasm so that visual information from a given eye is simultaneously transferred to both the ipsilateral and contralateral hemispheres. In contrast, in ectotherms and birds, the optic nerves undergo full

decussation, with all of the visual information transferred first from a given eye to the contralateral hemisphere. Moreover, inter-hemispheric commissures are relatively sparse in ectotherms and robust in mammals (Huber and Crosby, 1933; Jeffery and Erskine, 2005; Shanklin, 1930).

How might one demonstrate monocular control of eye movements at the behavioral level? One possibility is to provide each eye with a single, small moving target and to determine the eyes' capacity to simultaneously track the target monocularly. To this end, we chose a chameleon, *Chamaeleo chamaeleon* (Linnaeus 1758), as the animal model. While eye movements in chameleons are considered independent, the level of independence and division of attention are not known.

Kirmse (1988) tested chameleons for their ability to simultaneously and monocularly track two prey targets moving in opposite directions. He concluded that chameleons are unable to do
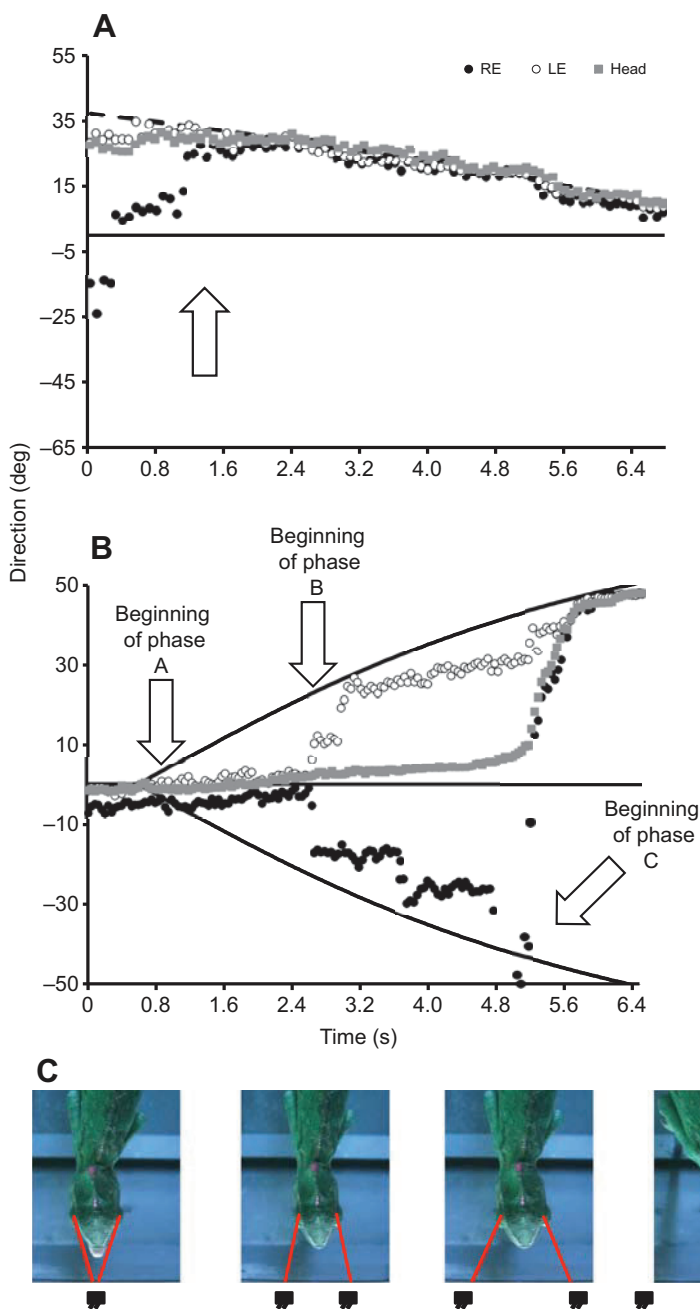

Fig. 1. Direction of gaze relative to target(s). (A) The direction of gaze in a single target test (STT). The dashed line indicates the target angular position. The instant of eye convergence is depicted by the arrow and is followed by binocular tracking. (B) The direction of gaze in a diverging target test (DTT). Phase A begins at the instant of target divergence. Phase B begins at the instant of eye divergence. Phase C begins at the instant of eye convergence (here, the right eye converged towards the left eye). *y*-axis: origin (0 deg) is the center of the screen; positive values, left side of the screen; negative values, right side of the screen; dashed lines, target direction; RE, right eye; LE, left eye. (C) A sequence of frames (from left to right, at 160 ms intervals) from a DTT. Gaze direction is depicted by the lines running from each eyeball to the screen. Initial eye convergence (far left) is followed by gaze divergence (two central frames) and a final convergence (far right). 'Prey' targets are black rectangles with two ventral appendages, depicted beneath each frame.
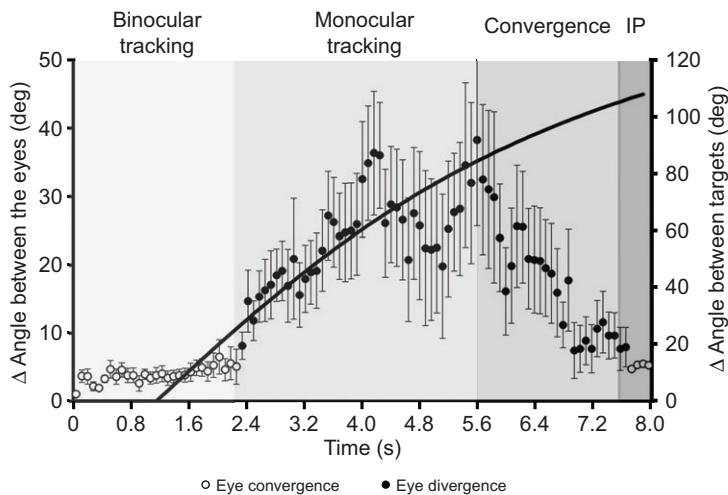
Fig. 2. Eye vergence as a function of angular difference between targets. The figure depicts the absolute magnitude of divergence of the targets (dashed line) and the absolute magnitude of vergence between the eyes (open circles, convergence; solid circles, divergence). Binocular tracking is the period before eye divergence (at ca. 2.0 s). Monocular tracking is the period from the onset of eye divergence to the onset of eye convergence (from ca. 2.0 s to ca. 5.6 s). Convergence is the period from the beginning of eye convergence until its conclusion (from ca. 5.6 s to ca. 7.5 s). IP, tongue initial protrusion toward one of the targets (at ca. 7.5 s). The mean of means±s.e. is given, *N*=7, 1–4 repetitions per individual.

this, but that their gaze alternates, so that when one eye tracks a target, the contralateral eye is 'idle'. In contrast to previous studies, we employed the chameleon's distinct pre-capture binocular fixation (Flanders, 1985, 1988; Harkness, 1977; Ott, 2001) as a clear starting point to ensure that both eyes were gazing at, and thus were attentive to, the same target at the very onset of each test. The subsequent monocular tracking of the targets required precise eye motion (e.g. smooth tracking) and 'division of attention' (Dukas and Kamil, 2001). We asked: (i) are chameleons capable of visually tracking two targets simultaneously and monocularly?; (ii) what are the gross and fine patterns of the eye movements during tracking?; and (iii) are there interocular differences in the movements during tracking?

RESULTS
Binocular and monocular tracking
When presented with a single moving target, the chameleon's eyes first converged and then remained relatively motionless in their orbits so

Fig. 3. Tracking precision. Tracking precision is determined by the duration of gaze relative to the target in the different phases of visual tracking. 'On target' means the point of intersection of the line of gaze with the screen was within one target width on either side of the displayed target. 'Over target' means the point of intersection of the line of gaze was more than one target width and distal to the displayed target. 'Under target' means the point of intersection of the line of gaze was more than one target width and proximal to the target. Mean proportions±s.e. are given, *N*=7. The results for the two eyes did not differ and were thus pooled. Results sharing the same lowercase letter do not differ significantly.

that subsequent tracking was performed by head movements (Fig. 1A). Overall, tracking of a single target (single target test, STT) was distinctly binocular for all chameleons and all tests.

When a single target was made to diverge into two targets (diverging target test, DTT), the eyes first gazed convergently at the single target (termed 'phase A'), then, once the target had diverged, the eyes showed clear gaze divergence, with each eye tracking the target on its respective side (termed 'phase B'). Finally, the eyes converged on one of the targets followed by an IP (termed 'phase C'; Fig. 1B). Interocular gaze angle in phase A was 3.33±0.88 deg, increasing to a maximum of 59.51±9.12 deg in phase B and finally decreasing to 5.21±1.83 deg in phase C (Fig. 2). While diverged (phase B), each eye spent significantly longer durations with the gaze directed at its respective side of the screen (χ^2_2=27.613, right eye: *P*=0.016, left eye: *P*<0.005) with no interocular differences (supplementary material Table S2).

In three specific tests (supplementary material Table S1), the eyes did not converge at the end of phase B and divergence continued until the targets vanished from the screen, with the interocular angle reaching ca. 105 deg. It was clear that the maximum possible angle of interocular divergence had not been reached because of the constraint of the targets disappearing from sight at the edge of the screen.

Tracking precision
Tracking precision was determined by comparing the points of intersection of the gaze axes with the screen and the target position on the screen. If the point of the gaze intersection was within one target width on either side of the displayed target, it was considered 'on target'. If the point of intersection was distal to or proximal to the above range, it was considered 'over target' or 'under target', respectively.

In binocular and in monocular tracking (i.e. STT and DTT), no interocular differences were observed in the relative durations of 'on', 'over' or 'under' target, over all tests. Therefore, the mean relative duration was calculated for each eye in each test (supplementary material Table S3). In binocular tracking, the relative duration of on target was significantly higher than the durations of under or over target (phase A of DTT: χ^2_2=15.527, *P*<0.001; STT: χ^2_2=18.233, *P*<0.001; Fig. 3; supplementary material Table S3).

In monocular tracking, during phase B of DTT, the relative duration of under target was significantly higher than that of over target (χ^2_2=13, *P*<0.005) but did not differ from that of on target (Fig. 3; supplementary material Table S3). Here also, no interocular differences were observed and the longest durations were found
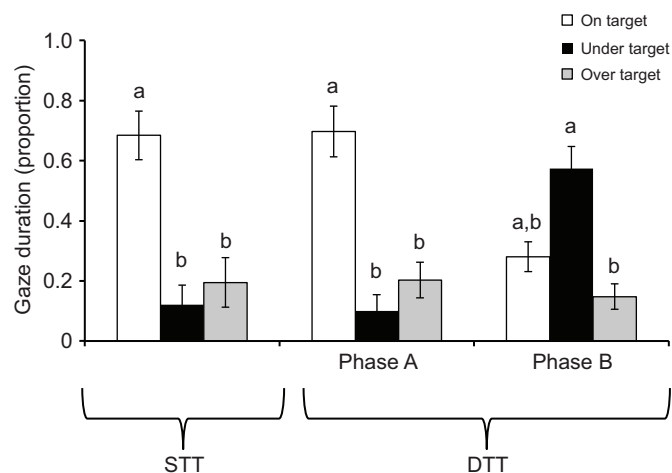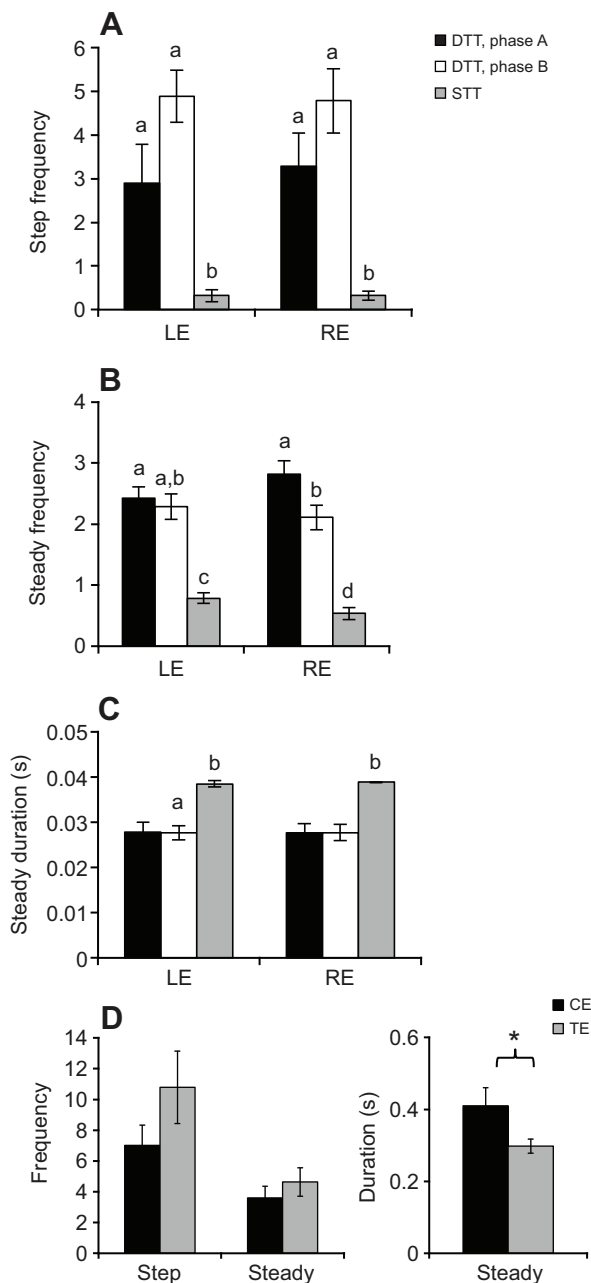
Fig. 4. Fine patterns of eye motion. The patterns comprised 'step' events and 'steady' phases. (A,B) The frequency of step and of steady and (C) the duration of steady for the RE and the LE. The results are for STTs and DTTs. Results sharing the same lowercase letter do not differ significantly. (D) Eye role, showing differences between the converging eye (CE) and the tracking eye (TE). The frequency of step events and of steady phases for the CE and TE for phase B in DTT (left) and the duration of steady phases (right) are shown. Frequency is given as the mean number of events per test. Duration was calculated separately within each phase of the DTT and in each STT and is provided as the number of frames; $N=7$ in DTT and $N=7$ in STT. *$P<0.05$. Data are the mean of means±s.e.

with the line of gaze in closest proximity under target ($\chi_3^2=34.525$, $P<0.001$; supplementary material Table S3).

Side preference

In most DTTs ($N=40/63$), the chameleons showed gaze convergence at the end of the test, leading to an IP; however, in the remaining tests ($N=23/63$), gaze directions remained diverged

(respective proportions: 0.63, 0.37). The frequency of the right eye converging to the left eye did not differ from the frequency of the left one converging to the right ($\chi_2^2=0.667$, $P=0.717$; supplementary material Table S4). The duration from the onset of convergence to its conclusion was 193.2 ± 51.2 ms (4.83 ± 1.28 frames) with no interocular difference (Wilcoxon: $Z=-0.447$, $P=0.655$; supplementary material Table S4). We analyzed the initial convergence of the eyes and the changes in the initial head motion in all the tests in which eye divergence–convergence was observed (13 tests). In 10/13 tests, the initial convergence of the eyes preceded the initial motion of the head, by 160 ± 80 ms (mean±s.d.).

Fine structure of gaze shifts

A preliminary analysis of the distribution of gaze directions showed two motion patterns. One comprised sequences with small shifts in gaze direction between consecutive frames, and we termed this pattern 'steady'. The other comprised brief, large interframe shifts in gaze direction, which we termed 'steps'. These fine patterns resemble smooth and saccadic tracking. A 'steady' phase was defined as a sequence in which angular differences in gaze direction between sampled frames (i.e. at 2-frame intervals) were less than 4 deg for a minimum of three successive measurements, while a 'step' event was defined as a gaze shift of 4 deg or more. Overall, most gaze shifts were of less than 4 deg (supplementary material Table S7). The frequency of step events in binocular viewing of single targets, both in the STT and in phase A of the DTT, was lower than during monocular viewing in the DTT. However, the frequency of step events in phase B of the DTT was significantly higher than in the STT (Fig. 4A; supplementary material Table S8). The frequency of the steady pattern was significantly higher in phase A than in phase B for the right eye, but not for the left eye. The frequency of the steady pattern in phases A and B of the DTT was higher than in the STT for both eyes (Fig. 4B; supplementary material Table S8). In phase B of DTT, we observed a high frequency of steady phases of relatively short duration (ca. 120–200 ms, 3–5 frames) and a low frequency of steady phases of relatively long duration (ca. 800–1200 ms, 20–30 frames; Fig. 5A).

The steady phase lasted significantly longer in the STT than in phases A or B of the DTT (Fig. 4C; supplementary material Table S8). Overall, interocular differences were significant only in the frequency of the steady pattern in the STT ($t_6=-4.583$, $P<0.005$; supplementary material Table S9).

The eyes' role: tracking versus converging

In DTTs, each eye either continued to track its respective target until it disappeared from the screen or, at the final phase (phase C), one of the eyes shifted its gaze from its original target to the contralateral target, leading to convergence. Convergence occurred in the majority of tests (40/63 for all tests, 15/23 for the analyzed tests). The eye that continuously tracked its target was termed the 'tracking eye' (TE) and the contralateral eye was termed the 'converging eye' (CE, Fig. 1B).

The TE and the CE showed different motion patterns, indicating that eye movements are role dependent rather than side dependent. Thus, in tests that ended with gaze convergence, the frequency of step events was significantly higher ($W=143.5$, $P<0.05$; supplementary material Table S10) and the frequency of the steady phases was significantly lower ($W=53$, $P<0.05$; supplementary material Table S10) than in tests that ended without convergence.

In tests that ended in gaze convergence, the duration of steady phases was significantly longer, and the frequency of steady phases was lower (but not significantly so) in the CE compared with the TE. The frequency of step events in the CE did not differ from that in the TE (Fig. 4D, Fig. 5B; supplementary material Table S10).
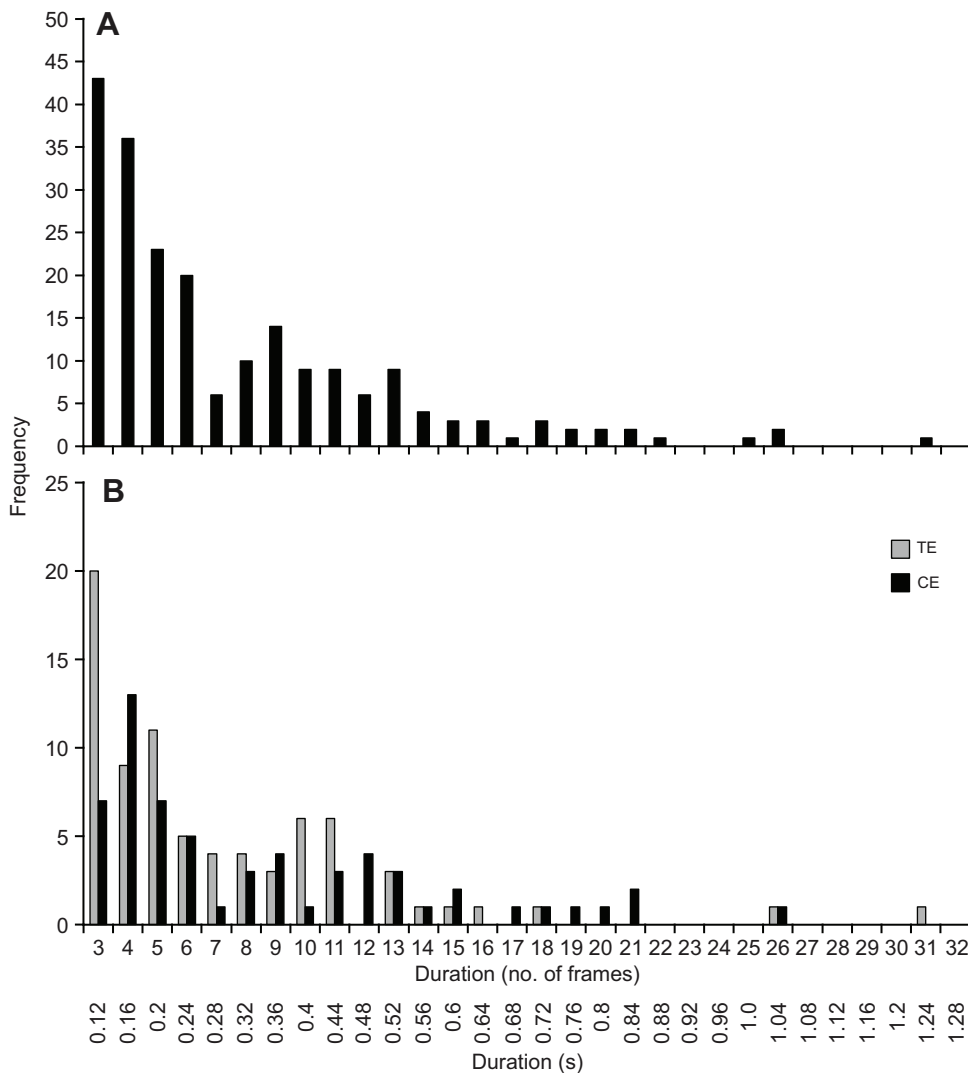
Fig. 5. The frequency distribution of steady durations. The frequency of steady durations in phase B of DTTs for the two eyes together (A) and separately for the CE and the TE only for tests ending in convergence (B).

During steady phases, continuous small changes occurred in the direction of gaze towards ('shifting with') or away from ('shifting away') the target or, alternatively, gaze direction did not change ('unshifted'; Fig. 6). The frequency of shifting with and of shifting away was significantly higher than the frequency of unshifted, over all DTTs (for tests ending with convergence: $\chi^2_2=34.462$, $P<0.001$; for tests ending without convergence: $\chi^2_2=10.231$, $P<0.05$; Fig. 7A; supplementary material Table S11). Over all tests, the frequency of 'steps toward' was significantly higher than the frequency of 'steps away' (respectively, $Z=-2.535$, $P<0.05$, and $Z=-2.314$, $P<0.05$; Fig. 8A; supplementary material Table S11). In tests ending with convergence, in the TE, but not in the CE, (i) the frequency of shifting with was significantly higher than that of shifting away ($Z=-2.510$, $P<0.05$; Fig. 7B; supplementary material Table S11), (ii) the frequency of steps toward was significantly higher than that of steps away ($Z=-3.294$, $P<0.005$; Fig. 8B; supplementary material Table S11). Finally, the CE and the TE did not differ in gain (mean±s.e.: 0.4±0.12 and 0.52±0.17, respectively; $Z=-0.153$, $P=0.878$, Wilcoxon rank test).

DISCUSSION
Vision is tightly linked with motion, and the acquisition of visual information is frequently performed by moving the eyes, head or body. Most studies on vertebrate eye movements have been conducted on mammals, specifically on species that have frontal eyes and conjugate eye movements, such as primates and cats (Martinez-Conde and Macknik, 2008; Zhou and King, 1998). However, in most vertebrates, the eyes are laterally placed in the skull and eye movements are disconjugate, as exemplified in fish (Fritsches and Marshall, 2002) and birds (Wallman and Letelier, 1993). Under these conditions, each eye is likely to gaze at sections of the visual sphere that do not correspond to the parts gazed at by the contralateral eye.

Our results clearly demonstrate that common chameleons are capable of performing simultaneous monocular tracking. Under the experimental conditions here, the eyes rapidly switched from binocular fixation to precise monocular tracking and then to final binocular fixation prior to IP (Fig. 1B,C). We further demonstrated that during binocular fixation of a stationary target and during binocular and monocular tracking of moving targets, there were subtle, hitherto undescribed patterns of eye movements. These comprised phases of longer duration with small gaze shifts ('steady'), resembling smooth pursuit movements, and events of short duration and large-magnitude gaze shifts ('steps'), resembling saccades. Such alternating patterns have been observed in other vertebrates. For example, in goldfish (*Carrassius auratus*), the eyes perform saccadic movements in the same direction as the head movement, and smooth rotational movements in the direction
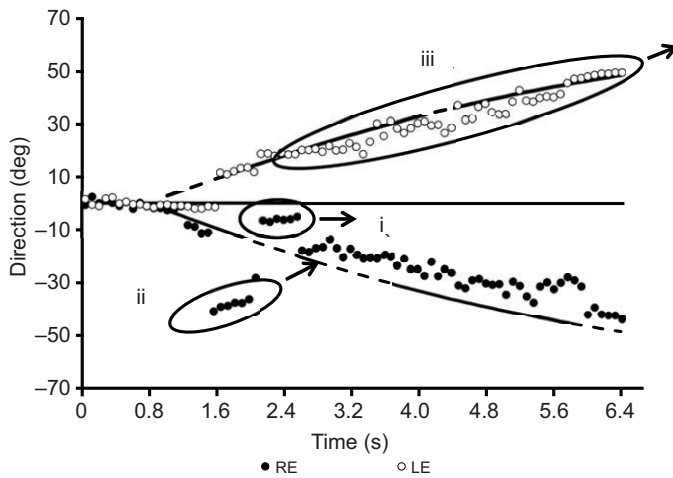
Fig. 6. Shifts in gaze direction. An example of shifts in gaze direction in a DTT. (i) 'Unshifted', the overall direction of gaze does not change; (ii) 'shifting away', the overall direction of gaze shifts in the direction opposite to that of target motion; (iii) 'shifting with', the overall direction of gaze shifts in the direction of target motion. In each case, the direction of target motion is indicated by the arrow.

opposite to the head (Easter and Stuermer, 1984). In birds, small moving targets elicit eye motions that alternate between slow phases, during which gaze is stabilized, and fast saccadic phases in the opposite direction (Land, 1999; Wallman and Letelier, 1993; Zeil et al., 2008). To the best of our knowledge, our results present the first documentation of smooth pursuit-like eye movements in response to a small moving target in a reptile.

In the chameleons, both target fixation and tracking were composed of steady and step phases. However, the frequencies of
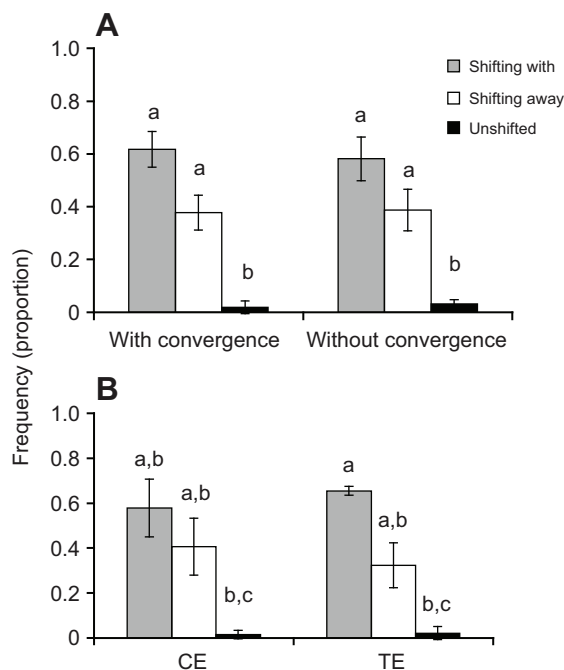

Fig. 7. Directionality of the steady phases. (A) The frequency of steady phases in a given direction, i.e. 'shifting with', 'shifting away' or 'unshifted', in the tests ending with or without convergence. (B) The frequency of steady phases in a given direction for the CE and the TE in the tests ending in convergence. Results sharing the same lowercase letter do not differ significantly (results are provided as mean proportions±s.e.).
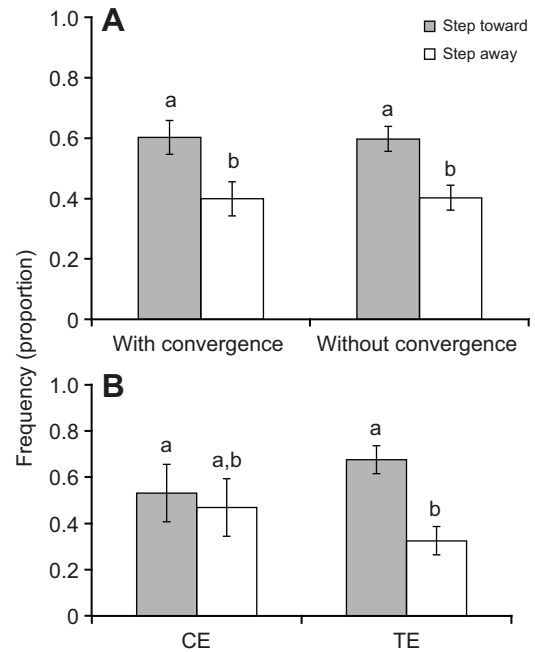

Fig. 8. Directionality of the step events. (A) The frequency of step events in a given direction in tests ending with or without convergence. (B) The frequency of step events in a given direction for all tests ending in convergence, for the CE and for the TE. Results sharing the same lowercase letter do not differ significantly (results are provided as mean proportions±s.e.).

these phases were significantly higher in fixating a stationary target compared with tracking a moving target, while the durations of the steady phase were significantly shorter in the former compared with the latter (Fig. 4; supplementary material Table S8).

Our results concerning the tracking of a single moving target agree only partially with those of Flanders (1985). While the eyes converge and 'lock' in their sockets and the tracking is by head motion (Fig. 1A), at the fine level, each eye continues to perform steady and step movements (Fig. 8B).

Gaze direction in the steady phases either changed with or opposite to the direction of the target, or it did not change at all. Changing with the direction of the target resembled the description of smooth pursuits (Lisberger et al., 1987; Souto and Kerzel, 2008); changing in the opposite direction to the target resembled drift eye movements – a slow, smooth wandering of the gaze that, unlike smooth pursuit, might occur without stimuli (Rashbass, 1961). Such drift movements are known in other vertebrates, e.g. primates, cats, rabbits and fish (Martinez-Conde and Macknik, 2008).

Behavioral studies on choice of eye use have been previously conducted. For example, in chess playing, the duration of fixation is a reliable predictor of the choice of next move (Reingold et al., 2001; Shadlen and Newsome, 1996). In our results, the patterns of eye movement differed in relation to context. In tests in which one eye converged to the other at the final stage, the frequency of step events and of steady phases was significantly higher than in tests that ended without convergence. Also, the duration of steady phases in the CE was longer than in the TE. These differences may well indicate that a stage of 'indecision' is reached in the CE that predicts its immediate abandonment of the target. However, the exact decision moment could not be predicted.

Interestingly, we found no evidence in the present study for lateralization of eye use. This is in contrast with previous studies in which we demonstrated that under binocular viewing of a moving
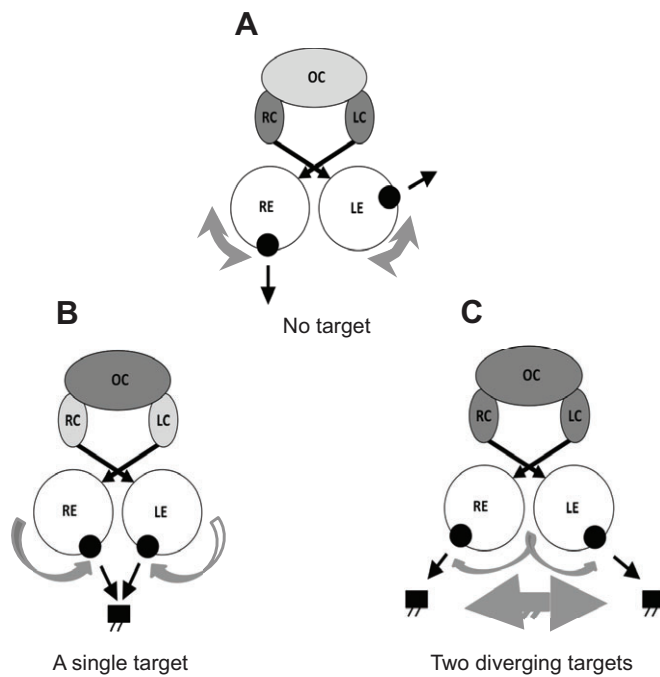
Fig. 9. A model for context dependence of eye movements in the chameleon. The model depicts the chameleon's capacity to switch between different patterns of eye movements under differing target conditions. (A) When scanning the environment without a specific target, eye movements are disconjugate. (B) When fixating a single moving target, the eyes converge binocularly and move in a coordinated manner at the gross level, yet show disconjugate patterns at the fine level of steady and steps. (C) When faced with two targets moving in opposite directions, each eye fixates monocularly on one of the targets. The eyes move in a conjugate manner at the gross level and show disconjugate patterns at the fine level. The frequency and duration of fine eye movements show a high coordination between the two. The model assumes a motor control over the separate monocular controls of the eyes. RE, right eye; LE, left eye; RC, right eye motor control; LC, left eye motor control; OC, overall motor control; solid rectangle, prey. Low and high levels of activation of the motor controls are depicted by light and dark gray, respectively; gray arrows indicate eye movements, black arrows indicate gaze direction.

threat, eye use is lateralized in terms of duration of gazing and frequency of eye shifts (Lustig et al., 2012a,b, 2013).

Our results clearly demonstrated that, at the gross level, monocular tracking movements were coordinated, with each eye tracking one target, as the targets moved in opposite directions. However, at the fine level, the spatio-temporal patterns of step events and steady phases between the eyes were disconjugate (Fig. 9). In the chameleon's switching between monocular and binocular viewing of a target, the convergence of one eye to the other was without any apparent 'hesitation' and lasted less than 0.2 s. This might indicate 'shared interocular knowledge' governed by a higher neural control system that synchronizes the two independent monocular units.

When tracking a target, the motor patterns displayed by the eyes differ with the nature of the stimulus. For example, when presented with alternating, high-contrast bars moving across most of the visual field (wide field), the eyes mostly perform typical, innate optokinetic nystagamus. This response is composed of alternating smooth tracking with target direction and fast saccade in the opposite direction (Land, 1999; Wallman and Letelier, 1993). However, if the stimulus is a small, slow-moving target, the eyes perform continuous smooth tracking movements (Souto and

Kerzel, 2008). Smooth tracking is especially well developed in primates in response to small targets (Takagi et al., 2000), whereas in non-primates (e.g. cats, rabbits and fish), it is observed in response to wide-field motion (Lisberger et al., 1987). The synergistic smooth pursuit and saccadic movements have been suggested as a solution for accurately determining target velocity (the smooth-pursuit phases) and position (the saccades phases) (Land, 1999; Orban de Xivry and Lefèvre, 2007; Wallman and Letelier, 1993; Zeil et al., 2008).

The capacity of birds and reptiles to switch between monocular and binocular viewing of targets (Flanders, 1985; Martin and Katzir, 1999; Ott, 2001; Röll, 2001; Wallman and Pettigrew, 1985) raises important questions at two levels: first, how do they create a unified visual world from two disparate, non-corresponding images that, for example, provide alternating monocular and binocular information in quick succession?; second, what is the structure and function of the underlying oculomotor control system? From the time of von Helmholtz (1896, cited in Ott, 2001), researchers have been intrigued by the question of whether binocularity is based on a single system that controls the two eyes simultaneously, or two separate monocular systems that are controlled at a higher level. Inherent to the latter is the question of the relative independence of monocular attention. Support for the latter is the oculomotor control system in humans: here, there are indications that eye movements are programmed and calibrated independently for each eye, whereas calibration of binocular coordination is achieved by a higher neural network. Malfunctioning of these processes could lead to heterotropia, a situation in which the eyes are not properly aligned with each other (Dell'Osso, 1994; Zhou and King, 1998). Support for the view that the basic organization of the oculomotor control system in vertebrates is monocular has also been obtained from studies on non-mammals, such as fish and amphibians (Walls, 1962), chameleons (Kirmse, 1988; Ott, 2001) and birds (Wallman and Pettigrew, 1985).

As observations across vertebrate groups accumulate, the emerging picture on eye movements seems to be that of a continuum of 'multiple solutions' (Dell'Osso, 1994). At one end, the binocular capacities of mammals, traditionally referred to as conjugate and hardwired, may not be so (Dell'Osso, 1994). Rather, their neural architecture may well allow the oculomotor system to function either as two independent systems or as a single binocularly conjugate system. This is supported by the observation that monocular muscle control in humans is generated by two neural integrators (Dell'Osso, 1994). Furthermore, while binocular coordination in mammals may be innate, its fine tuning requires training. At the other end, chameleons show the capacity to perform a wide range of innate conjugate and disconjugate eye movements. The results here highlight the importance of further investigating subtle patterns that may show conjugate movements at one level and disconjugate ones at another.

While this is the first demonstration of smooth monocular tracking of two targets, it may well be a model for other ectotherms (e.g. Fritsches and Marshall, 2002; Pettigrew et al., 1999) and birds in which the system allows switching between eye movement patterns.

MATERIALS AND METHODS

The research was conducted between September 2011 and October 2012 at the University of Haifa, Oranim campus, Tivon, Israel, under a permit from the Israeli Nature and Parks Authority (no. 2011/11411) and with approval of the Ethics Committee of the University of Haifa (no. 095/08).

First, we determined whether the direction of the monocular gaze corresponds to the general direction of the target. We then asked how accurate the monocular tracking is. Finally, we determined the subtle internal patterns of eye movements during tracking.

All the results are provided as mean of means±s.e., except for the directionality tests in which the results are provided as means±s.e. Results for durations are provided in seconds. The validity of determining the direction of gaze was tested as follows: a random sequence of 30 frames, extracted from a single test, was given to each of four researchers to provide an independent judgment of gaze direction for each eye in each frame. Inter-observer differences were low, with an overall s.d. of less than 1 deg for each eye.

Experimental animals

We used common chameleons (*C. chamaeleon*; *N*=13) collected from the botanical garden of Oranim campus between 2009 and 2011 and kept in an outdoor cage (Lustig et al., 2012a). For testing, chameleons were housed in an experimental room under a constant temperature of 26°C and a 12 h/12 h light/dark light regime. The light source consisted of one reptile UV fluorescent tube (Exo-Terra™, Castleford, West Yorkshire, UK) and one 40 W incandescent lamp per cage. For identification, each individual was marked with a small dot of colored nail polish on its back. During an experiment, the tested chameleon was randomly fed a single cockroach between tests, irrespective of its response. At the end of a testing day, all the chameleons were fed to satiation, but were not fed between experiments. Of the 13 chameleons, six were subjected only to the STT, two were tested with the DTT and five were tested under both conditions (supplementary material Table S1).

Experimental setup and procedure

Chameleons were first trained and tested for their response to computerized stimuli (Ketter Katz, 2014). The experimental apparatus was constructed so that viewing and responding to digital stimuli on an LCD screen could be performed from a predetermined position: the chameleon could approach the screen on a horizontal wooden dowel (diameter 1 cm), positioned so that its proximal end was 12 cm from the screen and perpendicular to it. The chameleon was videotaped with a camera at 25 frames s^{-1} with a Sony camera (NV-GS500) positioned 90 deg above the proximal end of the dowel. Overhead lighting was provided by a 40 W incandescent bulb and an Exo-Terra™ UV fluorescent tube (20 W, overall light intensity was 42–47 lx). The entire setup was covered with an opaque matte black fabric. Experiments were conducted between 09:00 h and 14:00 h, at 2 to 3 day intervals. To enhance the analyses of eye and head movements, small dots of colored nail polish were applied to the dorsal side of the fused eyelids and to the top of the head. At the beginning of each test, a single chameleon was lured from its home cage onto the distal end of the dowel in the experimental cage, using a live cockroach. Once on the dowel, the computer screen was turned on to display the computerized target (see below). A positive response was recorded if the chameleon displayed its natural predatory motor sequence of: (i) approaching the target, (ii) viewing the target binocularly and (iii) performing an IP of the tongue (Ott, 2001).

Stimuli

The computerized targets ('prey') were black rectangles (MatLab color values: red – 1, green – 0, blue – 1, hue – 200, sat – 240, lum – 0) with two ventral moving appendages (supplementary material Fig. S1), on a white background (MatLab color values: red – 255, green – 252, blue – 255, hue – 200, sat – 240, lum – 239). The target's size was 13×7 mm, and the subtending angle of its width at the dowel's proximal end was 6 deg. The targets and their motions were generated with MatLab (version 2009b and 2010a) and displayed on an Acer© 17 in LCD screen (AL1721, resolution 1280×1024 pixels) at the chameleon's approximate eye level.

In the STT, a single target continuously moved horizontally on the screen at a velocity of 1 cm s^{-1}. The position of first appearance of the target on the screen in each test was random. A test was concluded once the chameleon had responded positively to the target (i.e. had reached an IP), or after 2 min with no response.

The DTT began with a single, stationary target presented at the center of the screen. Once the chameleon had responded by an IP, the experimenter initiated the target's divergence into two separate targets. The diverging targets were identical in size and contrast to the original target and moved at 1 cm s^{-1}, but in opposite directions. A test was concluded once the chameleon had performed an IP toward one of the targets or once the targets had disappeared beyond the edge of the screen.

Analysis

Video sequences were extracted using Adobe Elements™ software and from these, single frames were extracted using MatLab. Gaze direction of each eye and the axis of the head were determined for every second frame using ImageJ (version 1.47). Eye gaze direction was determined from an imaginary line connecting the center of the externally observed eyeball and a colored dot on the central dorsal tip of the upper eyelid. Head axis was determined by the line connecting the rostral and occipital colored dots. The points of intersection of the imaginary lines extrapolated from the eyes and the head with the screen were recorded for subsequent calculation of the respective angles. Target position in DTT was recorded automatically by the software. Target position in STT was calculated as follows: the reference target position was derived from the direction of the head at the moment of IP. Target position in each preceding frame, to the beginning of the test, was calculated from the reference position, based on the known target velocity.

Eye movements

The angle between gaze direction of each eye and the sagittal plane of the head was calculated from the chameleon's distance to the screen and the point of intersection between the gaze and the screen. The summation of the two angles was termed the 'interocular angle'. The difference in eye–head angle between successive sampled frames was referred to as 'gaze shift'. Gaze 'convergence' or 'divergence' was determined by the distance between the points of intersection of the two separate gaze directions and the screen. If this distance was smaller than the head width, it was regarded as 'convergence'; if larger, it was regarded as 'divergence' (supplementary material Fig. S1).

Definitions of response phases

In tests with diverging targets, three phases were determined: phase A – from the beginning of the test, through binocular fixation, to the instant of IP; phase B (target divergence) – from IP through subsequent tracking, to the beginning of eye convergence on a target, or to target disappearance; phase C (eye convergence) – from the end of phase B to binocular viewing of the target and IP (Fig. 1B).

Gain and eye role

To determine the difference in gain between the CE and the TE, we sampled 10 steady phases for each eye, each >800 ms in duration. We calculated the gain for each sample from eye angular velocity/target angular velocity. To eliminate the effect of steps, we omitted the first and last measurements from each steady phase.

Statistical analysis

Analyses were performed on data obtained from seven chameleons, for phases A and B of the DTT and for the STT. The duration data for on, over and under target (see Results) were not normally distributed (Shapiro–Wilk test: phase B of DTT *P*=0.039, phase A of DTT *P*<0.001, STT *P*<0.001). Consequently, analyses were conducted using the Friedman test, while differences between the eyes were tested using the Wilcoxon test.

Analysis of eye directionality in the DTTs was conducted only for phase B of the test. The data were not normally distributed (Shapiro–Wilk test *P*<0.001) and the analysis was conducted using the Friedman test.

To determine the best explained variance in patterns of step events and steady phases, we tested combinations of the number of consecutive measurements and interframe angular shifts (supplementary material Table S5). The data showed no significant deviation from the normal distribution (Shapiro–Wilk test; supplementary material Table S6). Using repeated measures ANOVA, it was found that the combination of eye shifts of 4 deg in at least three consecutive measurements yielded the highest percentage of explained variance.

The DTT (N=7) and the STT (N=7) were performed with different individuals. Data for step and steady patterns for each individual, in phases A and B, were analyzed by paired t-test. Data for the STT were analyzed using a two-sample t-test with Bonferroni correction (0.05/3). To determine the differences in steady and step directionality (see Results) between tests that ended in convergence and tests that did not, we used the Friedman test for steady and a two-sided Wilcoxon test for step. To determine the differences in the directionality of steady and of step patterns between the CE and the TE, we used a two-sided Wilcoxon test. Statistical dependencies originating from repeated measurements per chameleon were ignored.

Supplementary material
Supplementary material available online at
http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.113084/-/DC1

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Table S1. The chameleons tested.

Chameleon	Test	Repetitions #	Analyzed
Bela	STT	20	1
	DTT	6	4
Bunny	STT	10	1
	DTT	12	4
Julie	STT	20	1
	DTT	9	4
Picollo	STT	20	1
	DTT	8	4
Tiny	STT	10	1
	DTT	10	4
Medussa	DTT	10	4
Daisy	DTT	8	4
Didi	STT	10	1
Fuad	STT	10	1
Java	STT	23	1
Maya	STT	8	1
Monicka	STT	20	1
Ursula	STT	20	1

STT, single target tests; DTT, diverging target tests.

Table S2. A comparison of directionality within and between the eyes.

Tested parameter	Results
Directional: right eye vs. left eye	right eye: 0.66 ± 0.14 left eye: 0.71 ± 0.09 $\chi^2_{(2)}$=27.613 p=1
Non-directional: right eye vs. left eye	right eye: 0.34 ± 0.14 left eye: 0.29 ± 0.09 $\chi^2_{(2)}$=27.613 p=1
Right eye: directional vs. non-directional	directional: 0.66 ± 0.14 non-directional: 0.34 ± 0.14 $\chi^2_{(2)}$=27.613 p=0.016
Left eye: directional vs. non-directional	directional: 0.71 ± 0.09 non-directional: 0.29 ± 0.09 $\chi^2_{(2)}$=27.613 p<0.001

Table S3. Comparisons between the left eye and the right eye in the proportion duration "on", "under" or "over'' target, during binocular tracking.

Tested parameter	Phase A	Phase B	Single target
"On target": right eye vs. left eye	right eye: 0.68 ± 0.14, left eye: 0.71 ± 0.14, Z=0 P=1	right eye: 0.29 ± 0.08, left eye: 0.27 ± 0.09, Z=-0.169 P=0.866	right eye: 0.69 ± 0.09, left eye: 0.68 ± 0.08, Z=-0.255 P=0.799
"Under target": right eye vs. left eye	right eye: 0.10 ± 0.10, left eye: 0.10 ± 0.09, Z=0 P=1	right eye: 0.59 ± 0.11, left eye: 0.56 ± 0.13, Z=-0.507 P=0.612	right eye: 0.12 ± 0.06, left eye: 0.12 ± 0.07, Z=-0.059 P=0.953
"Over target": right eye vs. left eye	right eye: 0.22 ± 0.12, left eye: 0.19 ± 0.13, Z=-0.105 P=0.917	right eye: 0.12 ± 0.08, left eye: 0.17 ± 0.10, Z=-0.676 P=0.499	right eye: 0.20 ± 0.09, left eye: 0.19 ± 0.08, Z=0 P=1
"On-" vs. "over-" vs. "under-" target for both eyes	"on": 0.70 ± 0.08, "under": 0.10 ± 0.05, "over": 0.20 ± 0.06, $\chi^2_{(2)}$= 15.527 P<0.001	"on": 0.28 ± 0.05, "under": 0.57 ± 0.07, "over": 0.15 ± 0.04, $\chi^2_{(2)}$= 13 P=0.002	"on": 0.68 ± 0.08, "under": 0.12 ± 0.07, "over": 0.19 ± 0.08, $\chi^2_{(2)}$= 18.233 P<0.001
The frequency of "under target" (given in target width)		3: 22.1 ± 4.9 6: 4 ± 2 9: 1.8 ± 1.1 12: 0.5 ± 0.5 $\chi^2_{(3)}$= 34.525 P<0.001	

Table S4. Comparisons (i) between the frequencies of eye converging to the right target, to the left target or not converging and (ii) between the durations of converging to the right eye or to the left eye.

Tested parameter	
Eye convergence to the right, to the left or to none of the targets	right: 0.26 ± 0.06 left: 0.39 ± 0.09 none: 0.35 ± 0.11 $\chi^2_{(2)}=0.667$ p=0.717
Duration of converging to the right vs. the left target	right: 5 ± 1 left: 4.4 ± 1.6 Z=-0.447 p=0.655

Table S5. The percentages of explained variance under the different combinations of the number of consecutive measurements and the angular inter-frame shifts.

Combination #	Number of consecutive measurements	Angular inter-frame shifts in eye axes	Percentage of explained variance (mean)
1	4	4	84.34
2	3	4	91.02
3	5	4	75.63
4	6	4	69.84
5	4	2	73.54
6	4	3	80.12
7	4	5	87.71
8	4	6	89.46

Table S6. Results of the Shapiro-Wilk normality test.

	Step frequency	Steady frequency	Steady duration
Right eye, phase A	0.178	0.376	0.111
Right eye, phase B	0.174	0.482	0.327
Right eye, single target	0.126	0.062	0.671
Left eye, phase A	0.854	0.518	0.802
Left eye, phase B	0.245	0.461	0.067
Left eye, single target	0.482	0.026	0.017

Table S7. The distribution of gaze shifts.

Gaze shift magnitude	Phase A	Phase B	Single target
1	right eye: 0.46 ± 0.09, left eye: 0.048± 0.08	right eye: 0.33 ± 0.05, left eye: 0.33 ± 0.06	right eye: 0.44 ± 0.04, left eye: 0.50 ± 0.03
2	right eye: 0.27 ± 0.05, left eye: 0.29 ± 0.05	right eye: 0.25 ± 0.03, left eye: 0.25 ± 0.03	right eye: 0.30 ± 0.02, left eye: 0.28 ± 0.02
3	right eye: 0.16 ± 0.05, left eye: 0.16 ± 0.06	right eye: 0.16 ± 0.03, left eye: 0.14 ± 0.03	right eye: 0.15 ± 0.01, left eye: 0.12 ± 0.02
4	right eye: 0.05 ± 0.03, left eye: 0.05 ± 0.04	right eye: 0.09 ± 0.02, left eye: 0.08 ± 0.02	right eye: 0.05 ± 0.01, left eye: 0.06 ± 0.01
5	right eye: 0.03 ± 0.03, left eye: 0.02 ± 0.02	right eye: 0.05 ± 0.02, left eye: 0.05 ± 0.02	right eye: 0.02 ± 0.01, left eye: 0.02 ± 0.01
6	right eye: 0.01 ± 0.01, left eye: 0.01 ± 0.01	right eye: 0.03 ± 0.01, left eye: 0.02 ± 0.01	right eye: 0.01 ± 0.01, left eye: 0.01 ± 0.00
7	right eye: 0.01 ± 0.01, left eye: 0.00 ± 0.00	right eye: 0.02 ± 0.01, left eye: 0.02 ± 0.01	right eye: 0.00 ± 0.00, left eye: 0.00 ± 0.00
8	right eye: 0.00 ± 0.00, left eye: 0.00 ± 0.00	right eye: 0.02 ± 0.01, left eye: 0.01 ± 0.01	right eye: 0.01 ± 0.01, left eye: 0.00 ± 0.00
9	right eye: 0.01 ± 0.01, left eye: 0.00 ± 0.00	right eye: 0.01 ± 0.01, left eye: 0.01 ± 0.01	right eye: 0.01 ± 0.00, left eye: 0.00 ± 0.00
Mean 10-19	right eye: 0.00 ± 0.00, left eye: 0.00 ± 0.00	right eye: 0.00 ± 0.00, left eye: 0.01 ± 0.00	right eye: 0.00 ± 0.00, left eye: 0.00 ± 0.00
Mean 20-29	right eye: 0.00 ± 0.00, left eye: 0.00 ± 0.00	right eye: 0.00 ± 0.00, left eye: 0.00 ± 0.00	right eye: 0.00 ± 0.00, left eye: 0.00 ± 0.00

(Mean of means ± s.e.)**.**

Table S8. The comparisons between phase A and phase B in diverging target test (DTT) and in single target tests (STT) for the frequencies of "step" and of "steady" and for the durations of "steady".

		Right eye	Left eye
Step frequency	Phase A vs. Phase B	Phase A: 0.13 ± 0.03 Phase B: 0.19 ± 0.02 $t_{(6)}$=-1.567 p=0.168	Phase A: 0.11 ± 0.03 Phase B: 0.19 ± 0.02 $t_{(6)}$=-1.719 p=0.136
	Phase A vs. Single target	Phase A: 0.13 ± 0.03 Single: 0.01 ± 0.00 $t_{(12)}$=3.288 p=0.006	Phase A: 0.11 ± 0.03 Single: 0.01 ± 0.00 $t_{(12)}$=3.312 p=0.006
	Phase B vs. Single target	Phase B: 0.19 ± 0.02 Single: 0.01 ± 0.00 $t_{(12)}$=7.257 p<0.0001	Phase B: 0.19 ± 0.02 Single: 0.01 ± 0.00 $t_{(12)}$=6.102 p<0.0001
Steady frequency	Phase A vs. Phase B	Phase A: 0.11 ± 0.00 Phase B: 0.08 ± 0.00 $t_{(6)}$=3.714 p=0.01	Phase A: 0.09 ± 0.00 Phase B: 0.09 ± 0.00 $t_{(6)}$=0.437 p=0.667
	Phase A vs. Single target	Phase A: 0.11 ± 0.00 Single: 0.02 ± 0.00 $t_{(12)}$=11.141 p<0.0001	Phase A: 0.09 ± 0.00 Single: 0.03 ± 0.00 $t_{(12)}$=6.883 p<0.0001
	Phase B vs. Single target	Phase B: 0.08 ± 0.00 Single: 0.02 ± 0.00 $t_{(12)}$=6.928 p<0.0001	Phase B: 0.09 ± 0.00 Single: 0.03 ± 0.00 $t_{(12)}$=6.697 p<0.0001
Steady duration	Phase A vs. Phase B	Phase A: 0.69 ± 0.05 Phase B: 0.69± 0.03 $t_{(6)}$=-0.07 p=0.947	Phase A: 0.7 ± 0.05 Phase B: 0.69 ± 0.04 $t_{(6)}$=0.109 p=0.917
	Phase A vs. Single target	Phase A: 0.69 ± 0.05 Single: 0.97 ± 0.01 $t_{(12)}$=-5.072 p<0.001	Phase A: 0.7 ± 0.05 Single: 0.96 ± 0.00 $t_{(12)}$=-4.902 p<0.001
	Phase B vs. Single target	Phase B: 0.69± 0.03 Single: 0.97 ± 0.01 $t_{(12)}$=-6.438 p<0.001	Phase B0.69 ± 0.04 Single: 0.96 ± 0.00 $t_{(12)}$=-5.902 p<0.001

Table S9. The comparisons of the frequencies of "step" and of "steady" and the duration of "steady", for the right eye and the left eye, for phases A and B of DTT and STT.

Step frequency	Phase A	right eye: 0.13 ± 0.03 left eye: 0.11 ± 0.03 $t_{(6)}$=0.523 P=0.620
	Phase B	right eye: 0.19 ± 0.02 left eye: 0.19 ± 0.02 $t_{(6)}$=-0.185 P=0.859
	Single target	right eye: 0.01 ± 0.00 left eye: 0.01 ± 0.00 $t_{(6)}$=0 P=1
Steady frequency	Phase A	right eye: 0.11 ± 0.00 left eye: 0.09 ± 0.00 $t_{(6)}$=1.296 P=0.242
	Phase B	right eye: 0.08 ± 0.00 left eye: 0.09 ± 0.00 $t_{(6)}$=-0.719 P=0.499
	Single target	right eye: 0.02 ± 0.00 left eye: 0.03 ± 0.00 $t_{(6)}$=-4.583 P=0.004
Steady duration	Phase A	right eye: 0.69 ± 0.05 left eye: 0.70 ± 0.05 $t_{(6)}$=-0.298 P=0.776
	Phase B	right eye: 0.69 ± 0.03 left eye: 0.69 ± 0.04 $t_{(6)}$=0.043 P=0.976
	Single target	right eye: 0.97 ± 0.01 left eye: 0.96 ± 0.00 $t_{(6)}$=0.518 P=0.623

Table S10. The comparisons (i) of the frequencies of "step" and of "steady" in tests that ended with or without convergence, and (ii) of the durations of "steady", between the converging eye (CE) and the tracking eye (TE).

Tests that ended in convergence vs. tests that did not	Steady duration	convergence: 8.14 ± 2.55 no convergence: 7.36 ± 1.93 Z=-0.62 P=0.950
	Step frequency	convergence: 0.44 ± 0.03 no convergence: 0.32 ± 0.04 W=143.5 P=0.036
	Steady frequency	convergence: 0.16 ± 0.01 no convergence: 0.19 ± 0.01 W=53 P=0.043
CE vs. TE	Steady duration	CE: 10.37 ± 1.33 TE: 7.45 ± 0.73 Z=-2.028 P=0.043
	Step frequency	CE: 7.02 ± 1.31 TE: 10.79 ± 2.37 Z=-1.439 P=0.150
	Steady frequency	CE: 3.6 ± 0.76 TE: 4.63 ± 0.92 Z=-1.892 P=0.058

Table S11. The comparisons of the frequencies of "steps" and of "steady" as a function of direction: (i) between tests that ended with or without convergence, and (ii) between the converging eye (CE) and the tracking eye (TE).

| Tested parameter	Steady frequency	Step frequency
All directional categories in tests that ended in convergence	shifting with: 0.61 ± 0.06 shifting away: 0.37 ± 0.06 unshifted: 0.01 ± 0.02 $X^2_{(2)}$= 34.462 P<0.001	toward: 0.60 ± 0.05 away: 0.39 ± 0.05 Z=-2.535 P=0.011
All directional categories in tests that did not ended in convergence	shifting with: 0.58 ± 0.08 shifting away: 0.38 ± 0.07 unshifted: 0.03 ± 0.01 $X^2_{(2)}$= 10.231 P=0.006	toward: 0.59 ± 0.04 away: 0.40 ± 0.04 Z=-2.214 P=0.027
directional categories in the CE	shifting with: 0.57 ± 0.13 shifting away: 0.40 ± 0.12 unshifted: 0.01 ± 0.01 $X^2_{(2)}$= 23.577 P<0.001	toward: 0.53 ± 0.12 away: 0.46 ± 0.12 Z=-0.546 P=0.585
directional categories in the TE	shifting with: 0.65 ± 0.09 shifting away: 0.32 ± 0.10 unshifted: 0.02 ± 0.02 $X^2_{(2)}$= 26.260 P<0.001	toward: 0.67 ± 0.06 away: 0.32 ± 0.06 Z=-3.295 P=0.001
"Shifting with" / step toward: CE vs. TE	CE: 0.57 ± 0.13 TE: 0.41 ± 0.12 Z=-0.826 P=0.409	CE: 0.53 ± 0.12 TE: 0.67 ± 0.06 Z=-1.024 P=0.306
"Shifting away" / step away: CE vs. TE	CE: 0.66 ± 0.09 TE: 0.31 ± 0.09 Z=-0.826 P=0.409	CE0.46 ± 0.12 TE: 0.32 ± 0.06 Z=-1.002 P=0.316
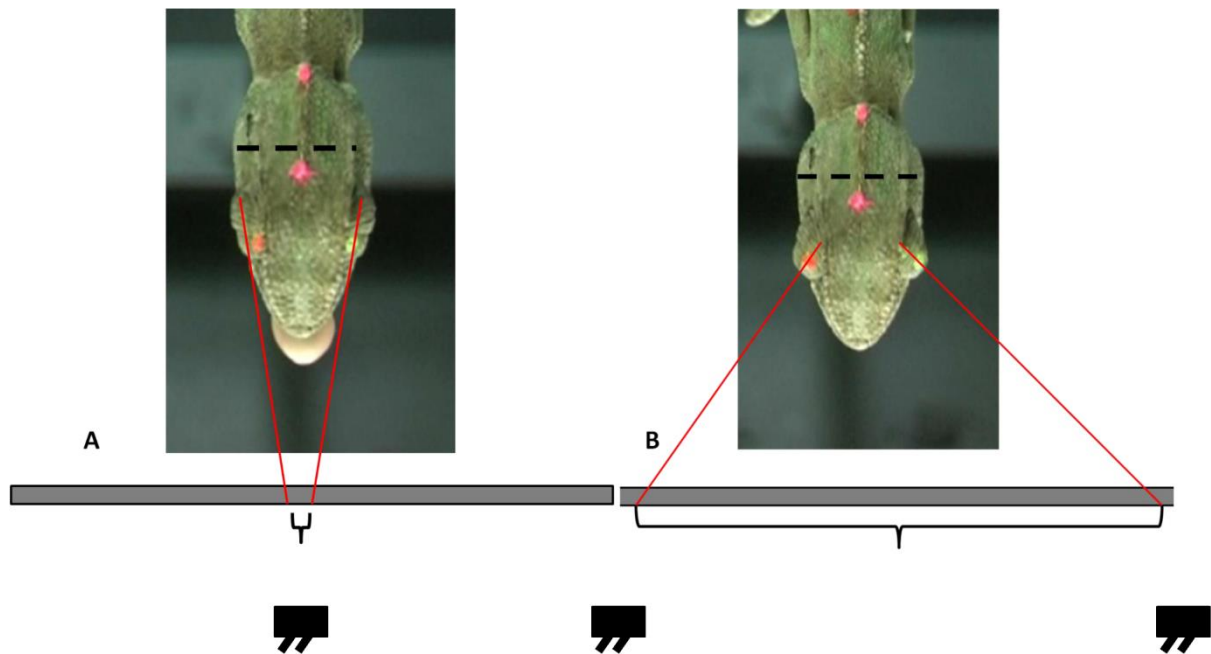
Fig. S1. Eye vergence movements under single target and two targets. (A) Eye convergence on a single target. (B) Eye divergence on two targets moving in opposite directions. Red lines- gaze axes; Horizontal hatched bars - head width; Horizontal solid bars - distance between intersection points of the gaze axes (extrapolated) on the screen. An example of the "prey" target is provided beneath each figure.