served when ribonuclease interacted with an activating antibody, as the entrapment of the antigen (ribonuclease) in a conformational form with a higher enzymatic activity. Thus, some evidence for metastable conformational forms of ribonuclease with altered kinetic properties exists.

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Eye Movements of African Chameleons: Spontaneous Saccade Timing

Abstract. *Despite asynchrony, saccades of left and right eyes of African chameleons had similar timing statistics. Prominent qualitative aspects of these statistics did not change if one or both eyes were masked. Evidently, an internal stochastic process regulated chameleon saccade generation.*

Although many animals scan their environments by rapid, jumplike eye movements called saccades, the only saccade patterns yet examined in detail come from humans (*1*). To gain insight into the temporal order of central nervous integration in a nonmammalian vertebrate, the African chameleon, I constructed frequency distributions of interval durations between successive chameleon saccades. The distributions (Fig. 1A) were indistinguishable from distributions taken from human subjects (*2*). Chameleons made most saccades randomly according to a constant-probability process whose rate did not vary despite perceptual restrictions as extreme as occlusion of one or both eyes.

In one obvious respect, chameleon saccade timing is more complex than human saccade timing. Chameleons can move their left and right eyes separately, in different directions, and with different amplitudes. Such independent eye movements are characteristic of the voluntary scanning movements of most vertebrate species (*3*). The independence of chameleons' eye movements is striking because their eyes protrude and are extremely mobile (approximately 200° horizontal freedom, 90° vertical freedom).

Since chameleons generally initiate saccades of left and right eyes asynchronously, one chameleon generates two sequences of saccade initiation times, one sequence for each eye. Such sequences were constructed from electrooculographic records of chameleon eye movements. Ten adult chameleons of three species, *Chameleo dilepis*, *C. jacksoni*, and *C. hohnelii*, provided more than 100,000 saccadic eye movements. (Figure 1C, although based on *C. dilepis* data, shows results typical of all three species.)

Two electrode pairs (1-mm Ag-AgCl disks moistened with conductive paste), placed horizontally on the orbital skin about each eye, measured the potential differences across left and right orbits. The horizontal component of an eye movement caused a change in the potential difference measured by its electrode pair. Saccadic eye movements caused characteristic rapid, steplike changes with amplitudes between 0.1 and 0.6 mV [compared with 0.2 to 0.8 mV for humans (*4*)]. Amplifiers with large time constants (3.4 seconds) amplified the left and right potential differences 1000-fold.

Electrooculograms (EOG's) of these amplified potential differences were made by filming them as traces on an oscilloscope screen, and by tape recording them for playback to a special saccade recognition circuit. This circuit passed only those EOG deflections caused by saccades. The saccade defining rules required that the deflection exceed a preset slope for a preset time (approximately 2 mV/sec for 10 msec). At its output, the circuit made rectangular pulses corresponding to the saccade-caused deflections in the input EOG. A minicomputer timed and tallied these pulses and stored the data for subsequent analysis by a general-purpose computer. The automatic recognition system found all saccades with horizontal amplitudes in excess of 1° and specified saccade initiation times to within 2 msec.

Each of ten recording sessions produced an unbroken pair of saccade time sequences 4.5 hours long. During the sessions, chameleons could move along a pair of dowels horizontally suspended in a large (1 m^3) electrically shielded cage. Because the dowels paralleled the transparent cage door, chameleons usually situated themselves parallel to the door with one eye facing outward, the other eye facing inward. This visual asymmetry concerned me until my data showed that it had no apparent effect on saccade timing. I easily occluded one or both eyes with bits of opaque black tape stuck over the eyes' palpebral fissures. Occluded eyes retained full mobility.

All recorded saccades were spontaneous—they did not compensate or stabilize changes in visual or acceleration fields caused by the chameleons' movements. Chameleons made most saccades while otherwise inactive. Moreover, their occasional movements were unaccompanied by visual tracking of the environment. The EOG's showed no smooth tracking eye movements whatever. The static environment and the typical slothful behavior of these animals ensured that sequences of spontaneous saccades were uncontaminated by ocular stabilizing movements.

As a first description of any stochastic process, the frequency distribution of interval durations between events is crucial (*5*). Intervals between successive chameleon saccades distributed unimodally with positive skew. The distributions had exponential tails (Fig. 1B). Poisson processes (simple stochastic processes by which events occur at constant low probability, independent of previous occurrences) generate intervals

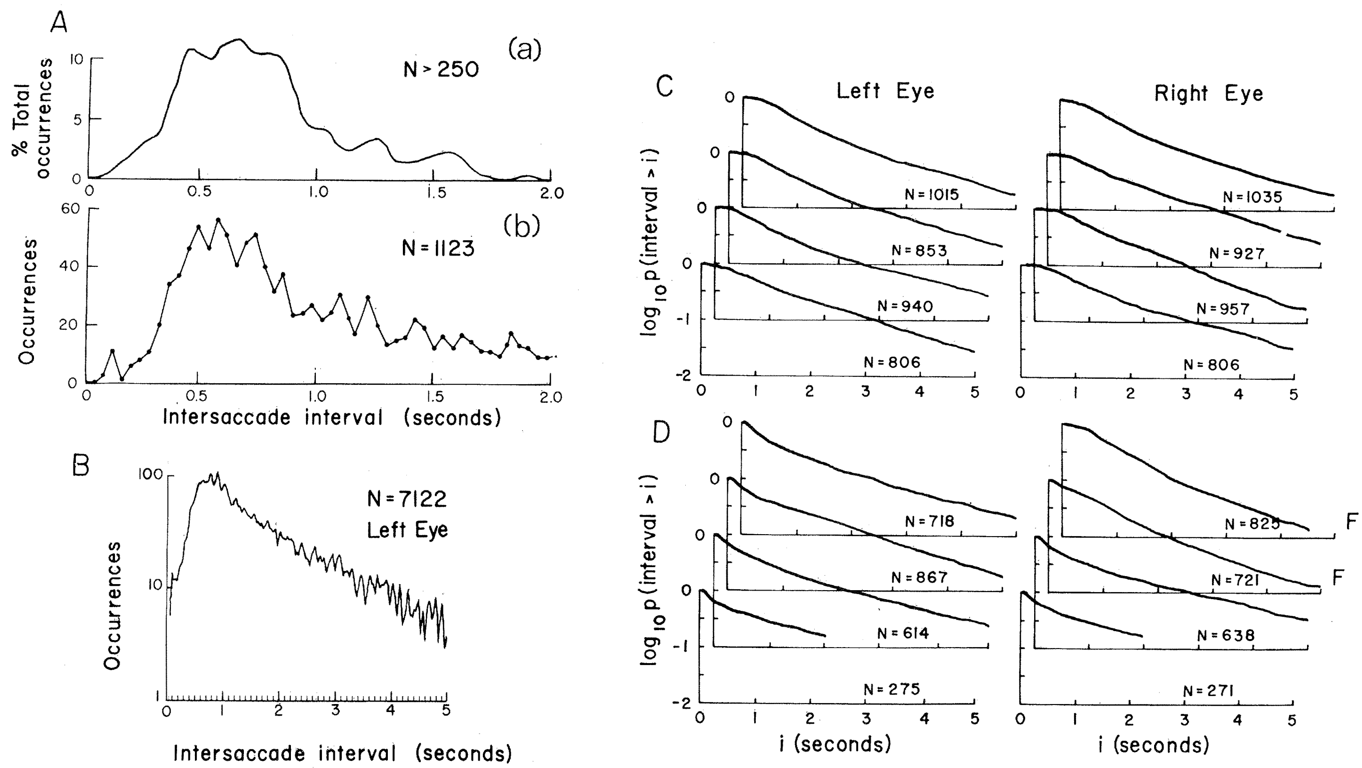

Fig. 1. Intersaccade interval distributions (A and B) and survivor functions (C and D). (A) Intersaccade interval distributions of *Homo sapiens* and *Chameleo dilepis*. (a) Data from a human wearing frosted contact lenses, redrawn from West and Boyce (*2*). (b) Data from a *C. dilepis*, hand-analyzed from movie films. (B, C, and D) Data from automated analysis of taped EOG's. (B) Semilogarithmic plot of a *C. dilepis* intersaccade interval distribution showing a linear tail. (C and D) Semilogarithmic plots of survivor functions. For (C) and (D), four curves per eye were assembled from consecutive 1-hour segments of a *C. dilepis* saccade sequence pair. First to last segments are represented on the page from bottom to top. The number of saccades (*N*) of each eye in each segment is shown. (C) Data from a chameleon with no masking of either eye. (D) Data from a chameleon whose left eye was occluded throughout the session, and whose right eye was likewise occluded, but freed (*F*) for the latter half of the session. (The bottom pair of survivor functions are truncated because of the small sample size.)

distributed as negative exponentials (*6*). I therefore hypothesized that chameleons created intersaccadic intervals longer than 1 second by a Poisson process.

The Poisson hypothesis predicted that the probability, *p* (after a saccade), of having to wait longer than some interval, *i*, until the next ipsilateral saccade would also decline as a negative exponential function. Estimates of these probability curves, *p*(*i*), termed "survivor functions" (*5*), are plotted semilogarithmically in Fig. 1C and clearly have exponential tails. Their slopes corresponded to the rate constant of the hypothetical driving Poisson process (approximately 0.2 to 0.4 per second). Similar tail slopes of survivor functions taken from contiguous segments of saccade sequences demonstrated integrity of the underlying stochastic process. Intervals longer than 1 second distributed independently. Together, these results confirmed that, by the time 1 second had elapsed after a saccade, a Poisson process dominated the timing of the next ipsilateral saccade.

Visual complexity of the static recording environments may have caused chameleons to initiate saccades in this way. But the hour-by-hour constancy I observed in some sequences (for example, Fig. 1C) militates against this possibility. Furthermore, statistics and distributions derived from concurrent left and right saccade sequences were always similar, even though the environment was strongly asymmetrical. For example, the chameleon which generated the saccade sequences of Fig. 1C spent most of the 4.5-hour recording session gazing out into the laboratory with his right eye, and into the shaded interior of the shielded cage with his left eye. Even so, left and right survivor functions were virtually identical.

To force the issue of environmental influence on saccade timing, I recorded saccade sequences from animals with one or both eyes completely occluded. The tail slopes of survivor functions from occluded eyes were the same as those from unoccluded contralateral eyes (Fig. 1D). The slopes were also the same as slopes from the same eye, before and after occlusion. Thus, in static visual environments, the chameleons initiated most saccades by a Poisson process evidently unaffected by visual input.

Whether by desire or inability, chameleons did not modulate the rate of this stochastic process. Since they were free to sleep and were relatively unrestrained, the data I collected represented truly spontaneous activity. Occasionally, there were long periods associated with sleep, during which there were no saccades. Saccadic activity in these records did not grade smoothly into and out of silence. Instead, saccades occurred in bursts. The total numbers of saccades generated by a chameleon in two equal periods of time were often different. But the tail slopes of the survivor functions were the same (Fig. 1D). Apparently, chameleon saccade generating systems occupied just two discrete states, "on" and "off."

Chameleons generated saccades spontaneously, whether or not their eyes were covered. The spontaneity of their eye movements suggested volitional control. But they timed most saccades according to simple, unseeing Poisson rules.

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Discrimination of Intermediate Sounds in a Synthetic Call Continuum by Female Green Tree Frogs

Abstract. *Male* Hyla cinerea *produce two distinctive calls. Acoustically intermediate calls are rare. Females discriminate between synthetic intermediates that differ by one cycle of amplitude modulation (50 per second). Processing appears to be continuous. The tree frog's auditory system thus provides a wide margin for the discrimination of its two principal signals.*

Most animals produce a relatively small number of discrete signals for intraspecific communication (*1*). The existence of repertoires of signals that intergrade (*2*) thus poses some important questions: To what extent, if any, do these intergraded signal systems increase the amount of information communicated? Do the animals using them possess some special sensory capabilities? Or, more generally, do the limited, discrete repertoires of most species indicate the inability of their nervous systems to produce and efficiently distinguish among a larger number of more similar signals? The answers to these questions depend on learning how animals deal with intergraded signals. How finely does an animal with a graded repertoire divide the continuum? How does an animal with discrete signals respond to intermediate signals?

Human speech is graded in its acoustic structure, and humans tend to perceive speech sounds that are intermediate along certain dimensions (for example, voice-onset time) in a nearly categorical manner (*3*). This means that intermediate sounds are usually identified ("labeled") as one or the other of the two end points of a continuum. Intermediates on the same side of a so-called phonetic boundary are very difficult to distinguish; intermediates on opposite sides of a boundary are readily discriminated even though the physical differences between them may be less than between intermediates on the same side the boundary (*4, 5*). At least one nonhuman primate with a graded vocal repertoire may treat some of its intermediate sounds in a similar fashion (*6*). Kuhl and Miller (*7*) showed that chinchillas, trained to distinguish the end points of a synthetic speech continuum and then presented with intermediate tokens, labeled these sounds in a manner similar to that of human subjects. Kuhl and Miller have suggested that categorical perception may simply reflect general psychophysical properties (constraints) of the (mammalian) auditory system rather than "special processing" mechanisms possessed by a species for the perception of its own signals (*8*). This issue remains unresolved not only because of the paucity of comparative data but also because differences in the methods of signal presentation and response criteria often preclude direct comparisons of the available studies. More specifically, we need to distinguish between an animal's ability to differentiate signals on the basis of some single property under "ideal" conditions and its performance in natural, complex contexts where redundant cues, noise, and speed of communication may become relevant (*9*). In any event, sensory mechanisms may restrict the number of discriminable signals (or phonetic segments) even in species with highly intergraded repertoires (*10*). It is thus tempting to speculate that the differences in the discrete signals of most animals reflect to some extent the resolving powers of their sensory systems. This report deals with the margin for error provided by the auditory system of a simple vertebrate for the discrimination of two of its discrete signals.

The vocal repertoires of most frogs and toads consist of unusually small sets of stereotyped signals (*1, 11*). The two principal vocal signals in the green tree frog (*Hyla cinerea*) are the mating and the pulsed calls, both of which are produced by males in breeding aggregations (*12*). Females are attracted to both kinds of calls in playback experiments, but they prefer mating calls. Pulsed calls are produced almost exclusively during agonistic interactions among males (*13*). Males occasionally produce transitional, acoustically intermediate calls (*14*). In comparison with pulsed calls, which are strongly amplitude-modulated (depth of modulation ≥ 75 percent) at about 50 per second for all or most of their duration, mating calls have a smooth amplitude-time envelope (*15*). Intermediate calls are strongly modulated for only part of their duration (Fig. 1A). These natural calls served as models for the generation of the synthetic call continuum (Fig. 1B) (*16, 17*). In one series of experiments females were given choices between the synthetic mating call [unmodulated (UM)] and the intermediates, and, in another series, between the modulated ($M = +7$) call and two of the intermediates (+4 and +5). Finally, females were given choices (four stimulus pairs) between intermediates. The sounds were recorded and played back with a stereophonic recorder (Nagra) (one kind of sound per channel); they were presented alternately (every 0.4 second), each from a separate speaker (Nagra DH) located 2 m apart. Gravid females were released individually from a small hardware-cloth cage located midway between the speakers where the intensities of the two sounds were equalized (75 dB with reference to 2×10^{-4} μbar). Experiments took place in a quiet (C-weighted ambient noise < 50 dB sound pressure level), dimly lit auditorium. Anechoic wedges (acoustic foam) minimized sound reflections in the test area. The criterion for a response was a female's touching a speaker or approaching it (to within 10 cm). This behavior reflects the natural courtship pattern; females typically initiate sexual contact with a calling male. Animals (fewer than 10 percent) that attempted to escape or failed to respond within 15 minutes were discarded. With two exceptions, the 122 animals that responded were tested in a single experiment in one of the three series described above (*18*). All animals were captured in amplexus on Wilmington Island, Georgia (20 km east of Savannah), between 1 June and 8 July 1977; they were tested within 24 hours of capture.

The synthetic mating call was preferred to +2, +3, +4, and +5 but not to +1 (Table 1). Females responded exclusively to +4 and +5 when the M (+7) call was the alternative stimulus (Table 1). The M call attracted some females in the absence of a competing stimulus. Thus most acoustically intermediate