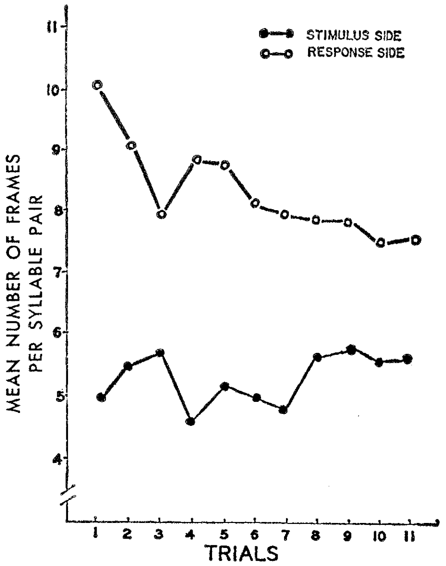

Fig. 1. Mean number of frames of stimulus and response as a function of trials.

(trials) to prevent serial learning, and we inserted two blank slides at the end of each trial to provide a 4-second intertrial interval. The subject was given a 1-minute rest at the end of every four trials and the session was terminated after 24 trials, or before that if he successfully anticipated the seven responses in any of the four orders.

We recorded eye movements continuously throughout the duration of the task by means of an eye-marker camera (*3*), mounted on the head, which consisted of a 2- by 8-mm motion picture unit and a periscope that transmitted a spot of light reflected from the cornea to a moving film. The developed film shows the paired-associate slides and, superimposed upon each, a bright circular spot indicating the position of actual fixation. We analyzed the data frame by frame, by examining the stimulus-response slides through a film viewer. This method of analysis was highly dependable, the between and within experimenter-reliability coefficients being 0.98 for a film of 24 trials, selected at random.

Sixteen of the 20 subjects reached the criterion of an errorless trial, the fastest doing so on the 11th trial. We have summarized the main findings in Fig. 1. The first 11 trials for all subjects are shown along the abscissa, while the ordinate represents the average number of frames per syllable-pair for those slides where the stimulus and response appeared together. The open circles represent response frames, the closed circles stimulus frames. For any given trial, total frames of stimulus and response may be calculated by adding the ordinate values for the open and closed circles. The difference between this value and 21 represents frames involving fixations of the central portion of the display. The two functions shown in Fig. 1 are not perfect mirror images of one another and this is reflected by a -0.43 correlation between stimulus and response frames.

We examined the findings shown in Fig. 1 by means of analysis-of-variance techniques and discovered that the two trend lines depart reliably from being parallel ($p < .001$), with time on stimulus remaining constant over trials and time on response becoming systematically shorter as learning progresses. This last trend has a chance expectancy of less than one in one thousand, an orthogonal polynomial comparison revealing no dependable nonlinear components. We obtained the same results by examining time on stimulus and response as a function of the first three of the four quarters of learning for those 16 subjects who reached the errorless-trial criterion. (We omitted the data for the fourth quarter because of their unreliability.) All 16 subjects showed less time on the response during the third quarter than during the first. Again, time on stimulus remained essentially invariant throughout the session.

In view of the fact that each subject saw the stimulus twice as often as the response, it is not surprising that the latter was scanned out of proportion to the former throughout the duration of the task. Nor were we surprised to discover less total time on stimulus and response during the latter stages of learning. This resulted from a tendency to fixate the central portion of the display, or even to look away, once a syllable pair had been learned. The phenomenon of most interest, however, that of the systematically decreasing ratio of response- to stimulus-time with trials, is clearly consistent with the two-stage hypothesis. This phenomenon reflects the transition from the response consolidation to the stimulus hook-up phase.

We also analyzed scanning behavior before and after the learning of each of the seven pairs and found what could be interpreted as additional support for the two-stage theory. Although there were no differences in time on the stimulus, all 20 subjects showed less time on the response after the pairs had been learned than before. This difference on the response side and lack of it on the stimulus side of the display is presumably due to a disproportionate amount of time on the response during stage one, even though the data presented before learning reflect both stages.

We were unable to reveal any reliable differences in scanning behavior between slow and fast learners, nor were we able to demonstrate any systematic changes in patterns of viewing the stimulus-response slides as learning progressed. Most subjects looked right-left-right and maintained this pattern throughout the duration of the session.

P. D. McCormack
E. J. Haltrecht

Department of Psychology,
Carleton University,
Ottawa, Canada

References and Notes

1. G. Mandler, *Psychol. Rev.* **61**, 235 (1954); L. Postman, in *Verbal Learning and Verbal Behaviour,* C. N. Cofer, Ed. (McGraw-Hill, New York, 1961), pp. 152–179; B. J. Underwood and R. W. Schulz, *Meaningfulness and Verbal Learning* (Lippincott, Chicago, 1960), pp. 92–94.
2. C. E. Noble, *Psychol. Rep.* **8**, 487 (1961).
3. N. H. Mackworth and E. L. Thomas, *J. Opt. Soc. Amer.* **52**, 713 (1962).
4. This research was supported by a grant-in-aid from the Associate Committee on Experimental Psychology of the National Research Council of Canada (grant APA-78) and by the Carleton University Arts Research and Publication Fund.

11 February 1965

Pupillary Response of the Screech Owl, Otus asio

Abstract. *The latent period of constriction in the owl is only half that in the human, and the latent period of dilatation is about equal to that in the human. Similarly, the rise time of constriction in the owl is much faster than that in the human. The owl system has the characteristics of a low-band-pass filter. The owl's frequency response is over an octave lower than that of the human, but its phase lags are shorter.*

Linear and nonlinear servomechanism theory has been used to describe quantitatively the dynamic characteristics of the human pupillary response to a small-signal visible light input (*1*).

This report presents the results of the application of this technique to the study of the pupillary reflex system of the screech owl, *Otus asio*.

The experimental technique and apparatus used in this study were those reported by Stark (*1*), with minor modifications. A controllable beam of visible light was allowed to fall upon the optical axis of the retina. Concentrically, a large-diameter beam of infrared light was allowed to impinge upon the eye. Changes in the amount of infrared light scattered from the iris were monitored as a measure of pupil area: the larger the area, the less the infrared return. Calibration was achieved by photographing the steady state pupil area and comparing with infrared-sensitive photocell output voltage. Dark adaptation preceded each experiment. The input and output signals were either fed on-line to a digital computer or stored on frequency-modulated tape for later analysis.

The owl's eye was chosen for study because it is large, has a yellow iris, cannot move, and reacts independently. The screech owl in particular was chosen as a laboratory animal because it is a relatively small animal and is easy to handle and constrain in the experimental apparatus. The owl was taped firmly in position in a cradle made from a soccer shin guard. One eyelid was pulled back to expose the eye fully. It was not necessary to restrain the nictitating membrane.

For open-loop experiments the input light was focused to a spot which, at the plane of the pupil, was smaller than the smallest area of the pupil. The feedback loop was then open at the point of disturbance, since adjustment of the pupil area has no effect upon the intensity of light striking the retina. To describe the dynamic characteristics of the reflex system, we measured the open-loop response to sinusoidal and step variations in input light intensity. For analysis, the pupillary reflex system was assumed to be a linear servomechanism. To enhance the validity of this assumption, the input light variations were restricted to a region which evoked only small-signal variations in pupil area.

Assuming that the system responds to total input light energy, that is, that an input spot of flux A and area B is an equivalent stimulus to an input spot in flux $2A$ and area $B/2$, the open-loop

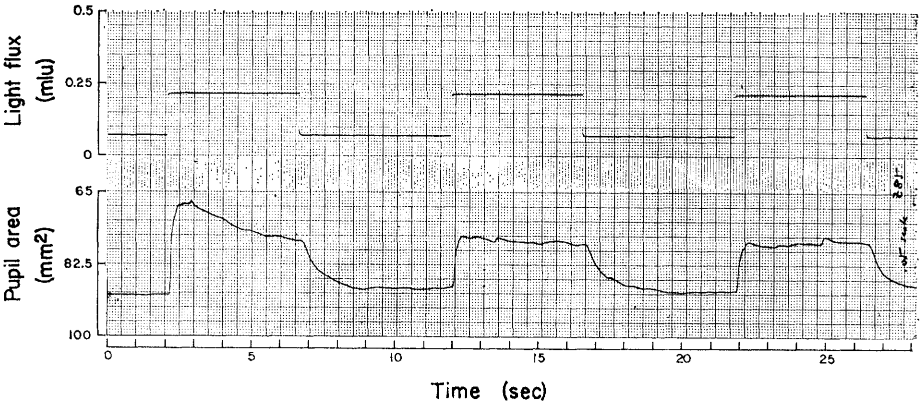

Fig. 1. Open-loop transient responses. Light flux measured at plane of pupil.

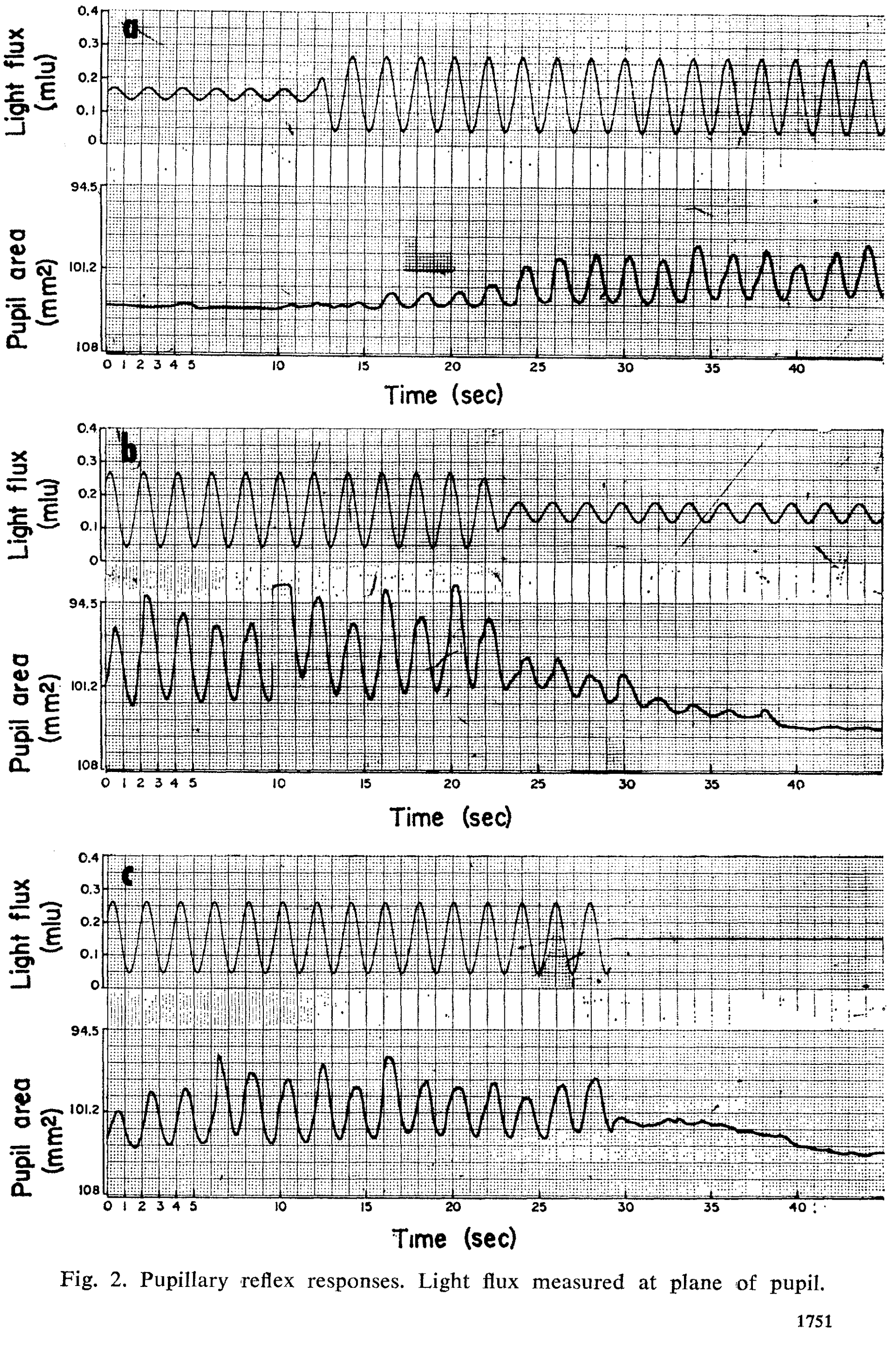

Fig. 2. Pupillary reflex responses. Light flux measured at plane of pupil.

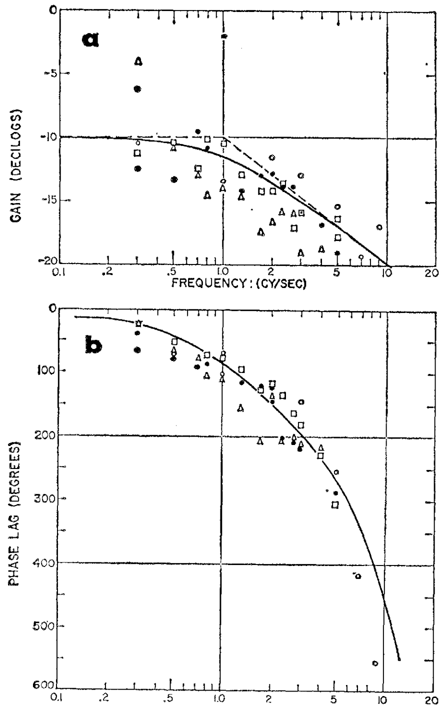

Fig. 3. Open-loop gain and phase lag of sinusoidally excited pupillary reflex. Symbols: □, run No. 1; △, run No. 2; ●, run No. 3; ○, run No. 4.

gain of the system may be defined as follows. Consider the case where $\bar{I}$ photons per second are impinging upon the retina and the pupillary system has been allowed to stabilize its response about an area $\bar{A}$. Then, let ΔI = change in the total number of photons per second striking the retina, and ΔA = change in the area. Under the equivalence assumption, the gain may be written:

$$G = \frac{\Delta A\,(\bar{I}/\bar{A})}{\Delta I} = \frac{\Delta A/\bar{A}}{\Delta I/\bar{I}}$$

The owl's pupil area has a range of 6 to 115 mm^2. Under our experimental conditions, the pupil area varied over the range 95 to 115 mm^2. The range of the human pupil area is 2 to 40 mm^2; under similar experimental conditions, the human pupil area varies over the range 16 to 30 mm^2.

Transient responses of the owl's pupil are shown in Fig. 1. Among the points to be noted is the short latent period: 0.05 to 0.10 second for constriction, 0.15 to 0.20 second for dilatation. There is also a high velocity of constriction as compared to the human. The velocity of constriction is greater than the velocity of dilatation and this asymmetry is also seen in the human. Changes in input amplitudes so as to obtain different response amplitudes demonstrate that the velocities of constriction and dilatation were directly dependent upon stimulus amplitude. Occasionally, marked overshooting and "ringing" were seen.

Adaptive processes which probably represent retinal light adaptation were seen after constriction. The time constants of these adaptive processes were dependent upon amplitude.

Noise was much less apparent in these recordings of the owl than in analogous human pupillary records. The noise also seemed to occur with larger amplitude in the constricted phase than in the dilated phase.

By performing experiments wherein the amplitude of the light step as well as the mean level of light were changed in order of magnitude by means of neutral density filters, it was clearly apparent that the effective stimulus was a percentage change of amplitude rather than the change in absolute value.

When driven with a sinusoidally varying intensity, most of the power of the output signal was in the fundamental frequency component of the input signal (Fig. 2). The lack of harmonic distortion argues in favor of the linear gain approximation derived above.

Low-frequency gain and mid-frequency gain were quite low (Fig. 3*a*). This means that the open- and closed-loop gains are not very different, a fact observed experimentally. There was a break frequency at 1 cy/sec and thereafter an attenuation with a slope approaching −1, or 10 decilogs per decade (6 decilogs per octave). The phase characteristics indicate that, in addition to the minimum phase lag element, there is also a nonminimum phase lag element due to the latent period. The minimum phase lag element is most likely due to the physiological mechanism involved in moving the thin sheet of iris muscle in the anterior chamber of the eye between the lens and the cornea.

From these graphical frequency response displays, we can construct a transfer function representing a linear lumped parameter approximation to the pupillary system in the frequency range studied:

$$G(s) = \frac{0.1\,e^{-0.15s}}{1 + 0.15\,s}$$

This consists of a low-frequency gain, a transport delay, and a simple lag element.

On a vector plot of gain and phase lag, the stability characteristics of the system can be seen. As is the human case, the system is stable, since a characteristic high phase lag is offset by a relatively low gain.

Figure 2 illustrates a time-dependent change in gain with change in stimulus amplitude. In other experiments, no "ringing" was observed after abrupt termination of a sinusoidal input.

It was stated above that under our experimental conditions the owl's pupil area is close to maximum. This leads to the prediction that a stimulus gain change would lead to a change in the mean size of the pupil, that is, that an increase in stimulus intensity would elicit a decrease in mean pupil area. Figure 2 shows an experiment where this was observed.

LEWIS G. BISHOP*
Zoology Department, University of California, Los Angeles
LAWRENCE STARK†
Neurology Section, Massachusetts Institute of Technology, Cambridge

References and Notes

1. L. Stark, "Stability, oscillations and noise in the human pupil servomechanism," *Proc. I.R.E.* (*Inst. Radio Engrs.*) **47**, No. 11 (1959).
2. We thank Dr. B. C. Abbott, University of Illinois, Urbana, for suggesting this study, and the Massachusetts Audubon Society for supplying the animals. Supported by Sperry-Rand Corporation Research Fellowship (to L.G.B.) and grants AF-49(638)-1313, MH-6175-02, and Nonr-1841(70) (to L.S.). The technical assistance of Julie Redhead is acknowledged.

* Present address: Applied Research, Autonetics, Anaheim, Calif.

† Present address: Bioengineering Department, University of Illinois, Chicago.

5 April 1965

Territorial Behavior among Puku in Zambia

Abstract. *Territorial behavior of a species of antelope, the puku,* Adenota vardoni *(Livingstone) consists of the defense by males during the mating season of relatively widely spaced territories on a "territorial ground." Females wander about on this area for the purpose of mating.*

Since it appeared plausible that the territorial behavior reported by Buechner (*1*) for a species of antelope, the Uganda kob, [*Adenota kob thomasi* (Neumann)], would also occur among the closely related puku, *Adenota vardoni* (Livingstone), I studied these antelopes in an area of 100 ha in the