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VISUAL, VESTIBULAR, AND MECHANICAL FACTORS IN CHAMELEON HEAD MOVEMENT

By

Martha Flanders

A DISSERTATION

Submitted to
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ABSTRACT

VISUAL, VESTIBULAR, AND MECHANICAL FACTORS IN CHAMELEON HEAD MOVEMENT

By

Martha Flanders

In the African chameleon, a moving cricket elicits a visually guided, pursuit head movement that aligns the tongue with the bait. Moving the chameleon's body elicits a vestibularly mediated, stabilization head movement that keeps the head stationary in space.

The independence of visual and vestibular head movements was tested by individually characterizing each, and comparing these characteristics to those of head movements made during combined bait and body movement. Results show a visual-vestibular interaction in which the timing of pursuit head movement is improved during combined bait and body movement.

Mechanical analysis showed that equal amplitude and frequency, visual and vestibular movements of the head relative to the body are mechanically similar, and suggested continuous neural control of head position.

ACKNOWLEDGMENTS

Thanks to Dr. James L. Edwards for financial support and laboratory space in the first three years of my graduate work. The research in Chapters 2, 3, and 4 was supervised by Drs. James L. Zacks (Psychology and Zoology), Erik Goodman (Electrical Engineering and Systems Science), and Robert P. Hubbard (Biomechanics and Metallurgy, Mechanics and Materials Science). Dr. James H. Asher, Jr. and Walter E. Chapelle, P.E. (my Daddy) helped with Appendices A and B, respectively.

Thanks again to Daddy for making the apparatus, and to Hank Wieferich for assembling the mechanical parts. Special thanks to Dr. Hubbard for guidance.

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CHAPTER 1: INTRODUCTION AND SUMMARY

The goal of this research was to find out what makes a lizard move its head the way it does. The African chameleon was an ideal subject for this motor control study, because of the conspicuous binocular head tracking exhibited by this lizard during its normal feeding behavior. Baby chameleons are born live and almost immediately begin track insects. Throughout life, the chameleon climbs on small branches as it aims both eyes and a projectile tongue at moving insects (Figure 1). Movement of the head relative to the body is guided by the vestibular system during body movement, guided by the visual system during insect movement, and always constrained by the mechanics of the head-neck system. The following chapters examine the relative contribution of each of these systems to coordinated head movement.

Chapter 2 gives a qualitative description of feeding behavior in the African chameleon, and a quantitative characterization of the pursuit head movement system. **Within a certain range of amplitudes and frequencies, a hungry chameleon will follow a cricket, moved back and forth sinusoidally, with a sinusoidal head movement and no apparent eye movement.** The head lags behind the cricket and does not move as far in either direction as does the cricket. An

Figure 1: **The African Chameleon in Nature.** The chameleon climbs on small branches as it hunts for insects. During locomotion or branch movement a vestibular reflex keeps the head stationary in space. A visually guided pursuit head movement follows a moving insect. Here, a female Chameleo senegalensis aims both eyes and a projectile tongue at a short-horned grasshopper as it lands on a leaf.

equation is derived to predict gain (amplitude of head movement/amplitude of bait movement), given the chameleon's time lag and the stimulus frequency. The most striking prediction of the equation, which is confirmed by the data, is that the head becomes aligned with the cricket just at the point when the head is momentarily stationary.

Chapter 3 presents the central theme of the dissertation. **The independence of visual and vestibular head movement systems is tested by individually characterizing each, and comparing these characteristics to those of head movements made during combined visual and vestibular stimulation.** The visual (pursuit) head movement system was characterized in Chapter 2. Head movement controlled by the vestibular system was characterized by rotating the chameleon's body back and forth sinusoidally, around the neck. Within ranges of amplitudes and frequencies the chameleons' vestibulo-collic reflexs (VCR) were observed to keep their heads stationery in space.

The hypothesis that visual and vestibular head movement systems are independent predicts that during combined body and bait movement the VCR will respond to body movement by stabilizing the head, so that the characteristics of the movement of the head in space will be the same as those of pure pursuit. When 10^{o} bait movement was combined with 5^{o} body movement, either in phase at the same frequency or at a lower frequency with no consistent phase relationship, the resulting movement of the head in space was sinusoidal, at the same frequency as the bait movement, and had the time lag/gain relationship characteristic of pure pursuit. However, in 17 of 18 trials, for a given chameleon, on a given day, time lag was shorter during body movement.

Chapter 4 tests and supports the hypothesis that **pursuit and VCR movements of the head relative to the body are mechanically similar and therefore place similar demands on the muscular system.** Since there is no movement of the head in space during perfect VCR, visual and vestibular head movements are mechanically similar only if the head's inertial resistance to acceleration is negligible. The comparison of inertial and elastic forces for sinusoidal head movement shows that the neck is highly elastic and inertial forces are negligible. Electromyographic data show similar muscle activity during pursuit and VCR movements, and support the importance of elasticity in the chameleon head-neck system.

CHAPTER 2: BINOCULAR HEAD TRACKING IN THE AFRICAN CHAMELEON

Introduction

The African chameleon has a unique feeding strategy. These arboreal lizards capture insects by shooting a long sticky tongue straight out of their mouths, off a specialized hyoid apparatus (Murphy, 1940). The chameleon scans its environment with large amplitude, independent, saccadic eye movements (Walls, 1942; Mates, 1978). When an insect is spotted, the head is aligned, both eyes come forward to fixate the target, and the hyoid is extended in what is known as the "initial protrusion" (Gans, 1967; Bellairs, 1970). During initial protrusion the chameleon decides how far to shoot its tongue by accommodation (focusing) rather than triangulation (as one might expect) (Harkness, 1977). The chameleon has a deep convexiclivate fovea that acts as a focus indicator (Harkness and Bennet-Clark, 1978) and may work along with short depth of field from iris dilation, and efference monitoring of motor commands to lens muscles, to help the chameleon judge distance.

When an insect moves past the chameleon during initial protrusion and binocular fixation, the chameleon moves its head, and not its eyes, in smooth pursuit. Foveation is a necessary part of pursuit, but an equally important goal is to align the tongue with the prey. Unlike mammals and fish, who pursue with visual fixation followed by counter-rotation of the eyes during head movement (Bizzi, et al., 1971; Lanchester and Mark, 1975), the chameleon often fixes its eyes in its head and pursues by performing head movement alone.

This chapter reports that within a certain range of amplitudes and frequencies, hungry chameleons will perform sinusoidal pursuit head movement, with no apparent eye movement. In spite of individual timing differences, and over their entire range of frequencies, all of the chameleons tested tracked sinusoidally moving crickets using a strategy that put the head at zero velocity when the bait was directly in front of it, and minimized retinal slip.

Methods

Five female Chameleo senegalensis, weighing between 20 and 60 gms., were obtained commercially and housed in a room with high humidity, 12 hr./day florescent lighting, and additional incandescent lights turned on as needed for basking and to adjust the temperature. Preferred body temperature was about 80-85°F (27-29°C) in the day, and 70°F (21°C) at night. The chameleons ate about six crickets/day. The crickets were fed a high calcium diet (Allen, personal communication).

The chameleons were pretrained to feed on a bait-moving apparatus (Figure 2). The chameleons clung to a stationary

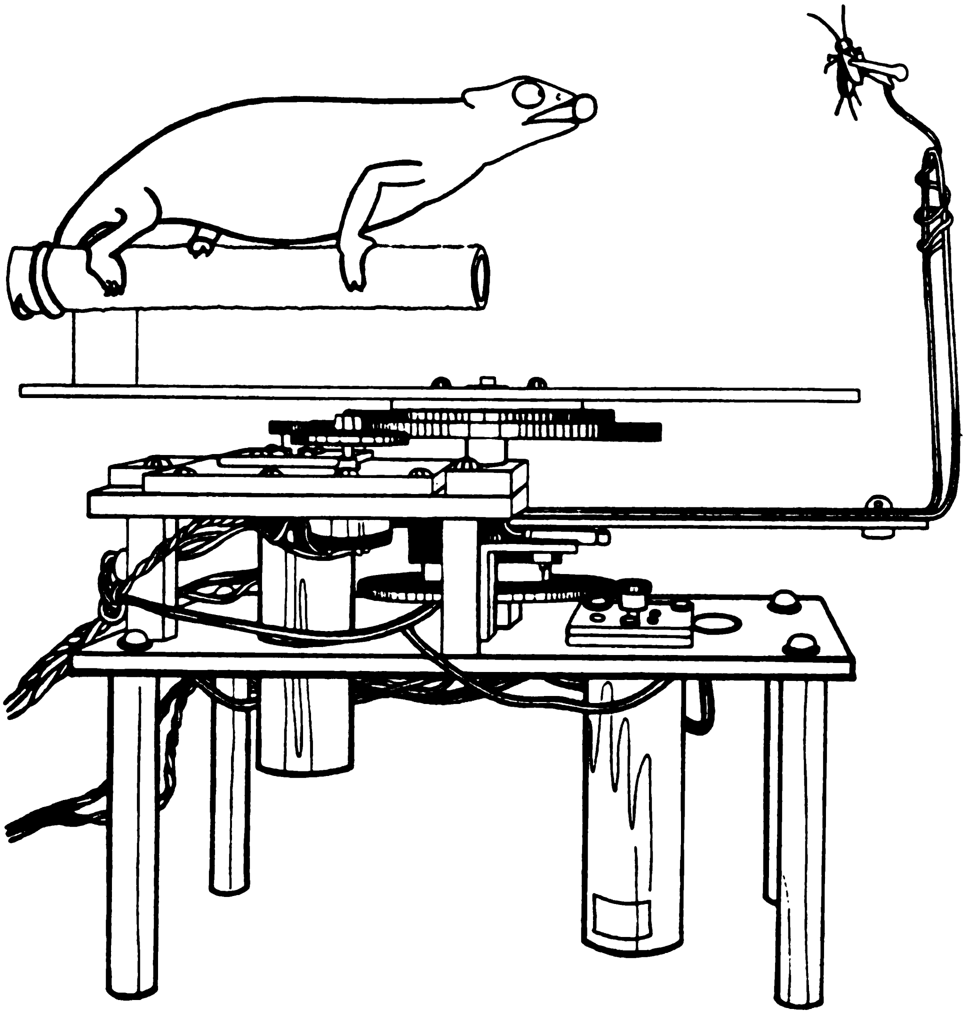


Figure 2: **The Motion Producing Apparatus.** With her tongue in initial protrusion, the chameleon clings to a movable perch and aims at a movable cricket. The forward position of the perch can be adjusted so that the angular, horizontal rotations of the cricket and/or perch (moved by gears and motors) are centered at the chameleon's neck. (Apparatus by Chapelle.)

perch and aimed eyes and tongues at moveable crickets (the bait and reward for pursuit). The bait was moved by a servomotor driven by a function generator chip. Angular, horizontal, sinusoidal motion between 0.5 and 4.0 Hz was produced with amplitudes up to about 20^{o}. As a chameleon grasped the perch, its position could be adjusted so that the axes of bait movement and head movement were concentric. Marks were painted on each animal's head and eye lids with black acrylic, to aid in position measurement.

The motions of the bait and head were recorded on 16 mm film at 50 f.p.s., with a telephoto/macro lens on a Bolex camera mounted about 2 meters above the apparatus. Ambient temperature was not controlled during film exposure but was usually near 85^{o}F (29^{o}C) due to incandescent spot lighting. A Lafayette stop motion projector was used to view the film. Pursuit sequences were projected onto an angular grid with the grid center at the center of the bait and head rotations. Generally the chameleons grasped the perch firmly and moved only their heads, but when small body movements occurred, the grid was adjusted frame by frame to keep the coordinate system centered at the chameleon's neck. Error introduced by moving the coordinate system was less than the error of position measurement off the grid (about $\pm 1.0^{o}$).

Film sequences containing at least three complete cycles of sinusoidal, steady state, pursuit head movement without eye movements were analyzed. A graphical technique was used to calculate the average amplitude gain of the head movement relative to the bait movement and the phase lag of the head movement (Appendix B).

Results

On film the motion data appeared as shown by the series of photographs in Figure 3A. Figure 3B places the photographs in one complete movement cycle, sampled at 1/4 sec. time intervals. The bait moves back and forth sinusoidally and the head follows in pursuit. Because chameleons do not move their eyes within the lids, the lines painted on the eye lids indicate that the eyes were fixed in the head during this cycle. Before initial tongue protrusion and during less vigorous pursuit, the chameleons sometimes locked one eye straight ahead while the other continued to scan the environment or moved in smooth or saccadic pursuit. Small conjugate saccadic movements were also observed. The behavior of the eyes was closely observed during each film exposure and measurements were taken only from cycles judged to be free of eye movement.

Figure 4 shows a representative pursuit sequence, as measured on the angular grid. Bait position (closed circles) and head position (open circles) are plotted frame by frame against time for five continuous cycles. Despite the error in measurement, pursuit head movements always appeared to be smooth and the data were well fitted by sine waves of the same frequency as the bait movement (Appendix A). In the frequency range from 1.0 to 2.8 Hz., the chameleons

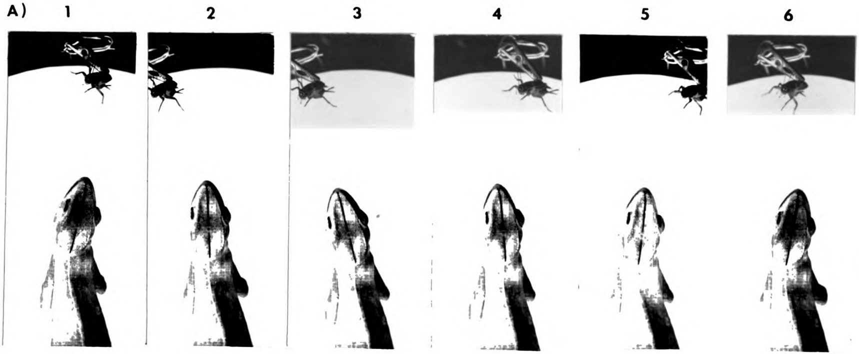
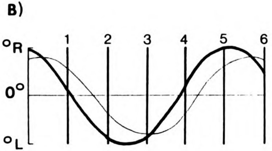


Figure 3: **Film Data.** Photographed from above at 1/4 sec. intervals, the chameleon (A) performs one cycle of pursuit head movement at 0.707 Hz., with a time lag of 130 msec., and a gain of about 0.8. The lines painted on the head and eyes aid in position measurement. The graph (B) approximates the location of each photograph (numbers 1-6) in the continuous angular motions of the bait (thick line) and head (thin line).



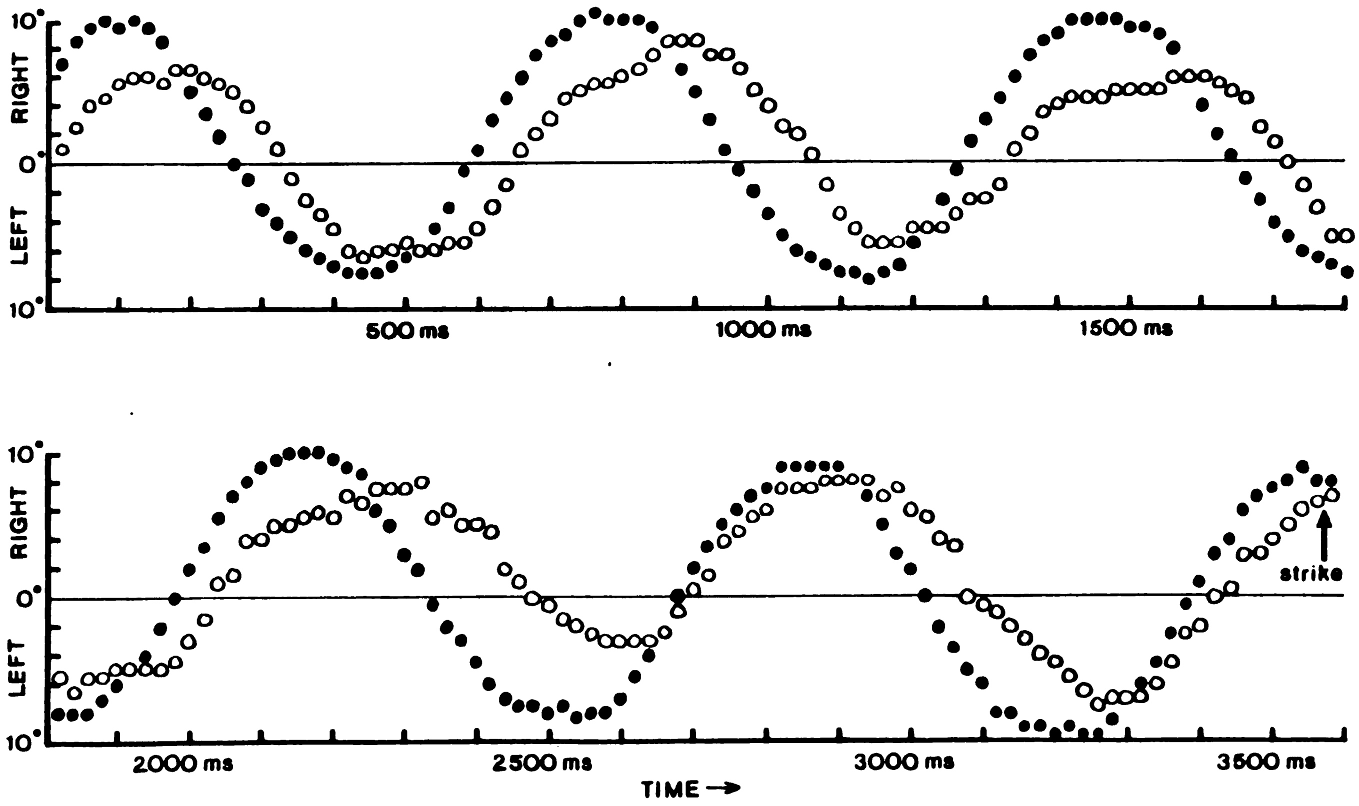


Figure 3: **Position vs. Time for Pursuit Head Movement.** Angular position of bait (●) and head (○) is shown at 20 msec. (one frame) intervals during a pursuit head movement at 1.4 Hz. Notice that the head is at peak displacement when bait and head are at the same position. After several cycles of pursuit the chameleon shot out her tongue to strike and eat the bait.

performed sinusoidal pursuit with a negative phase (or time lag, Δt), and an amplitude gain (the ratio between peak head displacement and peak bait displacement, H/B) less than one. Table 1 shows measured time lag and gain for the pursuit movements of five different chameleons duing 10° amplitude bait movement, on several different dates. The time lag of an individual chameleon varied little relative to differences between animals, and was not significantly correlated with frequency. The chameleons moved with large gains (near 1.0) at low frequencies, and with smaller gains at high frequencies.

The position vs. time record in Figure 4 shows that although the chameleon tracks the bait with a time lag, she uses an amplitude that puts the head at peak displacement (and zero velocity) when the bait and the head are at the same position. This phenomenon was observed in all five chameleons, even though time lags varied from 52.8 (Susan) to 144.4 (Bette) msec. and frequencies ranged from 1.0 to 2.8 Hz.

Figure 5 shows the observed pursuit strategy in the form of a generalized position vs. time graph. The bait movement (thick line) is followed by a pursuit head movement (thin line). B is the amplitude of the bait movement (about 10°). The head is at peak displacement when the bait and head are at the same position, so that head amplitude (H) depends on the time lag (Δt) and the period of a cycle. Time lag varies between animals and between trials, and the

Table 1: **Pursuit Data.** Characteristics of pursuit head movement with body stationary.

Date	Chameleon	f (Hz.)	Δt (msec.)	Measured H/B	Model H/B	ΔH/B
1/02	Susan	■ 2.8	89.3	0.25	0.21	+0.04
		■ 2.0	52.8	0.82	0.79	+0.03
		■ 1.4	59.5	0.86	0.86	0.00
2/08		■ 2.8	71.4	0.38	0.31	+0.07
		■ 1.4	55.6	0.82	0.88	-0.06
		■ 2.0	54.2	0.65	0.78	-0.13
		■ 1.7	66.1	0.72	0.76	-0.04
2/27		■ 1.4	61.5	0.88	0.85	+0.03
		■ 1.2	63.0	0.91	0.89	+0.02
2/08	Carol	X 1.0	108.9	0.81	0.78	+0.03
7/02		X 1.0	97.8	0.80	0.81	-0.01
2/08	Bette	✶ 1.0	144.4	0.66	0.61	+0.05
7/01	Hilde	▲ 1.0	90.6	0.90	0.84	+0.06
7/08		▲ 1.7	103.7	0.55	0.45	+0.10
7/03	Lisa	● 1.0	86.1	0.90	0.85	+0.05
7/04		● 1.4	93.6	0.70	0.67	+0.03
		● 1.0	76.1	0.77	0.88	-0.11
7/08		● 1.2	72.4	0.88	0.85	+0.03
		● 1.7	73.4	0.79	0.70	+0.09
7/13		● 1.4	80.9	0.72	0.75	-0.03
7/17		● 2.0	99.7	0.44	0.31	+0.13

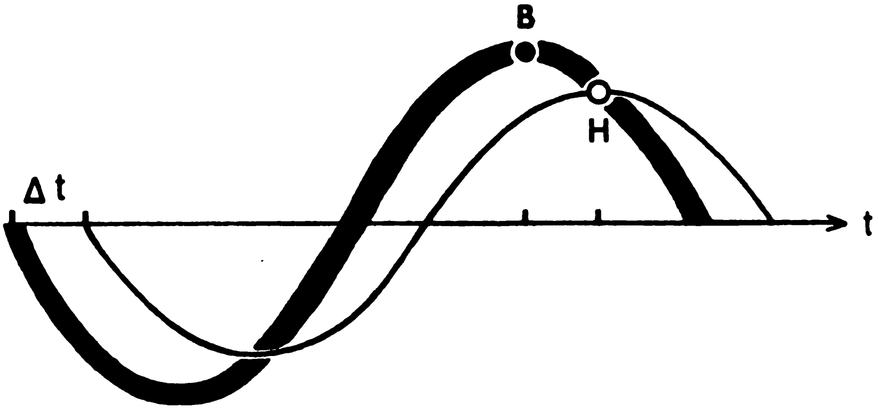


Figure 5: **The Pursuit Model.** Angular position vs. time for sinusoidal bait movement (thick line) and pursuit head movement (thin line) to the left (down) and right (up) of a zero position. Time lag (Δt) is shown at the zero crossing and again between the peak displacements. Amplitude gain (H/B) is predicted using the formula for point H (head amplitude) on the line with amplitude B (bait amplitude).

period of a cycle depends on the frequency set with the apparatus.

In order to quantitatively test the usage of this strategy, an equation was derived to predict amplitude gain (H/B), given time lag (Δt) and period (T) or frequency ($f=1/T$). The equation for predicted gain:

$$H/B = \sin 2\pi f[(1/4)T + \Delta t]$$

is derived from the angular position equation for sinusoidal motion:

$$\theta = A \sin 2\pi f(t),$$

where θ is angular position, A is peak displacement, and t is time. For position H, on the line with amplitude B,

$$H = B \sin 2\pi f[(1/4)T + \Delta t],$$

where (1/4)T is the time at point B and point H follows B by Δt.

Use of the head amplitude predicted by the model (rather than a larger or smaller head amplitude) minimizes the amplitude of the sinusoidal motion of the bait relative to the head (retinal slip for pursuit head movement without eye movement). This can be shown by representing a time lag - frequency combination as a phase angle:

$$\Psi = 2\pi f \Delta t$$

The motions of the bait (B) and head (H) can be represented as two vectors separated by the phase angle Ψ. Since $\vec{B}$ is a vector, it can be separated into two components: $\vec{B}_x$ is parallel to $\vec{H}$, and $\vec{B}_y$ is orthogonal to $\vec{H}$. The amplitude of the difference between the two sine waves (relative motion and retinal slip):

$$\vec{B} - \vec{H} = (\vec{B}_x - \vec{H}) + \vec{B}_y$$

is minimum when $\vec{H}$ is equal to $\vec{B}_x$. This occurs when

$$\begin{aligned} H &= B \cos \Psi \\ &= B \sin (90^{\circ} + \Psi) \\ &= B \sin 2\pi f[(1/4)T + \Delta t] \end{aligned}$$

as shown in the model.

Time lags of the five chameleons performing at frequencies between 1.0 and 2.8 Hz were used to calculate the gain predicted by the pursuit model equation for each pursuit sequence. The difference between measured gain and predicted (model) gain is shown in the last column of Table 1. The average difference between measured gain and model gain ($\Delta H/B$) was 0.018 which represents about a 0.18° overshoot of the predicted head amplitude. Using a t-test, this difference was not found to be significantly different from zero ($\alpha = .05$). (This test was also performed using an alternate measurement of time lag and the head undershot the model by 0.11°. See Appendix A.)

Figure 6 shows how well the data fit the model. Observed gains for each trial are plotted against the gain predicted for that trial, using time lag and frequency. Observed and predicted values have a significant positive correlation (correlation coefficient = 0.95). The y-intercept of the regression line, however, is significantly different from 0.00 (Snedecor and Cochran, 1971). This

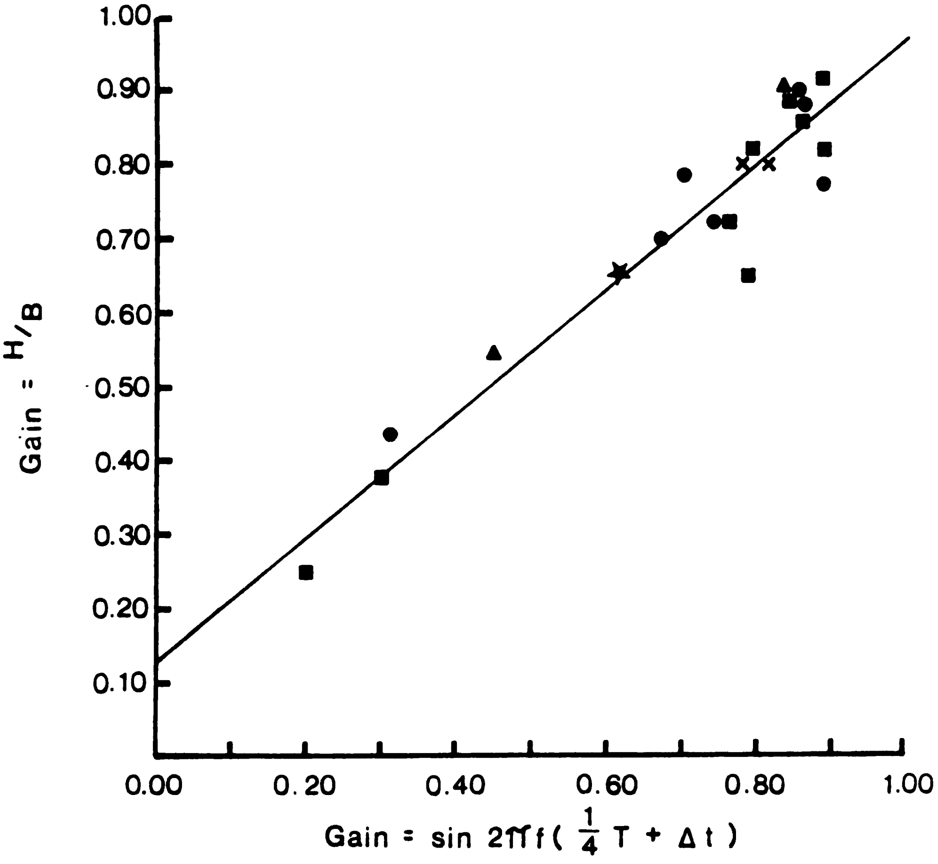


Figure 6: **Test of the Model.** Observed gain (H/B) vs. gain predicted by the model equation. Symbols represent trials shown in Table 2. A linear regression line is shown. Correlation coefficient = 0.95.

shows that low amplitude head movements overshot the predicted head amplitudes.

Head movements observed during 5° bait movement were also greater than predicted by using the model equation with $B = 5^{\circ}$. Susan and Lisa were tested with 5° bait movement, at 2.8 and 2.4 Hz respectively. In each case the chameleon's time lag was within her normal range (58.5 msec for Susan and 78.2 msec for Lisa), but the head overshot the amplitude predicted by the model by about 1.2°.

The range of frequencies and amplitudes used was limited by the chameleons' performances. At low amplitudes and low frequencies the chameleons struck and ate the crickets without performing three cycles of pursuit. At high amplitudes and frequencies the chameleons showed no head movement at all. For 10° bait movement, the frequency range of a chameleon was limited by her time lag. When a frequency-time lag combination represented a 90° phase lag, the model predicted a 0° head movement. For example, Bette, with her 144.4 msec. time lag, approached a 90° phase lag at 1.7 Hz. Thus it was impossible for the slower animals to perform pursuit head movements at high frequencies.

Figure 4 shows that after several cycles of pursuit the chameleon shot out her tongue to strike and eat the bait. The chameleons were most likely to hit the bait if they struck near peak head displacement, where the bait was in front of the head and moving slowly. The strike shown in Figure 4 was successful (a hit) for this reason, but the chameleons did not always choose the optimal time to strike, and often missed. For the trials in which the strike was recorded on film, the chameleons missed 69% of the time. Although the head was usually stationary when the bait was directly in front of it, it took about 40 msec. for the tongue, once fired, to travel its distance (and some additional time for motor commands to reach tongue muscles), so that by the time the tongue reached its target the bait had often passed. The fact that the pursuit system does not appear to take this additional time lag into account, and the variability in head position at the time of strike, suggest that the pursuit movement and the decision to strike are two separate processes.

Discussion

The study of pursuit head movement made in response to horizontal, sinusoidal bait movement, demonstrated that since head movement cannot track bait perfectly (due to a time lag), the chameleon uses a strategy that brings the head in line with the bait when the head is at zero velocity. Since the tongue must be shot straight out of the mouth, this might seem to be an ideal feeding strategy. But the chameleons often missed. (They very rarely miss stationary targets.) The head amplitude represented in the model minimizes retinal slip velocity and acceleration. Thus, the goal of the pursuit head movement system may be to foveate the prey and judge its distance, rather than to eat it.

Several lines of evidence suggest that the chameleon's pursuit head movement is visually guided by a continuous position tracking system. Interupting vision abruptly stops the head movement. The chameleon head-neck system is highly elastic (Chapter 4), and head movements did not (to the resolution of my measurement) contain free-swinging (or ballistic) segments. In nature the chameleon rarely encounters a cricket moving sinusoidally at a single frequency, but the experimental use of sinusoidal motion may have revealed a continuous position tracking system basic to pursuit.

Other authors have emphasized prediction in pursuit movement. Human smooth-pursuit eye movements follow target motions of low frequency with negligible phase lag due to sine wave prediction (Lisberger, et al., 1981). If the chameleons predicted the wave form of the bait movement rather than tracking it continuously, they should have improved their time lags from cycle to cycle (or from trial to trial). This was not seen. Lanchester and Mark (1975) argued against predictive pursuit for fish swimming toward falling bait, by modeling the path of the fish as one in which the mouth always points directly toward the bait. That study did not take into account a time delay between sensing the position of the bait and bringing the body into line with it. If fish have time lags between bait and head movement similar to those seen in chameleons, the movements that fit those authors' model were, in fact, predictive.

Further studies of chameleon head movement have shown that chameleons also use the pursuit strategy described above, for pursuit during the body movement. During passive body rotation, a chameleon's individual time lag was always shortened (Chapter 3) for higher gain, less retinal slip, and more successful strikes (improved pursuit performance).

CHAPTER 3: VISUAL AND VESTIBULAR INFLUENCES IN CHAMELEON HEAD MOVEMENT: CHARACTERIZING NEURAL INTERACTION

Introduction

In vertebrates, head and eye movements are guided by visual, vestibular and perhaps proprioceptive stimuli. A small, smoothly moving visual target is followed using pursuit head or eye movement systems. Movement of the entire visual field, relative to the eyes, is minimized using visually guided, compensatory (optokinetic) movements. During body or head movement, receptors of the vestibular system (utricle and semicircular canals) also mediate compensatory movements that work to stabilize the head (vestibulo-collic reflex, VCR) or eyes (vestibulo-ocular reflex, VOR) in space. Interactions between visual and vestibular movement systems have been studied extensively (Henn, et al., 1980) in the hope that they will reveal mechanisms basic to integrated sensory-motor function.

The fundamental problem in studying visual-vestibular interaction is recognizing visual and vestibular components of a movement guided by both stimuli. One approach is to individually characterize the visually guided movement and the vestibular, stabilization movement, and compare these characters to those of movements made during combined visual and vestibular stimulation. This tests the hypothesis that movements during combined stimulation are the sum of normal visual and vestibular movements. Rejection of this hypothesis is evidence for interaction between the two systems, while failure to reject supports their independence.

Investigations of smooth pursuit eye movement and VOR in primates, have been guided by the idea that VOR may be suppressed during head tracking to improve pursuit performance (Robinson, 1977). Lisberger, et al. (1981) characterized the pursuit system in monkeys, animals with nearly perfect VORs, and then combined oppositely directed visual and vestibular stimulation by rotating a visual target exactly with the animals' heads. The result was failure to reject the independence hypothesis. However, when visual and vestibular movements are exactly opposite, an infinite number of compromising interactions (vestibular suppression along with a change in pursuit) could give this same result.

Other investigators have rejected the independence of visual and vestibular movements. Bock (1982) tested human smooth pursuit and VOR in a conflict situation where visual and vestibular eye movements were in opposite directions, and concluded that eye movements were sometimes predominantly visual and sometimes predominantly vestibular (a switching type, non-linear interaction). In geckos, the combination of visual (optokinetic) and vestibular (vestibulocollic) stimuli in the same direction was found to improve the performance of one or the other or both systems (Meyer, et al., 1979).

Whether the visual-vestibular independence hypothesis is rejected or not, the with-or-without-body-movement paradigm does not always allow quantification of visual and vestibular components of a movement made during combined stimulation. The African chameleon, with reliable pursuit head movement characteristics, and a nearly perfect vestibulo-collic reflex (VCR), has exhibited separately recognizable visual and vestibular components of complex movement.

Methods

Data were taken from five female *Chameleo senegalensis*, obtained commercially and pretrained to feed on the testing apparatus (Figure 2). The apparatus allowed separate control of visual (cricket movement) and vestibular (body movement) stimuli. The chameleon's neck was centered over the axis of rotation of the apparatus as the cricket and/or the animal's body was moved back and forth sinusoidally at various frequencies (0.7 - 2.8 Hz) and amplitudes (10° cricket movement and 5° body movement), in the horizontal plane. Resulting head movements were filmed from above (16 mm, 50 f.p.s.). Films were projected onto an angular grid to measure cricket and head positions with an accuracy of about $\pm 1^{\circ}$.

Results

A representative pursuit performance is shown in Figure 7A. Angular positions of the cricket (closed circles) and the head (open circles) are plotted against time as the bait is moved 10^{o} to the right and left of a zero (straight forward from the stationary perch) position, and the head follows in a motion not significantly different from sinusoidal (Appendix A), with no apparent movement of the eyes relative to the head (Chapter 2). For a 10^{o} amplitude cricket movement, the frequency response of one chameleon's pursuit system (data from Lisa, Table 1) is shown in Figure 8 (closed circles). In Chapter 2 an equation was derived to predict gain (amplitude of head movement/amplitude of cricket movement, H/B) given time lag and frequency. The solid curved lines in Figure 8 show the gains that correspond with constant time lags according to this equation. Lisa performs pure pursuit with a time lag of around 80 msec.

VCR performance was measured by rotating the chameleons' perch sinusoidally around the neck with an amplitude of 5^{o} and no visual target. Vestibular reflexes are usually tested in the dark to exclude visual interactions, but because of the plasticity of vestibular function (Barr, et al., 1976) it is preferable to test VCR under conditions comparable to those used for combined visual and vestibular stimulation. The chameleon, well known for her independent, saccadic eye movements (Mates, 1978), excludes the possibility of visual interactions by failing to suppress


10°

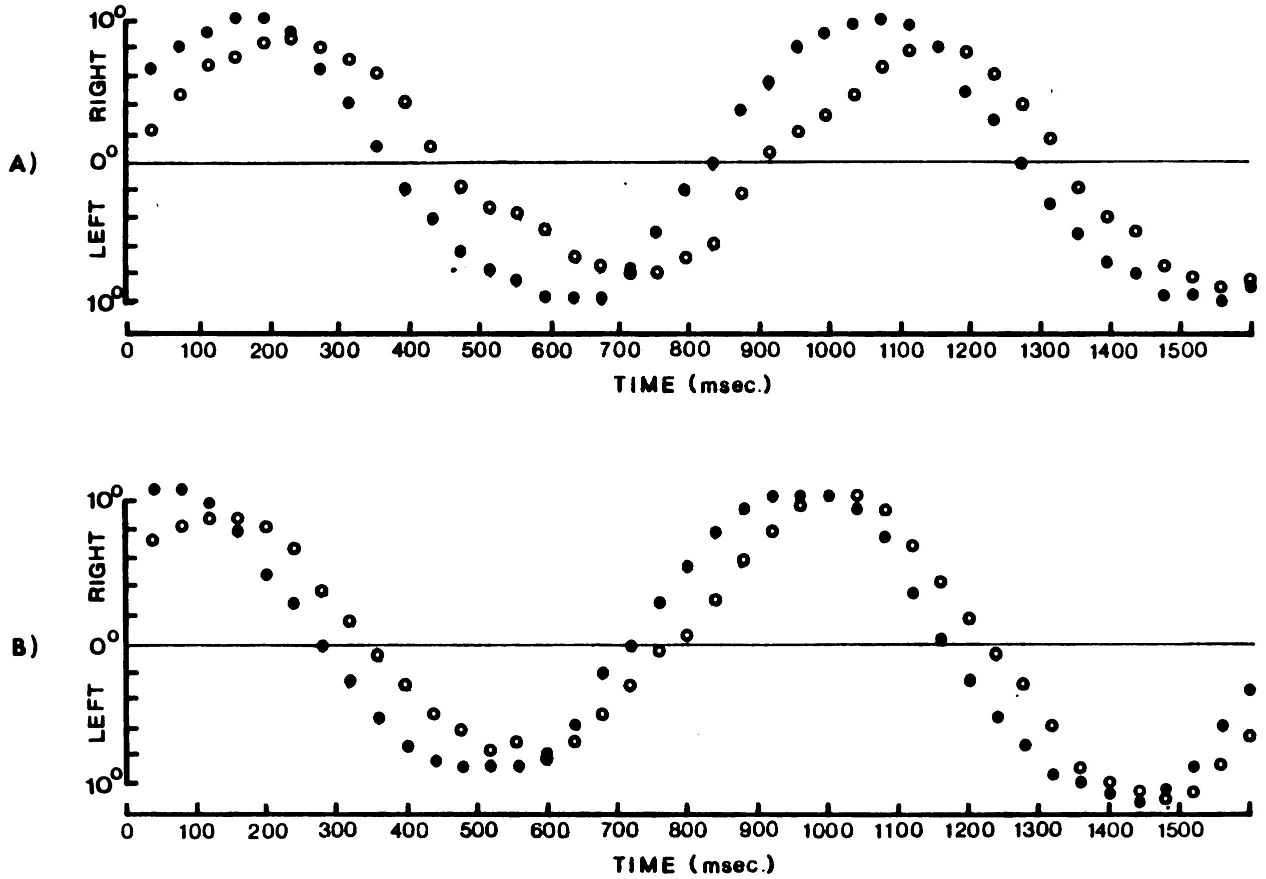


Figure 7: **Pursuit Head Movement with Body Stationary or Moved by Apparatus.** Angular position of bait (●) and head (o) in space is shown at 40 msec. (two frame) intervals during A) 1.0 Hz. bait movement, and B) 1.0 Hz. bait movement combined with 0.707 Hz. body movement.

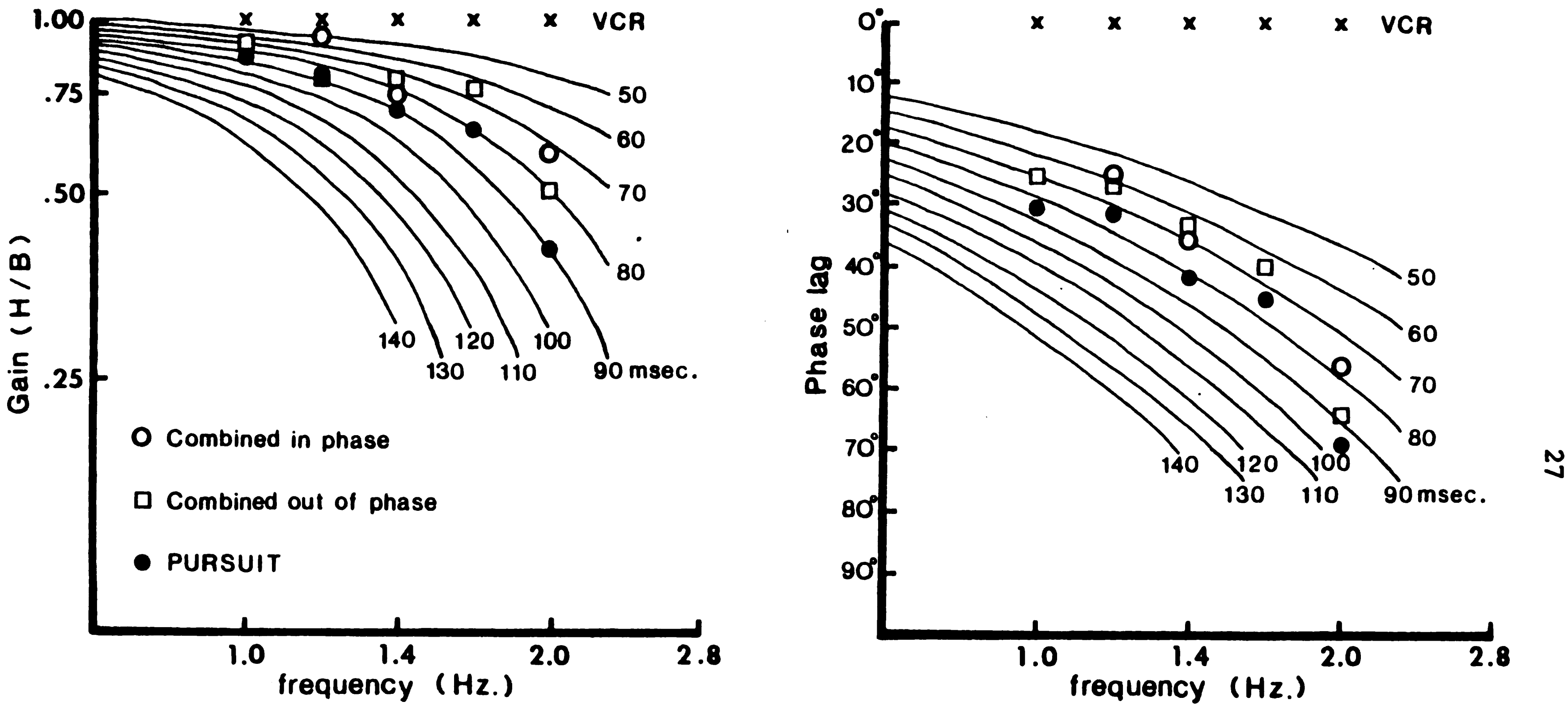


Figure 8: **Frequency Response for Sinusoidal Head Movement of One Chameleon.** Gain and phase characteristics are shown for sinusoidal head movement during body movement (VCR), bait movement (pursuit), and both (combined) body and bait movement. The curved lines are constant time lags on the phase vs. frequency graph, and the gains predicted by the pursuit model using these time lags.

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saccades during compensatory head movement, as would be expected for optokinetic stabilization (Pratt, 1982). The chameleons were observed to keep their heads stationary in space for several consecutive cycles of body movement, at each frequency. This excellent vestibular performance (shown in Figure 8 as a gain of 1.0 and a phase lag of 0°) was not surprising since the amplitude and frequencies used were similar to those produced by the chameleon's normal locomotion (measured on film in this laboratory).

According to the independence hypothesis, the combination of cricket movement with body movement (in the range of excellent VCR) will produce a head movement (in space) identical to that of pure pursuit. When 10° amplitude bait movement was combined with 5° amplitude body movement, either in phase at the same frequency, or at a lower frequency with no consistent phase relationship (as in Figure 7B) the resulting movements of the head in space were sinusoidal at the same frequency as the cricket movement (Appendix A) and amplitudes corresponded with time lags as predicted by the pursuit equation. For the 23 combined cricket and body movement trials shown in Table 2, predicted and observed head amplitudes had a difference not significantly different than 0.00 (t-test, $\alpha = 0.05$) and had a significant positive correlation (correlation coefficient = 0.85).

The frequency response for one chameleon's head movement during combined cricket and body movement (data from Lisa, Table 2) is shown in Figure 8 (open symbols). Open

Table 2: **Combined Data.** Characteristics of pursuit head movement with body moving in phase unless noted.

Date	Chameleon	f (Hz.)	Δt (msec.)	Measured H/B	Model H/B	ΔH/B
1/02	Susan	□ 2.8	49.6	0.45	0.64	-0.19
		□ 2.0	50.0	0.83	0.81	+0.02
		□ 1.4	63.5	0.99	0.85	+0.14
2/08		□ 2.8	49.6	0.70	0.64	+0.06
		□ 2.0	38.9	0.75	0.88	-0.13
		□ 1.7	44.6	0.80	0.89	-0.09
2/27		□ 1.4	47.6	0.82	0.91	-0.09
		□ 1.2	53.7	0.97	0.92	+0.05
7/01	Hilde	* Δ 1.0	83.3	0.88	0.87	+0.01
7/08		Δ 1.7	89.3	0.62	0.58	+0.04
7/02	Lisa	* ○ 1.0	65.6	0.93	0.92	+0.01
7/03		* ○ 1.0	70.0	0.93	0.91	+0.02
7/08		○ 1.2	59.8	0.99	0.90	+0.09
		* ○ 1.2	61.2	0.85	0.90	-0.05
		○ 1.7	64.9	0.83	0.77	+0.06
7/10		○ 1.4	83.0	0.73	0.75	-0.02
7/13		* ○ 1.4	66.9	0.79	0.83	-0.04
		○ 1.4	69.8	0.76	0.82	-0.06
7/17		* ○ 2.0	90.0	0.53	0.43	-0.10
		○ 2.0	77.4	0.62	0.56	-0.06
7/19		* ○ 1.4	72.6	0.79	0.80	-0.01
		* ○ 1.7	70.6	0.72	0.73	-0.01
		* ○ 2.0	91.0	0.56	0.41	+0.15

* 0.707 Hz. body movement.

circles represent body movement in phase with the cricket movement. Open squares represent body movement at 0.707 Hz. The combined cricket and body movement data fit the pursuit model (as shown by the correspondence of gain to time lag), but pursuit characteristics are improved during body movement.

In 17 out of 18 paired trials (same chameleon, same bait frequency, same day), time lags were shorter during body movement (Table 3). The average improvement of 13.75 msec. (s.e. = 2.17 msec.) was significantly larger than zero (t-test, α = 0.001). Time lags had been measured by calculating phase (Appendix B) and were remeasured by timing zero crossings and again found to be significantly improved (see Appendix A).

Discussion

In cases where the animal's body was moved in phase with the bait, improvement in gain (corresponding to improved time lag) could be interpreted as suppression of VCR. Vestibular suppression, however, does not explain the improved time lag of pursuit. Furthermore, during a body movement at a different frequency, suppression of VCR would make the pursuit movement more difficult, and would not be expected to give a sinusoidal head movement with improved characteristics (as shown in Figure 7B).

These results describe a significant interaction between pursuit and vestibulo-collic systems in which the VCR

Table 3: **Time Lags.** Paired trials from Tables 1 and 2 show shorter time lags during combined bait and body movement.

Pursuit Δt (msec.)	Combined Δt (msec.)	Pursuit Δt - Combined Δt (msec.)
89.3	49.6	39.7
52.8	50.0	2.8
59.5	63.5	-4.0
71.4	49.6	21.8
54.2	38.9	15.3
66.1	44.6	21.5
61.5	47.6	13.9
63.0	53.7	9.3
90.6	83.3*	7.3
103.7	89.3	14.4
86.1	70.0*	16.1
72.4	59.8	12.6
72.4	61.2*	11.2
73.4	64.9	8.5
80.9	66.9	14.0
80.9	69.8*	11.1
99.7	90.0*	9.7
99.7	77.4	22.3
$\bar{x}$ = 76.5 s.e. = 3.7	$\bar{x}$ = 62.8 s.e. = 3.6	$\bar{x}$ = 13.8 s.e. = 2.2

* 0.707 Hz. body movement.

continuously responds to passive body movement with perfect compensation, but the time lag of the pursuit system is improved during vestibular stimulation. If time lag represents neural processing time, the neuronal mechanism for improvement of this character could be synaptic facilitation, or recurrent excitation in pursuit circuits as proposed for prey catching behavior in frogs (Lara, et al., 1982).

Although there are obvious differences between VCR and VOR and between lizards and primates, the chameleon has offered a solution to the problem of recognizing the relative contributions of visual and vestibular systems to complex movement by showing an improved pursuit head movement during a different frequency body movement. In nature, the chameleon's survival depends on her ability to pursue and capture insects. A neural mechanism that allows her to run down a moving branch while aiming her tongue at a moving insect, would surely be adaptive.

CHAPTER 4: THE MECHANICS OF CHAMELEON HEAD MOVEMENT

Introduction

In producing head movement the chameleon's nervous system must take into account the mechanics of the neck. A shortening neck muscle may encounter viscous resistance to velocity, inertial resistance to acceleration, and friction. Displacement of the head is also resisted by passive elasticity of contralateral tissue, and, in the case of co-contraction, by active elastic force in antagonistic muscle.

Figure 9A shows the peak displacements of the chameleon's sinusoidal pursuit head movement (see Chapter 2 for details). Viscous resistance to movement is greatest at peak velocity, as the head passes through its zero position (straight ahead). For this sinusoidal head movement, inertial resistance to movement is greatest at peak displacement because this is where the neck muscles must change the direction of the movement (peak acceleration). The inertial force (due to the weight of the head) would tend to make the head continue in the same direction. The elastic restoring force is opposite to the inertial force and proportional to head displacement, so that it, too, is greatest at peak displacement.

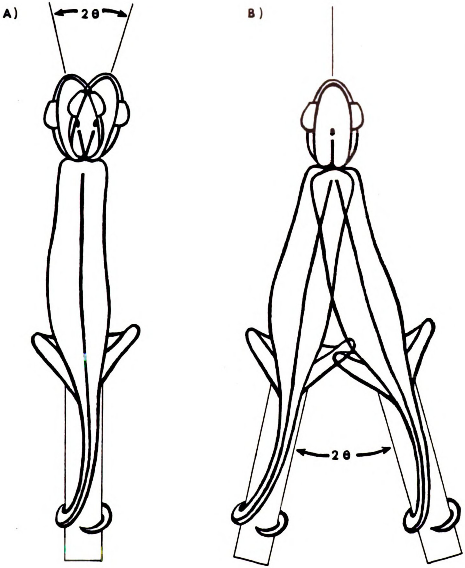


Figure 9: **Kinematically Identical Visual and Vestibular Head Movements.** A chameleon is viewed from above as she clings to the perch on the apparatus. Peak displacements of equal amplitude (θ) sinusoidal A) pursuit, and B) VCR movements of the head relative to the body are shown. The head is stationary in space during VCR and therefore encounters no inertial resistance to acceleration.

Figure 9B shows the peak displacements of the chameleon's head relative to the body as they occur during sinusoidal vestibulo-collic reflex (VCR) movement (Chapter 3). Again, viscous resistance to sinusoidal head movement is greatest at peak velocity (in this case, when the body passes through its zero position). During perfect VCR there is no movement of the head in space and the neck muscles therefore encounter no acceleration dependent resistance (due to the inertia of the head) to their shortening. The elastic resistance is proportional to the displacement of the head relative to the body, just as it is for pursuit head movement.

A series of experiments was done to test the hypothesis that kinematically similar pursuit and VCR movements are kinetically similar and therefore place similar demands on the muscular system.

Figure 9 shows pursuit and VCR movements of the head relative to the body that are kinematically similar, but because the head is stationary in space during VCR, they differ in their inertial kinetics. By comparing inertial and elastic moments (rotational forces) around the neck center at peak displacements of sinusoidal movements, this chapter demonstrates that inertial resistance to acceleration is negligible in the chameleon head-neck system. A limited electromyographic (EMG) analysis shows similar muscle activity during mechanically similar pursuit and VCR movements.

Methods

Experiments were performed on four African chameleons (*Chameleo senagalensis*). Three of the animals were tested under anesthesia (inhaled metofane) or after death (Nembutal overdose). These chameleons were numbered 1, 2, and 3 and weighed 56, 26, and 12 gms. respectively. The fourth chameleon, Lisa, weighed about 25 gms. and was tested live. Movement was elicited by the apparatus described in Chapters 2 and 3 (Figure 2).

To test the possibility of inertial head stabilization during body movement, the three anesthetized, freshly dead, or frozen and thawed chameleons were taped to the apparatus in a life-like position with head held horizontal by a suture at the center of rotation (the neck). The apparatus rotated the body with a maximum angular acceleration ($\ddot{\theta}$) of 27.6 rad/s^2 (2.0 Hz, 10° amplitude) and the head was filmed from above (Bolex, 16 mm, 50 f.p.s.) or observed directly.

To quantify moments around the neck due to inertia of the head and elasticity of the neck tissues, measurements were made on chameleons 1, 2, and 3. Elasticity of the neck tissues was measured at 85°F (a physiological temperature). A thread was sutured to each animal's nose and run over a pulley, so that various weights hung from the thread caused measurable head deflections. The pulley was moved so that the thread always pulled at a right angle to the long axis of the chameleon's head, in the horizontal plane. Weight was converted to torque around the neck joint using distance from neck to nose.

Mass moment of inertia (I) was estimated by approximating the head's dimensions to a circular cylinder with its center coincident with the head's center of gravity (Beer and Johnston, 1977). This estimate of I was probably greater than the actual because the chameleon has more air spaces in the nose than in the back of the head, and distance from the neck is important in weighting the volume. Also, head dimensions were overestimated to take into account the additional inertia of the tongue during initial protrusion (see Chapter 2). The center of gravity was located by hanging the head in several planes from threads, and estimating the intersection of straight lines extended from each thread. For mass measurement, the bodies were decapitated at the neck and behind the hyoid, and weighed wet.

Five additional formalin and alcohol fixed *Chameleo senagalensis* were dissected to locate probable neck lateral flexors for EMG experiments. Figure 10 is a dorsal view of the chameleon head and neck, with the superficial temporal and temporalis muscles (Mivart, 1870) removed from the large temporal fenestrae, to expose deep neck musculature. The EMG target muscle is indicated. This muscle originates on cervical vertebrae and inserts on the back of the skull. From the direction of the fibers, it is clear that this muscle should be the most effective lateral flexor of the group shown in Figure 10. The muscle that is cut and

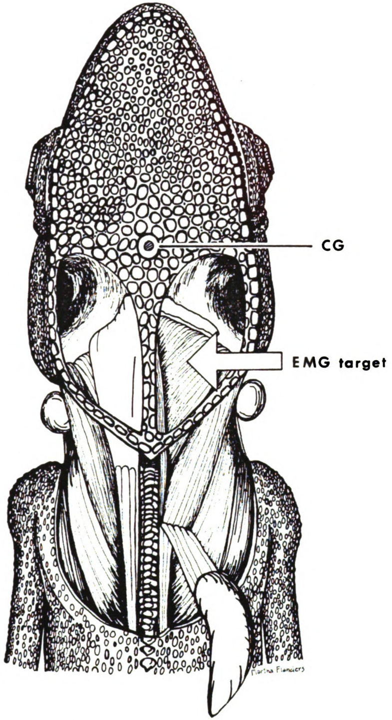


Figure 10: **Deep Neck Musculature.** Dorsal view of the head and neck of <u>Chameleo senegalensis</u>. Temporal muscles have been completely removed, and a muscle has been reflected on the right, to show the electrode target for the EMG experiment. The center of gravity (CG) is ventral to the parietal scale.

reflected on the right side of Figure 10, the EMG target, and the more medial, deep muscle shown on the right, were not described or named by Mivart (1870) in his classic dissection of *Chameleon parsonii* (a closely related species).

Fine wire, bipolar electrodes were inserted into neck muscles of the one restrained, live animal and muscular activity was recorded on magnetic tape and paper, along with traces from the apparatus (Figure 2) indicating bait or body position. Known characteristics of pursuit and VCR (Chapters 2 and 3) were used to calculate head position from these traces. Electrode placement was not verified, but all records were taken from the same two electrodes, in the same session.

Results

Sinusoidal rotation of the anesthetized or dead chameleons 1, 2, and 3 caused no measurable movement of the head relative to the body. This simple experiment demonstrated that passive elasticity at the neck joint was great enough to counteract the movement of head relative to neck due to inertia. The immediate conclusion from this finding was that vestibulo-collic stabilization movement is completely active, i.e., not aided by inertial stabilization.

When the chameleon's body was rotated around the neck (as reported above), the moment around the neck due to the inertia of the head, is proportional to the angular acceleration of the head in space. When the body is stationary and the head is rotated around the neck by lateral flexion (as in pursuit head movement), the moment due to inertia is, again, proportional to the angular acceleration of the head in space. Movement of the head in space at a given amplitude and frequency creates the same moment around the neck due to inertia, whether the neck is flexed or not. If moment at the neck due to elasticity is always much greater than moment due to inertia, then active muscle contractions during pursuit encounter minimal inertial resistance to their shortening.

Mass moment of inertia was calculated from measurements of head geometry, center of gravity and mass. The center of gravity was invariably ventral to the parietal scale (Figure 10) and between the ventral-caudal corners of the eyes. The head was about 20% of total body mass. For chameleons 1, 2, and 3, mass moment of inertia of the head was 3.1, 1.5, and 0.4 x 10^{-6} kgm^2, respectively. During a 1.0 Hz, 9^o amplitude movement (peak $\ddot{\theta} = -6.2\ r/s^2$) inertial moment around the neck was 19.0, 9.3, and 2.3 x 10^{-6} Nm, respectively (Beer and Johnston, 1977).

Neck elasticity (torque/deflection) is shown in Figure 11. Average error in deflection readings, calculated from repeated measures (Taylor, 1982) was about 2.0^o. Chameleon 1 (square symbols), the animal with the largest inertia, also had the stiffest neck; chameleon 3 (stars) was the lightest and most flexible. Chameleon 2 was freshly killed when the data were taken; the others had been frozen and

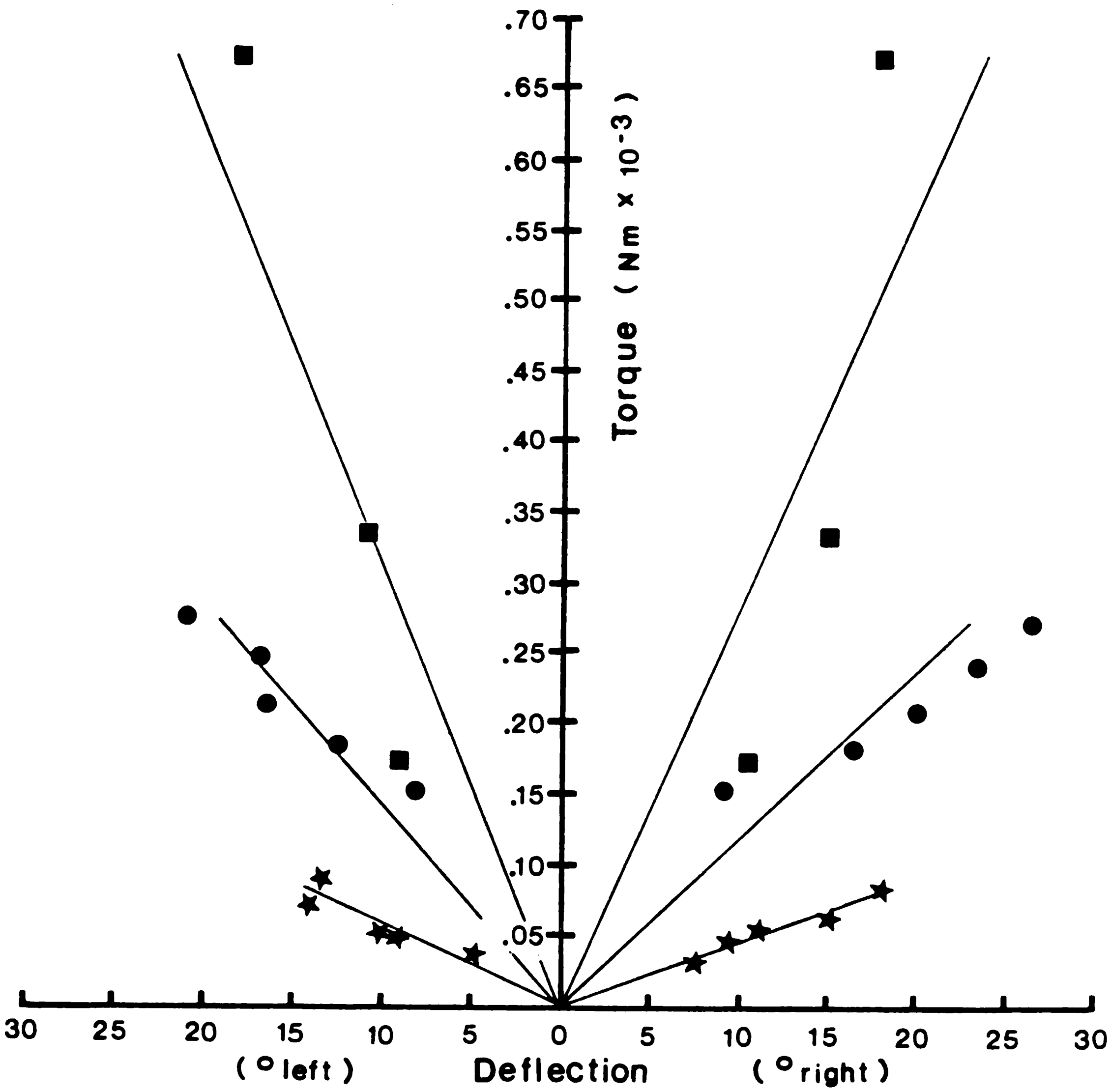


Figure 11: **Neck Elasticity.** Torque vs. neck angle for dead chameleons 1 (■), 2 (●), and 3 (✶) as measured by pulling the head to the left or right with a known force. Lines are estimated by eye.

thawed. An earlier estimate of elasticity in the fresh tissue of chameleon 1, showed a slightly stiffer neck. In life, active muscle tone should make the neck even stiffer.

The lines in Figure 11 were fitted by eye and originate at zero because the neck was straight when the applied torque was zero. It should be noted, however, that in the zero head position there are equal and opposite moments due to elasticity of the right and left neck tissues, that are at least as great as the moment due to inertia produced by passive body rotation. Although elasticity estimates are rough, data from Figure 11 show that during a pursuit head movement, the moment due to elasticity is much greater than the moment due to inertia. The elastic force opposing a 9° head displacement was about 0.29, 0.13, and 0.05×10^{-3} Nm for chameleons 1, 2, and 3 respectively. The ratio between elastic force and inertial force for these three animals was 15:1, 14:1, and 22:1.

Limited EMG results suggest that mechanically similar pursuit and VCR movements are mediated by similar patterns of muscle contraction. Figure 12A shows EMG activity in right and left lateral flexors during a VCR head movement. The thick line is a 1.0 Hz, 9° amplitude, passive body movement created by the apparatus. During this time Lisa held her head stationary in space, so that the thin line represents movement of the head relative to the body. The muscle activity is centered around peak displacement to counteract elastic resistance.

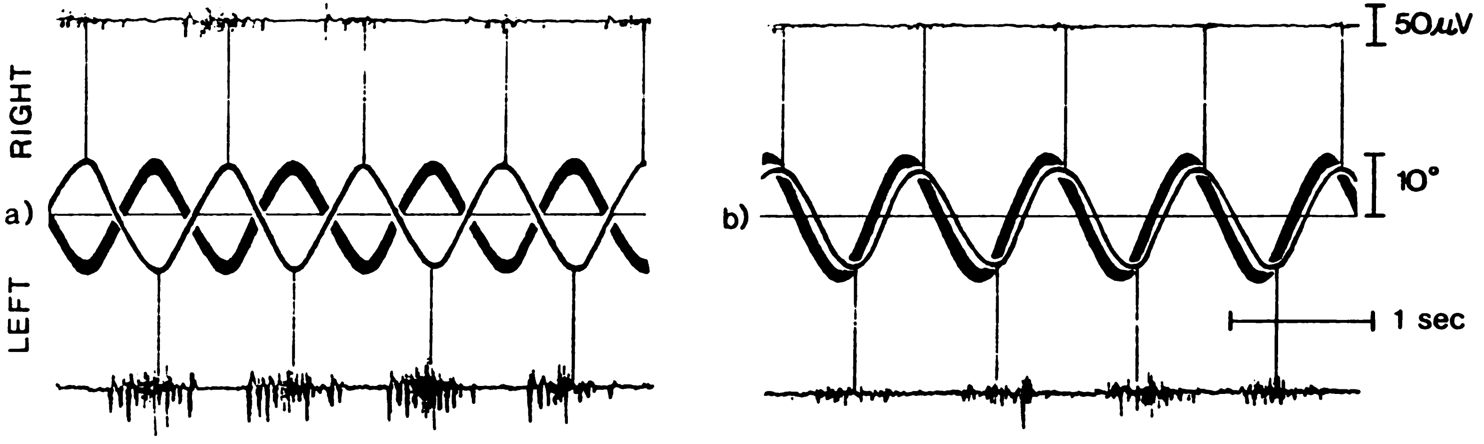


Figure 12: **Muscle Activity During Mechanically Similar Vestibular and Visual Head Movements.** EMG of right and left neck muscles during the movement of the head relative to the body shown by the thin line. A) VCR: thick line shows body movement. B) Pursuit: thick line shows bait movement. Muscle activity is centered around peak head displacement.

Figure 12B shows a mechanically similar pursuit head movement (thin line) following an apparatus produced bait movement (thick line). Since there is negligible inertial resistance to pursuit head movement, the activity centered around peak displacement, again, counteracts elastic resistance to displacement. Although there is less movement artifact in the pursuit EMG (electrode leads were taped to the body), the actual muscle signal appears to be very similar to that recorded for VCR. Figure 13A and B compare the muscle signals for VCR (A) and pursuit (B) movements at a higher graph speed, along with the actual polygraph traces from the apparatus (the thick lines in Figure 12). Figure 13C shows several cycles of VCR during which the chameleon had both eyes closed (excluding the possibility of a visual contribution to head stabilization).

Discussion

Results of all three experiments suggest that kinematically similar visual and vestibular movements are also kinetically similar and mediated by similar muscle contractions. Passive body rotation of anesthetized and dead animals showed that elasticity was greater than inertia. Quantification of these parameters was in agreement with this result. EMG patterns were similar for VCR and pursuit movements and again showed the importance of elastic resistance to displacement.

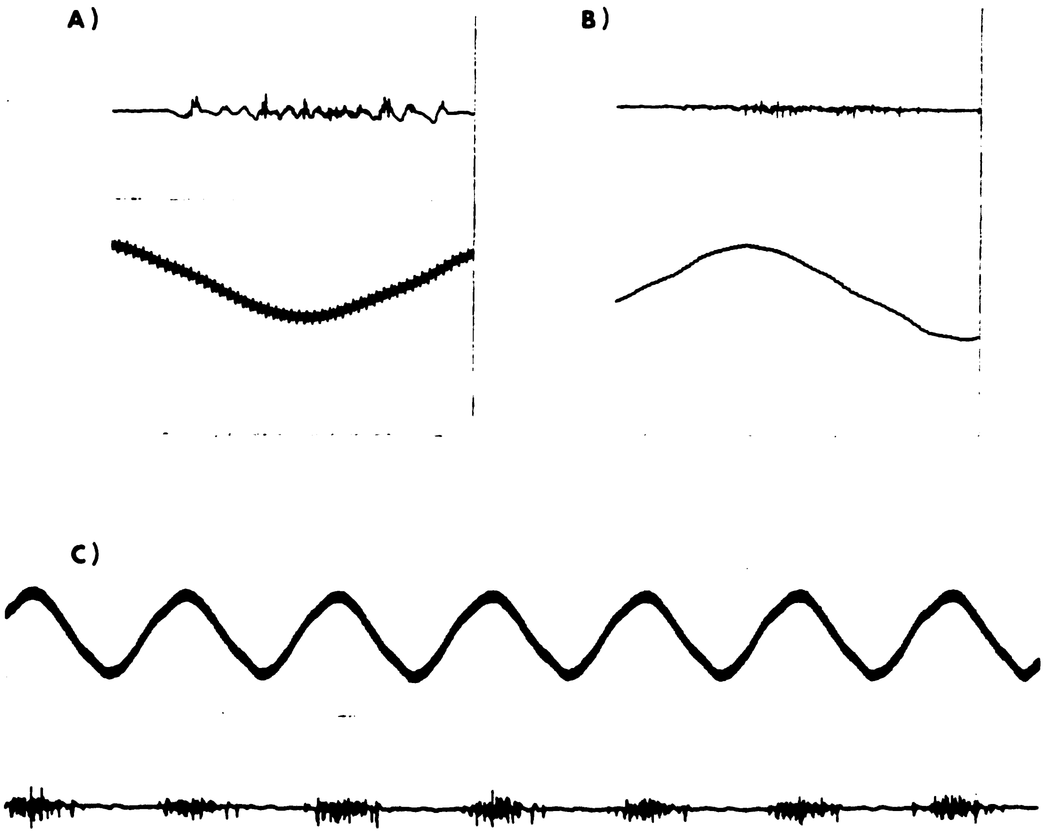


Figure 13: **EMG Data.** Records from Figure 12 run at a higher graph speed to show that although there is more movement of the base line during VCR (A), the high frequency muscle signal is similar to that of pursuit (B). Curved lines show angular position of the body (A and C) and bait (B) across time. During the seven cycles shown in C, the chameleon kept her head stationary in space with both eyes closed. Scale is shown in Figure 12.

Viscous resistance to velocity was not measured in this system. Moment due to viscosity is zero at peak displacement of a sinusoidal movement (since velocity of the head relative to the body is zero), and viscosity, therefore, was unimportant in the comparison of inertial to elastic forces. Although the EMG analysis was limited, the results do not show much activity during peak velocity, as would be expected if viscosity were a significant resistive force. Friction in the neck joint also was not measured. In a study of monkey head-neck mechanics, friction was measured and was found to be negligible (Bizzi, et al., 1978).

In the chameleon, head stabilization during body movement is completely due to active muscle contraction. Furthermore, since there is no passive movement of head relative to body within normal acceleration limits, it is unlikely that the stretch reflex contributes to stabilization. Proprioceptive information from the actively moved head should be the same in VCR and pursuit situations.

The importance of neck elasticity in this system is consistent with the spring model for motor control (Bernstein, 1967; Bizzi, et al., 1976). According to this theory, head (or limb) position is controlled by adjusting the stiffness (or resting length) of antagonistic muscles. On the other hand, inertia and viscosity are not negligible at all joints. Other theories of motor control stress the use of momentum in movement coordination (Greene, 1982; Goodman and Kelso, 1983).

APPENDICES

APPENDIX A

STATISTICAL ANALYSIS

Statistical analysis was used to address a number of questions underlying the assumptions and conclusions reported in the preceding text:

1. Is the head movement sinusoidal?

Use of the equation:

$$H/B = \sin 2\pi f[(1/4)T + \Delta t]$$

to predict gain (Chapter 2), was based on the assumption that both the bait movement and the head movement were sinusoidal. The movement of the bait was apparatus controlled and had been checked on an oscilloscope by cross plotting it with a known sinusoid to assure that it was sinusoidal. For each set of data the bait and head positions were graphically cross plotted for points in time (Appendix B) and were used only if they could be fitted (by eye) with an ellipse. This Lissajous method gave a qualitative check to make sure all movements were roughly sinusoidal. Five out of 49 trials that were analyzed, were not used because they were not fitted by an ellipse. Upon review of the film it was discovered that during these 5 trials the cricket was not well clipped to the apparatus and was vibrating as it was moved.

To quantitatively test the assumption that all head movements were sinusoidal, the Lissajous graphs were reviewed to select the worst (or least well fitted by an ellipse) performance of each chameleon. For each of these trials head position vs. time data were fitted with a sine wave generated by the following formula:

$$\Theta = H \sin 2\pi f(t)$$

where θ is angular position (in degrees), H is the amplitude of the head movement (in degrees), f is frequency (in Hz), and t is time (reported in intervals adjusted from 1/21 sec. to 1/24 sec. to match the film speed of a given trial).

Carol's worst head movement occurred on 7/02 (Table 1) This trial was fitted with a sine wave of the formula:

$$\theta = 8 \sin 2\pi\ (1)\ (1/22)$$

by using a t-test (Steel and Torric, 1980) to test the hypothesis that the difference between measured head positions and those generated by the equation was 0.00° (H_0: $\bar{d} = 0.00°$, H_1: $\bar{d} \neq 0.00°$). Table 4 shows position points generated by using this formula, reported at 1/22 sec. (two frame) intervals. Figure 13 shows this rectified sine wave plotted on an angular position vs. time graph (closed circles). Actual data from Carol's pursuit head movement is shown in the second column of Table 4. The rectified head movement is plotted in Figure 14 (open circles). For each point in time head position was subtracted from the position on the true sine wave (third column, Table 4) and these deviations were averaged. The average difference between the sine wave and the head movement ($\bar{d}$) in this case was

Table 4: **Sinusoidal Motion.** A sine wave generated using the equation for sinusoidal motion is compared to a representative pursuit head movement. The absolute values of angular positions ($|\theta^\circ|$) are shown at 45 msec. (two frame) intervals.

$\|\theta^\circ\|$ sine wave	$\|\theta^\circ\|$ head	$\|\theta^\circ\|$ sine wave - $\|\theta^\circ\|$ head
2.3	1.5	0.8
4.3	3.5	0.8
6.0	5.5	0.5
7.3	7.0	0.3
7.9	7.5	0.4
7.9	8.0	-0.1
7.3	8.0	-0.7
6.0	6.5	-0.5
4.3	4.5	-0.2
2.3	1.5	0.8
0.0	1.5	-1.5
2.3	3.5	-1.2
4.3	4.5	-0.2
6.0	6.0	0.0
7.3	7.0	0.3
7.9	7.5	0.4
7.9	7.5	0.4
7.3	7.5	-0.2
6.0	6.5	-0.5
4.3	5.0	-0.7
2.3	3.5	-1.2

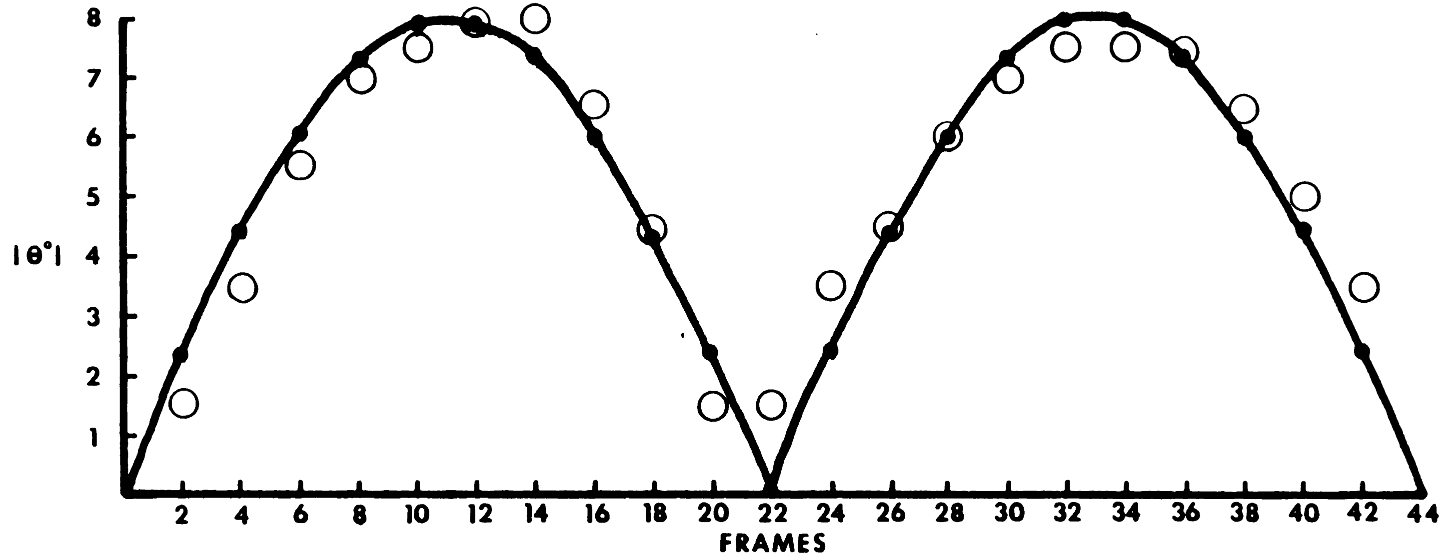


Figure 14: **Test for Sinusoidal Motion.** Position data from Table 4 are plotted against time to show the difference between a rectified sine wave (●) and a rectified head position record (○).

-0.11°, leading to a failure to reject $H_0:\bar{d} = 0.00$ ($n = 21$, $s_{\bar{d}} = 0.15$, $t = 0.73$).

Susan's performance on 2/08 at 2.8 Hz. (Table 2) was also given a t-test to see if the head's deviation from sinusoidal motion was significantly different from 0.00°. In this case the head movement was fitted by the formula:

$$\theta = 5.5 \sin 2\pi\ (2.8)\ (1/24)$$

with 18 data points ($\bar{d} = 0.49^{\circ}$, $s_{\bar{d}} = 0.39^{\circ}$) the calculated t value ($t = 1.25$) was less than the critical value ($t_{(.05)15} = 2.131$) leading to a failure to reject the hypothesis that the head movement was sinusoidal.

Hilde's performance on 7/01 (Table 2) was fitted using the formula:

$$\theta = 7 \sin 2\pi (1)\ (1/21)$$

The hypothesis that $\bar{d} = 0.00^{\circ}$ was, once again, not rejected at the $\alpha = .05$ level of significance ($n = 18$, $\bar{d} = -0.33^{\circ}$, $s_{\bar{d}} = 0.21^{\circ}$, $t = 1.56$).

Lisa's head movement on 7/03 (Table 3) was found to be significantly different from a sine wave of the formula:

$$\theta = 9 \sin 2\pi (1)\ (1/22)$$

($n = 18$, $\bar{d} = 0.54^{\circ}$, $s_{\bar{d}} = 0.22^{\circ}$, $t = 2.45$) at the $\alpha = .05$ level, although not at the $\alpha = .02$ level ($t_{(0.05)15} = 2.131$, $t_{(0.02)15} = 2.602$).

The one set of data taken from Bette was extremely well fitted by the Lissajous ellipse, so it was not necessary to perform a t-test in this case.

Failure to reject the hypothesis that all but one of the worst head movements were sinusoidal supports the assumption that all head movements were sinusoidal.

2. Are the estimates of time lag obtained using a second method of measurement, significantly different than those reported in the preceding text?

Time lags reported in the preceding text and used to test the pursuit model (Chapter 2), and to support the conclusion of decreased time lag during body movement (Chapter 3), were calculated by the Lissajous method (Appendix B). This analysis used all of the data points for bait and head movement in a given trial, to give an estimate of phase lag, which was converted to time lag using frequency.

A second estimate for time lag in each trial was obtained by calculating the average number of frames between the zero position crossings of bait and head movements. Since a frame lasted about 22 msec. and time lags were usually less than 100 msec., this method gave a rather rough estimate. For the pure pursuit data (Table 1) the average time between pairs of zero crossings had a standard deviation that ranged between ± 0.0 and ± 22.4 msec.

The estimates of time lag calculated by the two methods were found to be significantly different from each other at the $\alpha = .05$ level (although not at the $\alpha = .02$ level). A t-test was used to test the hypothesis that the average difference between the two groups of measurements was 0.00 msec. (H_0: $\bar{d} = 0.00$ msec., H_1: $\bar{d} \neq 0.00$ msec.). For pursuit data, the average difference ($\bar{d}$) was 6.21 msec. ($n = 21$, $s_{\bar{d}} = 1.94$ msec.) leading to a t value of 3.21*. For combined stimulation data, the two groups of measurement were again significantly different ($n = 23$, $\bar{d} = 4.17$ msec., $s_{\bar{d}} = 1.54$ msec., $t = 2.71$*). These differences in msec. measurements represent an error of about 7%.

In 34 of the 44 trials the time lag calculated through Lissajous analysis was larger than that measured from zero crossings. This difference probably represents a systematic error: ellipses could have been drawn too round, or the number of frames between zero crossings counted too conservatively, or both. Notice that although the two groups of measurements are significantly different, the average difference (6.21 msec or 4.17 msec, above) is less than the average error of zero crossing measurements (± 9.6 msec.).

In spite of the significant difference between methods of measuring time lag, either estimate can be used in the pursuit model (Chapter 2) to predict the amplitude of head movement. Use of Lissajous data predicts a head movement with a slightly larger amplitude than that observed ($n = 21$, $\bar{d} = 0.18^\circ$, $s_{\bar{d}} = 0.14^\circ$), while use of zero crossing data predicts a head movement of a slightly lower amplitude ($n = 21$, $\bar{d} = -0.11^\circ$, $s_{\bar{d}} = 0.17^\circ$). In both cases the difference between predicted and observed head amplitudes was not significantly different from $\bar{d} = 0.0^\circ$ (for the Lissajous estimate of Δt, $t = 1.26$; for the zero crossing estimate of Δt, $t = 0.65$, $\alpha = .05$). These convergent results support the validity of the model.

In Chapter 3 (Table 3), Lissajous time lags were compared for pursuit with and without body movement to show that the difference between the two ($n = 18$, $\bar{d} = 13.75$ msec., $s_{\bar{d}} = 2.17$ msec.) was significant ($t = 5.26^{**}$). This treatment difference is more than twice the difference between the two measurement systems, and furthermore, comparison of zero crossing time lags for the same 18 trials, shows the same trend ($\bar{d} = 11.77$ msec., $s_{\bar{d}} = 2.65$ msec., $t = 4.43^{**}$).

In Figure 15, Lissajous time lags (top) and zero crossing time lags (bottom) are plotted against frequency for three different chameleons with (open symbols), and without (closed symbols) body movement. The variance of the zero crossing data (251.4 msec.^2 with body movement, and 347.8 msec.^2 without) is larger than the variance of the Lissajous data (221.8 msec.^2 with body movement, and 242.0 msec.^2 without). The regression lines show that in each case, time lags are decreased during body movement. The zero, or negative slopes of the regression lines are an artifact of the fact that only the faster animals will perform at higher frequencies. Regression lines for individual animals have positive slopes, and only in the case of Lisa's performance during body movement (the open circles, phase or zero crossing) is the time lag data significantly correlated with frequency (correlation coefficient = 0.69, $\alpha = 0.05$).

Although the difference between Lissajous and zero crossing measurements of time lag for each trial is significantly different from $\bar{d} = 0.0$ msec., the extra measurement

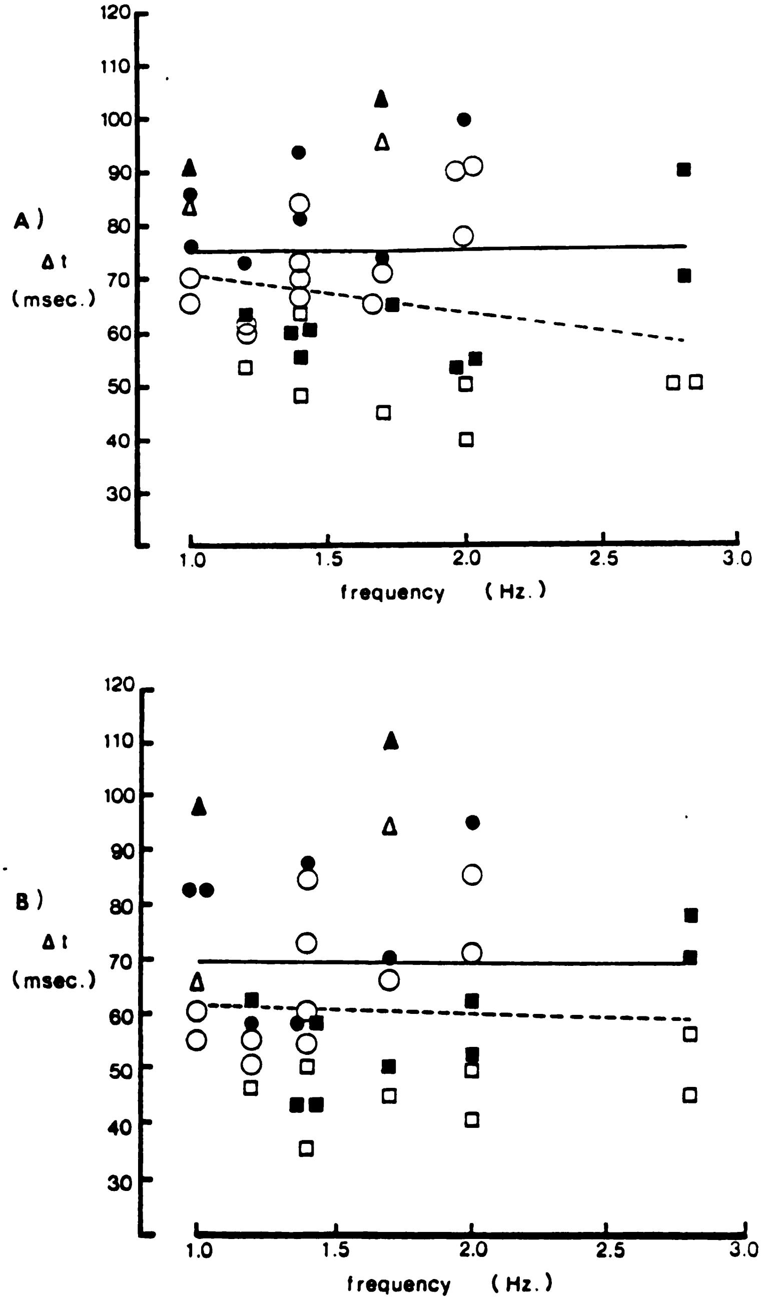


Figure 15: **Linear Regressions of Time Lag vs. Frequency.** Time lags for three chameleons were measured by A) phase and B) zero crossings. Symbols represent trials shown in Tables 1 and 2. Solid lines are regressions for pursuit with body stationary. Dotted lines are regressions for pursuit during body movement.

of time lag has served to support the validity of the pursuit model, and the conclusion of decreased time lag during body movement.

3. Are the data normally distributed around their means?

Use of parametric statistics presupposes that the data are normally distributed around their means. A Kolmogorov-Smirnov test (Sokal and Rohlf, 1969) was used on several groups of data to test the null hypothesis that the data are normally distributed.

The use of a t-test to conclude that the average difference between model gain and measured gain is not significantly different from $\bar{d} = 0.00$, assumes that the underlying population of gain differences is normally distributed. For pure pursuit data, with observations more than five standard deviations from the mean trimmed, d_{max} (.3370) was less than the critical value (.3376 for $n = 18$, $\alpha = .05$) leading to a failure to reject the hypothesis of normally distributed data. For combined stimulation, however, the data distribution was found to be significantly different from normal ($d_{max} = .3505$, critical value $= .3376$, $n = 15$, $\alpha = .05$). For this population of gain differences, the variance is probably larger than it would be if the data were normally distributed. This makes it more difficult to reject $H_0{:}\bar{d} = 0.00$.

Performances of individual chameleons might be expected to be normally distributed around their own means; and if a large enough group of chameleons were tested, the data should be normally distributed around a group mean. Susan's pursuit data are not significantly different from being normally distributed (d_{max} = .3449, critical value = .45427, n = 8, α = .05), and her average gain difference is not significantly different from d = 0.00 (n = 8, $\bar{d}$ = -0.04, $s_{\bar{d}}$ = 0.02, t = 1.66, α = .05). It is probable that not enough chameleons were tested, to make the group data normally distributed in the case of combined stimulation (3 chameleons for combined stimulation, compared to 5 for pursuit data).

Other sampling problems may have contributed to data's not being normally distributed: 1) the chameleons were not uniformly sampled, i.e., more data were taken from some than others; 2) the fit of the model might have a frequency dependence, and frequencies were not uniformly sampled (see Tables 1 and 2).

In spite of these sampling problems, measured gain is significantly correlated with model gain (as reported in Chapters 2 and 3), and the ratio of measured gain/model gain (although not normally distributed) is not significantly different from 1.00 (n = 44, $\bar{y}$ = 0.96, $s_{\bar{y}}$ = 0.04, t = 1.00, α = .05).

The use of a t-test to conclude that time lags were significantly shorter during body movement (Table 3-1) assumes that time lag differences are normally distributed. Use of the Kolmogorov-Smirnov test on this population led to a failure to reject the hypothesis that the data are normally distributed (d_{max} = 0.2097, critical value = .32733, n = 16, α = .05).

Although there are inherent problems in the use of heterogeneous data, and small sample sizes, it seems probable that the populations underlying the collected data are normally distributed and therefore, it is reasonable to use parametric statistics in this thesis.

APPENDIX B

LISSAJOUS ANALYSIS

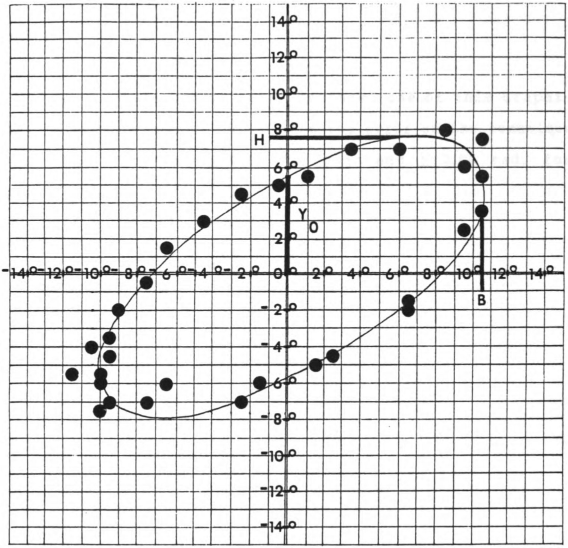
Lissajous analysis (Malmstadt and Enke, 1963) was used to calculate the gain and phase of the sinusoidal head movement that followed sinusoidal bait movement (see Figures 6 and 9). This analysis makes use of the fact that the mathematical formula for an ellipse can be derived from two sine waves, one in the x dimension and another in the y dimension. For a bait movement with amplitude B and a head movement with amplitude H, the formulas for x and y coordinates are:

$$x = B \sin \omega t$$

$$y = H \sin (\omega t + \Psi)$$

where $\omega = 2\pi f$ rad./sec., and $\Psi = 2\pi f \Delta t$ rad. f is the frequency of the sinuosoidal bait and head movements (in cycles/sec.), and Δt is the time lag of the head movement (in seconds).

Figure 16 shows bait and head positions cross plotted for points in time during a typical pursuit head movement. The data were fitted (by eye) with an ellipse. Gain was determined, as shown, by taking the ratio of maximum y and x positions, H/B. Phase lag, Ψ, was determined by using the x and y equations at the point where $\sin \omega t = 0$, and solving for Ψ:



Gain = H / B

Phase = $\sin^{-1} Y_0 / H$

Figure 16: **Gain and Phase Calculation.** Head (H) and bait (B) positions are cross plotted to determine gain and phase by the Lissajous method.

$$x_0 = 0$$

$$y_0 = H \sin \Psi$$

and thus

$$\Psi = \sin^{-1} y_0/H.$$

For a given set of data, repeated use of this graphical, Lissajous method showed that the error of the technique (Taylor, 1982) was ± 0.02 for gain and ± 0.05 rad. for phase.

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