

# Earthquake Prediction by Animals: Evolution and Sensory Perception

by Joseph L. Kirschvink

**Abstract** Animals living within seismically active regions are subjected episodically to intense ground shaking that can kill individuals through burrow collapse, egg destruction, and tsunami action. Although anecdotal and retrospective reports of animal behavior suggest that although many organisms may be able to detect an impending seismic event, no plausible scenario has been presented yet through which accounts for the evolution of such behaviors. The evolutionary mechanism of exaptation can do this in a two-step process. The first step is to evolve a vibration-triggered early warning response which would act in the short time interval between the arrival of *P* and *S* waves. Anecdotal evidence suggests this response already exists. Then if precursory stimuli also exist, similar evolutionary processes can link an animal's perception of these stimuli to its *P*-wave triggered response, yielding an earthquake predictive behavior. A population-genetic model indicates that such a seismic-escape response system can be maintained against random mutations as a result of episodic selection that operates with time scales comparable to that of strong seismic events. Hence, additional understanding of possible earthquake precursors that are presently outside the realm of seismology might be gleaned from the study of animal behavior, sensory physiology, and genetics. A brief review of possible seismic precursors suggests that tilt, hygrometry (humidity), electric, and magnetic sensory systems in animals could be linked into a seismic escape behavioral system. Several testable predictions of this analysis are discussed, and it is recommended that additional magnetic, electrical, tilt, and hygro-sensors be incorporated into dense monitoring networks in seismically active regions.

## Introduction

One of the major goals of seismology is to determine whether fault zones generate any hint of impending earthquakes. Recent discussions in the literature on this topic have been mixed, with some question as to whether large earthquakes are by their very nature unpredictable (e.g., Geller, 1991a, 1991b; Geller *et al.*, 1997a, 1997b), or whether we simply need a more complete record of geophysical and geochemical data in earthquake prone areas (Park, 1996; Aceves and Park, 1997). Unfortunately, data of this sort has gathered slowly due to the rarity of large seismic events, the limited spatial distribution of continuously recording instruments, and the large number of variables that could be recorded.

It is clearly impractical and prohibitively expensive to record continuously a random variety of physical and chemical parameters near all possible earthquake epicenters. Even focused work on the San Andreas Fault at Parkfield, California, which was the probable epicenter of the 1857 Fort Tejon earthquake (Sieh, 1978) and the site of semiperiodic magnitude 6 earthquakes (Bakun and McEvilly, 1984) demonstrates the cost and elusive nature of this recording problem (Roeloffs and Langbein, 1994). Hence, virtually all inferences about possible precursory phenomena must come

from the occasional lucky observation or must be gleaned from anecdotal reports obtained after the fact. In an attempt to systematically evaluate such observations, the International Association of Seismology and Physics of the Earth's Interior (IASPEI) organized a subcommission on earthquake prediction with the task of evaluating these precursory events through a peer-review process and creating a preliminary "List of Significant Precursors" (Wyss, 1991; Wyss and Booth, 1997), commonly referred to as the "List." Between 1989 and 1997, a total of about 40 nominations were made and evaluated by this subcommittee. The five cases placed on the preliminary List included foreshocks, preshocks, seismic quiescence before large aftershocks, radon decreases in ground water, and ground water level increases (Wyss, 1997). Six of the nominations that were not accepted for the List in the first two rounds dealt with various electromagnetic phenomena.

Given these difficulties in directly measuring preseismic phenomena, it seems worth asking whether information about seismic precursors might be available from a totally different, nongeological source: animal behavior. No nominations for the IASPEI List were considered involved data

from animal behavior, although the topic has certainly generated past interest (e.g., Gans, 1976; Tributsch, 1982). Claims of human sensitivity prior to earthquakes have also muddled this field, perhaps irreparably, given some of the patently absurd claims that have been made (e.g., headaches in northern California predicting earthquakes in Nicaragua, as described by Clarke, 1996). In discussions with geophysical colleagues, a commonly raised objection to the concept that animals might detect earthquake precursors is the fact that the life spans of most animals are much shorter than the typical repeat time of large seismic events. Hence, they are unlikely to *remember* any precursory signals. However, animal behavior is particularly susceptible to genetic control, so much so that an entire scientific journal, *Behavior Genetics*, is devoted to the topic. Through the course of random mutation and natural selection, rare events that episodically kill or reduce the fitness of even a small fraction of the breeding individuals of a species can lead to the evolution of mechanisms to avoid such mortality—this is best known in the case of disease. Organisms can also evolve behaviors that enhance survival and fitness, such as the well-known escape responses from predators and fire. Many of these involve sophisticated pattern recognition abilities. Work during the past 50 years has demonstrated that a large number of complex behavioral responses exhibited by animals are in fact under genetic control. Behavioral genetic systems, like all genes, are ancient fossils that preserve information that has helped survival of the lineage over the past 3.5 billion years. Behaviors as complex as the honeybee waggle dance language are instinctive, appearing spontaneously even in populations of the insect raised without the benefits of experienced, adult worker bees. Many examples are known where a sensory input (through vision, hearing, touch, smell, etc.) elicits a “fixed-action” response, causing an immediate and essentially involuntary, reflex-like reaction. These range from escape responses to mating behavior, and they occur in animals as diverse as flatworms, insects, and mammals. Note that behaviors of this sort are *not* learned—they are inherited, shaped through the long, slow process of random mutation and natural selection. It is therefore not necessary for the event that triggers the response to have happened within memory of any living individuals within a given population. The proper question is therefore best expressed within the context of population genetics: Is it reasonable for a seismic-escape behavior pattern to evolve, and can such a genetic system be maintained in the face of selection pressures operating on the time scales of damaging seismic events?

Previous biological analyses dating back to the mid-1970s concluded that an innate (genetically based) seismic-escape response was unlikely to have evolved in animals, due to the impression that earthquakes were “. . . too rare to establish a selective advantage that might permit genetic fixation of such a characteristic,” and the question of “. . . whether most species could take successful evasive action even if they had advanced knowledge of an impending earth-

quake” (Gans, 1976). Both of these concerns need re-evaluation. First, in 1975 we had only rudimentary knowledge of the frequency of moderate and large seismic events. In California and many other areas we now realize that great earthquakes occur with average repeat intervals of 100 years or so (Dolan *et al.*, 1995; Sieh, 1996). Although moderate earthquakes of  $M \sim 6+$  affect smaller geographic areas, they are more numerous and may dominate the local seismic hazards for an area. Furthermore, zones of high seismic activity have existed on Earth for at least the past two billion years or more, as they are a byproduct of plate tectonic processes. A small selection pressure acting over a vast interval of geological time can be just as effective at gene fixation as is stronger selection acting over a shorter time interval. Second, evasive action can, in many instances, reduce mortality during an earthquake. Earthquakes can kill animals or reduce their fitness in a variety of ways, from direct physical shaking (e.g., causing burrows to collapse, shaking eggs out of nests, breaking honeycomb, etc.) to indirect action of mudslides and tsunamis. Fitness can also be reduced in the interval after an earthquake as a result of the disruption of normal behavior from aftershocks. For many organisms, behavioral action taken prior to an earthquake could reduce mortality: fish and cetaceans leaving coastal zones, rodents exiting from collapsible burrows or dwellings, bees swarming, parents delaying egg-laying, etc.

This article stems from similarities in this list of possible pre-earthquake behavior to those unusual behaviors which have been reported for animals in the days, hours, and minutes prior to an earthquake. The book by Tributsch (1982) documents many of these observations in depth on a global scale. The similarity of behaviors reported by cultures as diverse as those in the Middle East, South America, and Asia lends at least some credibility to the hypothesis that a biological earthquake warning and/or prediction system may exist. If so, there must be a plausible route by which such a system could have evolved.

One major process through which complex biological systems evolve is to take an existing genetic pattern that evolved for one function and to link or adapt it for a different role. The new system is then gradually debugged and improved through the process of random mutation and natural selection. This evolutionary pattern has been termed exaptation (Gould and Vrba, 1982). For a seismic-escape response to develop in this fashion, an organism would need to combine an existing escape, panic, or “exit from the burrow” behavioral pattern with one or more appropriate sensory inputs to trigger the reaction. This reduces to three fundamental questions: (1) Has anything like a seismic-escape response already been established in the behavioral genetic repertoire of animals? If so, how could it have evolved? (2) Are there occasional precursory physical or chemical events, detectable at the surface of the earth, which might signal an impending earthquake? If so, have animals evolved the sensory abilities needed to detect them? (3) Can such a seismic-escape response gene system be maintained within a popu-

lation in the face of random mutation and genetic drift between significant seismic events? Each of these questions is addressed in this article.

### Has a Seismic Escape or “Early Warning” Response Already Evolved?

Virtually all animals possess instinctive responses to escape from predators and (for land animals) from fire; in humans these responses are known as panic and are associated with the rapid release of adrenaline, which heightens sensory awareness and temporarily blocks sensation of pain. Numerous observations exist of animals displaying panic in the few seconds prior to the onset of strong ground shaking. Tributsch (1982) lists many such examples, including dogs barking, nervous cats jumping out of windows, birds screaming, rats running out of their holes, bees swarming, etc. Such behavior immediately prior to an earthquake is not difficult to explain, as seismic *P* waves travel faster through the crust than the associated *S* waves by roughly 2–4 km/sec. If organisms are sensitive enough to detect vibrations accompanying the arrival of *P* waves, that sense could provide enough of a warning to trigger a death-avoiding response immediately prior to the arrival of the more damaging *S* waves. Only in very close proximity to the epicenter will the shaking start without appreciable warning. As moderate to large earthquakes like Loma Prieta can cause liquefaction at distances of 50+ km (Pease and Orourke, 1997), it is reasonable to infer that burrow collapse could be triggered in loose topsoil at greater distances. Hence, animals that live tens of kilometers from the epicenter have several seconds after detection of the *P* wave to escape the effects of the energetic *S* waves. Although anecdotal in nature, these observations support the hypothesis that a potential seismic-escape response is present in the behavioral repertoire of animals, and that it can be released at least by the sensory perception of low-frequency vibration.

In the case of *P* wave arrivals, the sensory ability that triggers the seismic-escape response is clearly acoustical or mechanical in nature, and it is even felt by humans on occasion (K. Sieh, personal comm., 1998). At least some extant rodents (e.g., California kangaroo rats) use low-frequency seismic “footdrumming” as a method of communication between burrows to mark territorial boundaries and to notify predatory snakes that their presence has been discovered (Randall, 1997; Randall and Lewis, 1997; Randall and Matocq, 1997). As both snakes and rodents have the ability to detect and respond to these vibrations, and sensory systems are in general highly conserved, the ability to detect these low-frequency signals was probably present in the last common ancestor of reptiles and mammals. It may well be a primitive feature of all vertebrates.

The evolution of a *P*-wave triggered seismic-escape response is not difficult to conceive, particularly via the process of exaptation previously described. A cursory survey of the field of neurophysiology demonstrates that predator–

prey interactions are largely responsible for driving the ability of animals to detect environmental signals almost down to the thermal noise limit (Block, 1992). Evidence of predatory activity in the fossil record extends back to the latest Precambrian at about 545 My ago, as indicated by predatorial borings in the shells of the first primitive mollusks (Bengtson and Zhao, 1992). Given the enormous selection pressure of predator–prey interactions, evolution should have perfected the auditory and tactile sensitivity of animals to the point where *P*-wave arrivals could be perceived within a geologically short interval of time. Evolutionary exaptation of these senses to yield a seismic-escape response would then be a very small change, linking these two existing systems (vibration sensitivity and predator escape) to yield a new behavior that minimizes mortality from seismic activity. As a wide variety of vertebrates (from fish to mammals) display behaviors consistent with the presence of this basic system (Tributsch, 1982), it probably evolved prior to mid-Ordovician time.

### Are There Other Physical or Chemical Events at the Earth’s Surface That Signal Impending Earthquakes, and Is It Plausible for Animals To Detect Them?

Once a *P*-wave-triggered seismic-escape system is in place (e.g., it reaches genetic fixation within a population), a similar process of exaptation can occur to link it to any other sensory signals that an animal might perceive prior to an earthquake. This step, if it has occurred, represents the transition from an *early warning* response to a true *predictive* response. My reasoning is as follows. Close to an earthquake epicenter, the *P* waves may be energetic enough to cause liquefaction and burrow collapse on their own, prior to arrival of the *S* waves (Lin, 1997). In these areas, a *P*-wave-triggered response alone would not be of much use for avoiding or minimizing seismic effects. On the other hand, if there are other precursory signals within the realm of an animal’s sensory perception, then random genetic mutations in the behavioral genes may occasionally link detection of this signal to the *P*-wave-triggered early warning response. This evolutionary exaptation could then be refined and improved by natural selection. During the past billion years, this may have happened many times, in many disparate lineages, depending upon how good an organism’s sensory perception processes had become.

As already noted the IASPEI preliminary list of significant earthquake precursors includes five geophysical nominations, three of which are seismic in nature (foreshocks, preshocks, and seismic quiescence before major aftershocks). The other two relate to a decrease in radon concentration and an increase in ground water levels (Wyss, 1997). As noted by Wyss (1997), this list does not preclude the existence of other geophysical or geochemical precursors; it simply represents the set of lucky observations obtained so far that meet minimal thresholds for statistical reliability. The problem at hand is to try to extend these suggestions in

a fashion which may lead to testable predictions concerning animal behavior.

For this purpose it is useful to examine the set of ancillary cases (some of which have not yet been nominated for the IASPEI consideration) as well as the admittedly anecdotal descriptions of animal behavior prior to earthquakes. Note that the goal of this exercise is *not* to nominate these for IASPEI consideration, but to encourage experimental tests of the relevant stimuli on suitable animal populations to see if they are capable of releasing panic-like seismic-escape behavior. Viewed from this perspective, at least four possible candidates for animal sensitivity can be gleaned: (1) ground tilting, (2) humidity changes, (3) electrical currents, and (4) magnetic field variations. These are considered in detail next.

#### Ground Tilting

Apparent tilt precursors prior to strong earthquakes have been reported in Japan and China, and several were included in formal IASPEI nominations (e.g., cases 5, 6, and 16 reviewed in Wyss [1991]). However, the magnitude of these precursors appear to be in the range of a few *micro*-radians, acting over several hours before the earthquake. In the vertebrates, the vestibular system in the inner ear is the main organ that mediates the detection of verticality, and the sensitivity of this response has been best studied in humans. Using a joystick-controlled gymbol system Bisdorff *et al.* (1996) found that normal human subjects typically needed tilts of  $6^\circ$  ( $\sim 0.1$  radian) or more from verticality to respond to this stimulus. Humans are therefore unlikely to detect tilting prior to earthquakes. On the other hand, many organisms have much better vestibular systems than do humans. Anatomically, these are particularly well developed in subterranean rodents as compared to aboveground rats (Lindenlaub *et al.*, 1995), and the use of a high-resolution vertical sensitivity as part of a multi-component navigational system in animal homing has been suggested seriously (Phillips, 1996). Unfortunately, few behavioral measurements of tilt sensitivity have been made in nonhuman animals, so there are at present no published data capable of refuting the hypothesis that animals close to an epicenter could detect an impending event in this manner. Also, shallow soils are often subjected to compaction and other nonseismic deformation, which add noise to any signal an animal might want to detect. On the other hand, extraordinarily accurate tilt meters are inexpensive and easy to implement (Westphal *et al.*, 1983).

#### Humidity Changes

The recognition that changes in groundwater level might sometimes provide clues to an impending earthquake suggests that associated changes in local humidity might be detected by animals. If the groundwater level rises significantly due to preseismic dilatancy, it must displace air from the pore spaces in the process. This moist air would then escape upwards and increase the humidity of air in soil and

burrows, and perhaps in the surface boundary layer on top of the soil. If water level changes are detectable in groundwater wells, it ought to be similarly detectable via humidity measurements in the soil.

The process of humidity reception in animals is known as hygroreception. Spiders and insects possess hygrosensitive sensilla that consist of specialized receptor cells with hygroscopic hair-like structures that detect humidity and/or temperature fluctuations (Sayeed and Benzer, 1996; Tichy and Loftus, 1996). Vertebrates appear to detect humidity through their olfactory system. Controlled laboratory experiments have shown that desert rodents are able to detect seed caches buried in dry sand based on variations of only a few percent of their water contents (Vanderwall, 1993).

Animal detection of impending earthquakes through hygroreception might therefore be possible in arid environments. It is, however, difficult to see how this method would work in rainy areas like Japan, which have uniformly high levels of humidity both in the soil and the air. It is also difficult to understand how the pattern of a preseismic humidity change would differ from that generated by an impending storm. On the other hand, Tributsch (1982) notes that some of the behaviors displayed by animals before earthquakes resemble their prestorm behavior, so this may be a component in their preseismic behavior. Digital hygrometers are on many commercially available home humidifying systems, and would be inexpensive to put in the field.

#### Electrical Currents

The presence of electrical and optical precursors prior to earthquakes is at present an area of intense, if controversial, research. Specific claims have been made in Greece of successful predictions, but the seismic community is understandably skeptical (see the May 27, 1996, issue of *Geophysical Research Letters*, which was devoted to this VAN technique). However, the existence of "earthquake lights" associated with seismic events has been noted and discussed often (Derr, 1973; Lockner *et al.*, 1983; Hedervari and Noszticzius, 1985; Lockner and Byerlee, 1985; Derr and Persinger, 1986; Ouellet, 1990). Earthquake lights were photographed during the extensive 1966 earthquake swarm in Matsushiro, Japan (Derr, 1973, 1986), and in southern Washington state (Derr and Persinger, 1986). Derr (1973) notes that lights have been reported before, during, and after the earthquakes. Although laboratory studies of rock fracture suggest optical emission via an exoelectron excitation process (Brady and Rowell, 1986), good explanations for how the atmospheric luminescence can persist for periods of several minutes have not been provided. Presumably, some form of crack propagation coupled with ion flow and perhaps fluid movement could be responsible for both electrical and optical effects.

In terrestrial animals, electrical sensitivity is rather low compared to marine or freshwater animals due to the high resistivity of air. High voltages are perceived through the

secondary effects of shock and/or the electrostatic action on feathers or hairs. In contrast, aquatic animals such as sharks, rays, and some fish often have exquisite electrical sensitivity due to specialized organs used both for communication and prey location (Bullock, 1982). In the elasmobranch fish (sharks and rays), a specialized receptor system in the ampullae of Lorenzini has, in fact, reached the thermal noise limit with the ability to perceive *nanovolt* changes in electrical fields (Kalmijn, 1974); these are comparable to the voltage of a flashlight battery applied across the Atlantic Ocean. Thus, the extensive reports reviewed by Tributsch (1982) suggesting an electrical link to anomalous behavior in fish before earthquakes merits serious experimental consideration, and could well have been incorporated into pre-seismic behavioral triggering in these and other aquatic animals. Similarly, nocturnal animals would have no difficulty detecting earthquake lights by simple visual signals. If some of these signals happen prior to significant seismic events, exaptation could link them to a pre-existing escape response.

#### Magnetic Field Variations

Ultra-low frequency (ULF) magnetic field variations are perhaps the least understood class of possible earthquake precursors, representing about 6 of the 40 nominated cases in the IASPEI List (Wyss, 1997); none has yet made the short List. Many other examples and thorough discussions of possible mechanisms for producing these magnetic precursors have been reviewed (Park *et al.*, 1993; Park, 1996; Mueller and Johnston, 1998). Furthermore, as noted later, some studies have employed proton-precession magnetometers that are not capable of recording the most interesting data in the .01–5 Hz region (e.g., Mueller and Johnston, 1998). Most of these studies arose from luck—magnetic observatories just happened to be recording some features of the geomagnetic field for other reasons when the earthquake occurred, and as such they often experienced power failures and data gaps as a result. (Coseismic data loss is one factor preventing inclusion on the formal List.) It should be noted that a major problem with recording ULF magnetic signals of this sort is that the magnetic field anomalies tend to follow an inverse cube power law with distance from the source, as expected from a dipole. Hence, meaningful data can only be obtained when recording instruments with adequate sensitivity and bandwidth just happen to be present very close to the epicentral area. Two of these lucky observations include the recording of a persistent 23 nT magnetic field anomaly a few days prior to the 1978  $M_s$  7.0 Alay earthquake (Shapiro and Abdullabekov, 1982; Park *et al.*, 1993), and a very fortuitous, broadband spectral recording of the 1989  $M_s$  7.1 Loma Prieta earthquake made by a group at Stanford University (Fraser-Smith *et al.*, 1990; Bernardi *et al.*, 1991).

As noted later, the Alay and Loma Prieta events are particularly important for the question of earthquake prediction by animals, as the precursory signals lie within, or very close to, the measured behavioral threshold limits for magnetic field perception by animals. The Loma Prieta data par-

ticularly merit detailed discussion here, as the recordings provide information about the spectral characteristics and amplitudes of the geomagnetic field changes in nine frequency bands between 0.01 and 10 Hz, at a distance of only 7 km from the epicenter. Rather than recording the data continuously (as is typical for a seismogram), magnetic field characteristics were stored as “geomagnetic activity indices,” which were the set of logarithms (base 2) of the 30-minute averages of the power in each frequency band. r.m.s. field amplitudes can be reconstructed using a calibrated conversion table (Fraser-Smith *et al.*, 1990; Bernardi *et al.*, 1991). These data show a significant elevation in magnetic activity in the .01–5 Hz frequency range starting about two weeks prior to the earthquake, with peak amplitudes in the 1–3 nT range. About three hours before the event, however, the largest signals exceeded the dynamic range of the instrument, with peak r.m.s. fields *exceeding* 6 nT as measured in the 0.01–0.02 Hz band. As this represents a time average, peak field levels could easily have been much higher. Unfortunately, about eight hours worth of the coseismic and subsequent data were lost due to power failure caused by the earthquake.

Sensory detection of this level of geomagnetic variation by some animals is neither an improbable nor an impossible event. One of the most surprising developments in the field of sensory neurophysiology during the past 25 years has been the discovery of geomagnetic influence on behavior in a phylogenetically diverse assemblage of organisms (a topic which has been reviewed extensively elsewhere by Kirschvink *et al.*, 1985; Kobayashi and Kirschvink, 1995; Wiltshcko and Wiltshcko, 1995; Kirschvink, 1997). In parallel with the growing experimental data on magnetoreceptive organisms, the biophysical basis of the response was found to be due to small crystals of the ferrimagnetic mineral, magnetite ( $\text{Fe}_3\text{O}_4$ ), which are formed biochemically. Crystals of this biogenic magnetite used for orientation were first discovered in the magnetotactic bacteria (Blakemore, 1975, 1982; Frankel and Blakemore, 1984), where they are held together in linear chains so that their individual magnetic moments will sum together. The resulting magnetostatic orientation energy per cell typically exceeds thermal noise (kT) by factors between 10 to several thousand. Neurophysiological studies have also revealed similar magnetite crystals in honeybees (Gould *et al.*, 1978), pigeons (Walcott *et al.*, 1979), and fish (Walker *et al.*, 1984), which, in the best preparations, are also aligned in linear chains as they are in the magnetotactic bacteria (Mann *et al.*, 1988). Subsequent electrophysiological studies in fish and birds have identified the ophthalmic branch of the trigeminal nerve as the main conduit of magnetic field information to the brain, from magnetite-based receptors located in the frontal regions of the head (Semm and Beason, 1990; Walker *et al.*, 1997). More recently, lipophilic dyes and scanning laser confocal reflection microscopy have been used to identify some of the magnetite-containing cells at the distal termini of the trigem-

inal nerve, which appear to be highly specialized for magnetoreception (Walker *et al.*, 1997).

As is the case for many other sensory systems, behavioral data indicate that some animal groups have extended the sensitivity of their magnetoreceptor systems down essentially to the thermal noise limit. Biophysical models of this limit for magnetointensity perception, given the typical quantities of magnetite measured in animals, are on the order of 100 pT (Kirschvink and Walker, 1985). At least two plausible evolutionary driving factors can be envisioned for producing an ultrasensitive magnetoreceptor system. The first involves selection for long-distance homing ability in migratory animals. Magnetic field inclination and total intensity of Earth's dipole field vary in a regular fashion with latitude, and sensory perception of these components can be selected upon to improve homing and navigation abilities in an essentially continuous fashion. As the resolution of the overall system improves (presumably through the addition of additional receptor cells and better information processing), other navigational features present in the geomagnetic field can aid in their navigational abilities, spurring additional selection for increased sensitivity. Birds have long been known to be disoriented at magnetic anomalies (Walcott, 1978), just as cetacean (dolphin and whale) stranding events preferentially happen at magnetic anomalies along coastlines (Klinowska, 1985; Kirschvink *et al.*, 1986; Kirschvink, 1990). Most of the positional variance observed in fin whales migrating at sea is explained by their avoidance of high magnetic fields and field gradients, suggesting that they use the marine magnetic lineations as a normal part of their navigational system (Walker *et al.*, 1992). Analyses of these data imply sensitivity to intensity fluctuations in the range of a few nT.

The second evolutionary factor which could drive magnetoreception to, or help keep it at, the thermal noise limit involves use of the diurnal variations in the geomagnetic field as a timing cue. Nocturnal animals and those that live or nest in dark cavities (like honeybees) are not always able to set their internal circadian clocks with sunlight, as is typically done by most animals. Although the geomagnetic field at most localities on the Earth's surface is fairly stable at night, solar heating of the ionosphere begins at daybreak and produces electric currents which are active during most of the daylight hours. These lead to a periodic shift in the magnetic field components at the surface on the order of 50 to 100 nT, with regular variations according to season and latitude (see Skiles, [1985] for a review). Direct evidence exists that honeybees can actually use this information as a timing cue. Lindauer (1977) presented compelling evidence that bees raised in a constant-condition flight room were able to maintain track of their internal biological clocks, despite the absence of visual, thermal, humidity, and other signals relating to day/night cycles. This time-keeping ability was disrupted on days with magnetic storms, implying that their time-keeping abilities were based on the 20–50 nT diurnal variations of the geomagnetic field. This basic effect was

replicated by Gould (1980), who was able to shift the diurnal cycle artificially through the use of a 23-hour synthetic geomagnetic diurnal variation generated by a fluxgate-controlled coil system. In mammals, further evidence for this link between circadian rhythms and ULF magnetic variations comes from studies of melatonin synthesis. Melatonin is the main hormone in animals which controls the sleep/wake cycles; its production by the pineal gland is suppressed both by light and by weak, ULF shifts in the magnetic field (Reiter, 1994).

Experimental data from honeybees further demonstrate that the geomagnetic sensory system has evolved to the level where the Alay and Loma Prieta magnetic anomalies could probably be detected, both in frequency and sensitivity. The discovery that bees can be taught to discriminate artificially generated magnetic fields in laboratory settings (Walker and Bitterman, 1985) led to measurements both of the threshold sensitivity (Walker and Bitterman, 1989) and the frequency response of the receptor systems (Kirschvink and Kobayashi-Kirschvink, 1991; Kirschvink *et al.*, 1992, 1997). Figure 1 shows a compilation of these data, which indicate that the honeybee magnetoreceptor system is tuned to respond best to frequencies below 10 Hz, with sensitivity in the low nT range. Tributsch (1982) reports observations of unusual swarming behavior of bees about 15 minutes prior to the onset of strong earthquakes.

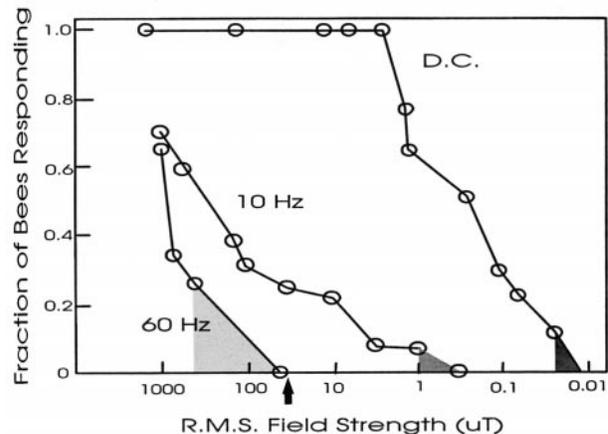


Figure 1. Behavioral measurements of the ability of honeybees to discriminate extremely low frequency a.c. magnetic fields. This figure shows the proportion of honeybees able to discriminate the given field stimulus. The data for the nine honeybees exposed to the d.c. field are from Walker and Bitterman (1989), and those from 11 honeybees tested at 60 Hz a.c. and 15 honeybees at 10 Hz a.c. are from Kirschvink *et al.* (1997). Shaded intervals at the lower end of each curve show the area of uncertainty between the performance of the best animal at that frequency and the subsequent level at which the animal did not discriminate. For comparison, the black arrow indicates the approximate magnitude of the d.c. geomagnetic field in Pasadena (45  $\mu$ T). The honeybee magnetoreception system is tuned for maximum sensitivities below 10 Hz.

Evolution of this highly sensitive magnetoreception system is an interesting problem. Primitive, early eukaryotes presumably inherited their magnetite-based magnetotactic responses from their bacterial ancestors, maintaining its use for providing a constant rudder against the randomizing influence Brownian motion (Torres de Araujo *et al.*, 1985). The presence of nearly identical magnetosome-chain structures in higher animals, and their use in geomagnetic orientation, is most easily explained as the result of common descent (Chang and Kirschvink, 1989; Kirschvink, 1989). However, as the musculature and locomotor abilities improved in primitive animals, there would be selection for more accurate homing and orientation abilities. In most sensory systems this is accomplished by increasing the number of receptors and the complexity of the neural circuits that extract environmentally relevant information. An increased number of neurons not only results in better accuracy of the directional signals present in the magnetic field, but it also permits extraction of the total *intensity* of the local magnetic field (Kirschvink and Gould, 1981; Kirschvink and Walker, 1985), which is a scalar parameter and hence independent of the orientation of an animal. As the average north/south gradients in total intensity are in the range of 5–10 nT/km, natural selection for enhanced navigational accuracy ought to drive the system to the point where magnetic anomalies in the Earth's crust could be used as navigational reference signals. The ability noted earlier that honeybees keep track of time in dark cavities by detecting diurnal variations in the geomagnetic field is probably an example of where this high-resolution sensory system was exapted for a completely different purpose than for which it originally evolved. A similar exaptation of this high-resolution magnetic sensitivity for time-keeping is not unlikely in nocturnal burrowing animals, some of which are known to have a good magnetic sensory system (e.g., African mole rats [Burda *et al.*, 1990; Wiltchko and Wiltchko, 1995]). Once this low-frequency, high-resolution magnetic sensory system has evolved, its further evolutionary exaptation to trigger an existing seismic-escape response is possible. Highly evolved pattern recognition is also possible, as is common in the vertebrate hearing and visual systems. As species of all major subgroups of the vertebrates display this high-resolution magnetic intensity sensory system, it must have evolved prior to their divergence (Ordovician time).

#### Can a Seismic-Escape Response System Be Maintained Within a Population?

The time scale for a genetic system to evolve and be fixed in a population depends upon the relative selection pressure (the differential survival) that the ability provides the individuals within the population, as well as the length of time over which the selection pressure operates. Hence, a behavioral trait that is nearly neutral in terms of natural selection for most of the time, but during a rare event provides a significant chance of increased survivability, can in

theory produce a highly evolved system. In fact, modern refinements of the principal model of evolution (the neutral theory of Kimura) have led to what is now called the nearly neutral theory, in which most competing copies of a particular gene (alleles) in a population drift along with no net positive or negative effect over the course of many generations *except when a fluctuation or event in the environment selects heavily for their presence* (Gillespie, 1984; Ohta, 1996; Ohta and Gillespie, 1996). The net effect is to increase the likelihood that the genes will eventually be fixed in the population. This pattern of “episodic selection” could arise as a natural consequence of mortality generated by the repeat patterns of earthquakes.

A simple Monte-Carlo simulation demonstrates how a system of this sort can lead to the fixation and maintenance of a seismic escape response gene. For the model presented here, we consider a population of burrowing animals, such as California's kangaroo rats (*Dipodomys* sp.), which live in and around the San Andreas Rift (Best *et al.*, 1996). In the terminology of population genetics (e.g., Crow and Kimura, 1970), fixation is the process through which a trait or gene initially present in only a small fraction of the population comes to dominate, or “fix” itself, as being present on both copies of the proper chromosome in each breeding individual of a population. Once fixed, it is fairly stable against being displaced by new mutation. In the absence of selection pressure or mutation, the ability of any particular copy of a gene to make it to the next generation is a chance process. As most animals are diploid (two copies of each chromosome), each parent randomly contributes only one of their two copies of each gene to their progeny. Consider now a situation where one of the behavioral genes (call it A) acts to link a sensory input to an established response that minimizes mortality resulting from an earthquake. Individuals with only the other allele for this gene, denoted a (e.g., the aa genotype), do not produce this response, whereas either heterozygous (aA or Aa) or homozygous (AA) individuals with the trait will respond. According to the neutral theory of population genetics (Crow and Kimura, 1970), in the absence of selection and mutation the relative levels of the gene will do a random walk, with less frequent alleles usually being lost from the population. We are interested, however, in the nearly neutral case, where only once in many generations the trait A enhances the survivability of any individual that possesses it. Given the anecdotal behavioral evidence that a P-wave-triggered escape response has already evolved in animals, the most important question concerns the level of relative selection required to maintain the trait in the population.

Figure 2 shows typical results for a simple, first-order Monte-Carlo simulation in which the breeding population size is held constant at 10,000 individuals, with a 50-generation (or year) recurrence interval for a seismic event large enough to cause mortality via burrow collapse, run for 1000 generations. At each seismic event, we assume that any individual with at least one copy of allele A survives and is

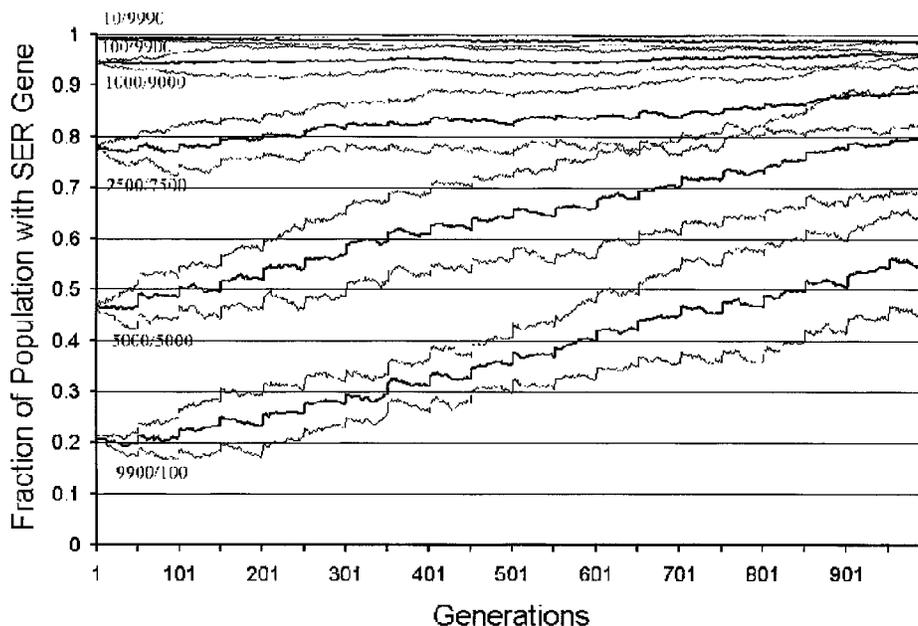


Figure 2. Results of Monte-Carlo simulations on the stability of a seismic-escape response trait under conditions of episodic selection. In these simulations, the effective breeding population is held constant from generation to generation at 10,000 diploid individuals, with equal numbers of males and females. To move from one generation to the next (breed), one female and one male are selected randomly from the “parental” generation using a uniform random-number generator, and each parent randomly gives one of its alleles to the progeny. (Individual parents can have many offspring). This process is repeated until the new generation has reached 10,000 individuals, whereupon it is randomly divided into equal numbers of males and females. After every 50 generations, a “seismic event” is introduced in which the phenotype of each individual is examined. Individuals with at least one A allele are allowed to reproduce as normal, but 10% of those which lack it (aa) are killed randomly (e.g., marked so that they are skipped in the next breeding cycle). Each simulation was allowed to run for 1000 generations, and repeated with identical starting conditions 10 times. Results were averaged at each generation, and are shown on the figure as families of three curves, the mean (bold lines)  $\pm$  1 standard deviation at each generation.

In order to test the genetic stability of a seismic escape response, and its ability to be fixed within a population using these parameters, individuals in the initial populations were all homozygous (either all AA or aa). This was done to simulate the situation where a small group of genetically similar individuals migrated into a new area, thereby infecting the existing population with seeds of the other genotype. In this figure, the five simulations started with (aa, AA) ratios of 10/9990, 100/9900, 1000/9000, 2500/7500, 5000/5000, and 9900/100, respectively, and can be distinguished by their initial starting values on the ordinate. Note that the phenotype fractions shown after one generation are much higher than in the seed population, as the initial homozygosity is lost completely in the first random breeding operation. Individuals with genotypes of aA, Aa, and AA all have the seismic-escape gene, and are protected from the random seismic death.

In the first simulation, which starts with only 10 individuals having the aa genotype, virtually all individuals in every subsequent generation are protected from seismic death with at least one copy of the A gene, and all of the a alleles are gradually lost within a few hundred generations. (This curve is indistinguishable from the top line on the graph.) In the first two simulations, so few aa phenotypes exist in the population that the net results approach those expected from simple random genetic drift. In the following simulations, however, a significant number of aa individuals are blocked from breeding every 50 generations so that the fraction of individuals protected by the A gene increases rapidly with time.

In these simulations, a 10% mortality for the aa genotype once every 50 generations is a rather small factor. As an example in the 2500/7500 simulation near the middle of the chart, only about 230 of the aa individuals were blocked from breeding between the 50th and 51st generation, out of a total of 500,000 random matings during the 50 generations involved; this is an average selective factor of only 0.046%.

able to reproduce in the next generation. During each seismic event, 10% of all individuals without any copies of the A allele are “killed” (e.g., blocked from reproducing in the simulation). Each simulation was repeated 10 times, and the results were shown as the mean occurrence of the A phenotype, plus or minus one standard deviation at each generation.

Simulations in which the a trait (no seismic-escape response) is present in small amounts indicate that it is quickly eliminated from the population even after only a few dozen seismic events, even for only a 10% advantage of the competing A genes expressed only once every 50 years (a net selective advantage of only  $\sim 0.05\%$ ). Hence, a seismic-escape response system should be genetically stable once fixed within a population. Similarly, when homozygous AA individuals are introduced at low levels into a population of initially pure aa, the A phenotype has a very high chance of reaching fixation within a geologically short interval of time. Simulations with a lower selective advantage simply take a longer time to reach fixation, with a greater chance of random loss in the process.

It is conceivable that not all activity of such an escape response gene might be beneficial—a false alarm during the daytime hours, for example, might lead to increased predation among nocturnal rodents, and not all earthquakes generate a local tsunami, etc. These factors obviously balance on average against any beneficial effects of the response. Genes that are more detrimental than beneficial tend to be weeded out with time. However, the model presented here is overly simplistic as it involves only one trait, and the rather complex behavioral systems observed today are most likely the end result of hundreds of millions of years of evolution of dozens of interacting gene systems. It is this complexity that makes it possible for animals to achieve rather sophisticated pattern recognition abilities, much in the way that neural nets can be trained. Evolutionary fine-tuning of these patterns for a seismic-escape response would result in fewer false alarms. One obvious test of this is to see if animals are able to distinguish *P* waves from *S* waves; an *S* wave from a distant earthquake would not signal impending burrow collapse, although it might be of comparable energy to that of a local *P* wave from a close event.

### Discussion

The analysis presented here implies that if there are occasional precursors to earthquakes that animals could detect, behavioral patterns could evolve to minimize associated mortality. Several considerations exist that make this more plausible than might otherwise be thought. First, plate tectonics (the driving force for most earthquakes) has operated for at least the past two billion years on Earth. Hence, the surface environment has been subjected to repeated strong shaking with repetition on the 100- to 10,000-year time scales, perhaps even higher on active plate margins. Second, these effects are not limited to plate boundaries. Even many

mid-continent areas experience seismic events in this time frame (e.g., New Madrid, Missouri AD 1811–1812; Lisbon, Portugal AD 1755 [Demoulin, 1996; Johnston and Schweig, 1996]). Third, and as already noted, strong seismic events are indeed capable of inducing significant mortality in existing populations, particularly in near-shore, burrowing, and egg-laying organisms. Fourth, if taken at face value, anecdotal reports of peculiar animal behavior before earthquakes (Tributsch, 1982) are compatible with evolution of a basic seismic-escape response sometime before the divergence of the animal phyla nearly one billion years ago (Runnegar, 1982; Wray *et al.*, 1996; Ayala and Rzhetsky, 1998). As the geological evidence of burrow formation goes back nearly 540 million years, as shown from trace fossil evidence in rocks of Early Cambrian age (McIlroy and Heys, 1997), burrow collapse as a mechanism of seismic mortality should date back at least this far. The distant ancestors of all mammals (synapsids) who survived the Permian/Triassic mass extinction 250 million years ago were apparently burrowing animals living along the tectonically active margin of the ancient supercontinent of Gondwanaland (Smith *et al.*, 1993). Their fossil remains are almost always found as pairs of animals in collapsed burrows (Smith *et al.*, 1993; Smith, personal comm., 1997). Thus, mammals in particular have had over 250 million years in which to refine their seismic-escape response and link it via exaptation to additional sensory signals. As a general rule, genes that control evolutionarily ancient processes evolve much more slowly, and are influenced far less by genetic drift, than are more recent additions to the genome. Hence, one would expect a seismic-escape response system to be evolutionarily conserved.

Several lines of experimentation could help test these ideas. First, we need to study animal behavior associated directly with the ground shaking associated with seismic events. Although it is obviously impractical to sit and wait for suitable earthquakes to happen, the introduction of broadband seismometers during the last decade has provided excellent and detailed recordings of ground motion during several large earthquakes (Landers, Northridge, Kobe, etc.). Just as these records are being used to test building designs and revise earthquake safety guidelines (e.g., Heaton *et al.*, 1995), controlled shake-table experiments could be done on laboratory populations of burrowing animals from seismically active zones; some of California’s endemic kangaroo rats would be good candidates. These experiments would establish a baseline of animal behavior for comparison with reactions of other stimuli. Following this, a variety of field-based experiments could be done on the same species, in which candidate precursory geophysical and geochemical signals are given artificially to determine which, if any, are capable of triggering similar behavioral reactions. The exaptation model outlined here would predict some similarity in the evoked behavioral response between shaking and other stimuli linked to seismic-escape activity. In particular, simple back-of-the-envelope calculations indicate that it would be relatively easy to modulate the magnetic field

within a 100-m diameter coil system to the levels indicated by the Alay and Loma Prieta magnetic precursory events; this could be done with minimal disturbance around a natural kangaroo rat warren in the field. Even though the exact seismomagnetic patterns were not recorded prior to these events, enough information is available from the Loma Prieta earthquake to produce a family of complex waveforms with similar spectral characteristics to those recorded just prior to the main event. Studies like this should be done. Ultimately, knowledge of the complete genome sequence of these animals might yield clues to the triggering mechanism and sensory patterns that elicit seismically triggered fixed-action responses, but we may need to wait 20–50 years before the genetic basis of innate pattern recognition is understood.

Finally, seismologists should not limit their recording and monitoring efforts solely to ground motions, which has historically been the case. For the ultimate goal of earthquake prediction, there is no substitute for detailed records of possible precursory signals associated with strong seismic events. As such, it is silly to depend upon serendipitous observations such as those from Alay and Loma Prieta. Although some focused magnetic studies exist (e.g., Mueller and Johnston, 1998), the proton precession magnetometers typically used do not operate in the interesting frequency range (0.01–5 Hz) flagged by the Loma Prieta data. In Southern California, the TriNet/Terrascope stations maintained by Caltech, the U.S. Geological Survey, and the CDMG have several 24-bit data channels which are not presently in use. These ought to be equipped with inexpensive sensors to monitor tilt, geoelectrical potential, humidity, and magnetism, and the magnetic signals should be recorded continuously at least through 10 Hz. As an example, the per-unit cost of fluxgate magnetometers, with sensitivities in the 50–100 pT range, has dropped precipitously in recent years due their development for use in intelligent vehicle highway systems (IVHS). Although not as sensitive as the induction coil systems used to record the Loma Prieta event (Fraser-Smith *et al.*, 1990), they are far less expensive, have adequate sensitivity to detect nT-level changes, and are unlikely to go off-scale as did the Stanford equipment. These could be deployed easily on the TriNet/Terrascope system in Southern California and perhaps elsewhere.

### Acknowledgments

I thank C. Allen, E. Brodsky, L.K. Hutton, H. Kanamori, D. Prothero, Tom Heaton, and Tim Raub for helpful comments. Work on magnetoreception in my laboratory has been supported generously by the Electric Power Research Institute (EPRI-WO-4307-03), and partially by the NIH and the Fetzer Foundation.

### References

- Aceves, R. L., and S. K. Park (1997). Cannot earthquakes be predicted, *Science* **278**, 488–488.
- Ayala, F. J., and A. Rzhetsky (1998). Origin of the metazoan phyla: molecular clocks confirm paleontological estimates, *Proc. Natl. Acad. Sci. USA* **95**, 606–611.
- Bakun, W. H., and T. V. McEvelly (1984). Recurrence models and Parkfield, California, earthquakes, *J. Geophys. Res.* **89**, 3051–3058.
- Bengtson, S., and Y. Zhao (1992). Predatorial borings in late Precambrian mineralized exoskeletons, *Science* **257**, 367–369.
- Bernardi, A., A. C. Fraser-Smith, P. R. McGill, and O. G. Villard (1991). ULF magnetic field measurements near the epicenter of the Ms 7.1 Loma Prieta earthquake, *Phys. Earth Planet. Interiors* **68**, 45–63.
- Best, T. L., R. K. Chesser, D. A. McCullough, and G. D. Baumgardner (1996). Genetic and morphometric variation in kangaroo rats, genus *Dipodomys*, from coastal California, *J. Mammal.* **77**, 785–800.
- Bisdorff, A. R., C. J. Woisley, D. Anastasopoulos, A. M. Bronstein, and M. A. Gresty (1996). The perception of body verticality (subjective postural vertical) in peripheral and central vestibular disorders, *Brain* **119**, 1523–1534.
- Blakemore, R. P. (1975). Magnetotactic bacteria, *Science* **190**, 377–379.
- Blakemore, R. (1982). Magnetotactic bacteria, *Annu. Rev. Microbiol.* **36**, 217–238.
- Block, S. M. (1992). Biophysical aspects of sensory transduction, in *Sensory Transduction*, Marine Biological Laboratory, Woods Hole, Massachusetts, D. P. Corey and S. D. Roper (Editors), Rockefeller University Press, 424.
- Brady, B. T., and G. A. Rowell (1986). Laboratory investigation of the electrodynamics of rock fracture, *Nature* **321**, 488–492.
- Bullock, T. H. (1982). Electroreception, *Annu. Rev. Neurosci.* **5**, 121–170.
- Burda, H., S. Marhold, T. Westenberger, R. Wiltshcko, and W. Wiltshcko (1990). Magnetic compass orientation in the subterranean rodent, *Cryptomys hottentotus* (Bathyergidae), *Experimentia* **46**, 528–530.
- Chang, S.-B. R., and J. L. Kirschvink (1989). Magnetofossils, the magnetization of sediments, and the evolution of magnetite biomineralization, *Annu. Rev. Earth Planet. Sci.* **17**, 169–195.
- Clarke, T. (1996). *California Fault: Searching for the Spirit of a State Along the San Andreas*, Ballantine Books, New York, 417 pp.
- Crow, J. F., and M. Kimura (1970). *An Introduction to Population Genetics Theory*, Harper & Row, New York, 591 pp.
- Demoulin, A. (1996). Clastic dykes in East Belgium—evidence for Upper Pleistocene strong earthquakes west of the Lower Rhine rift segment, *J. Geol. Soc.* **153**, 803–810.
- Derr, J. S. (1973). Earthquake lights: a review of observations and present theories, *Bull. Seism. Soc. Am.* **63**, 2177–2187.
- Derr, J. S. (1986). Luminous phenomena and their relationship to rock fracture, *Nature* **321**, 470–471.
- Derr, J. S., and M. A. Persinger (1986). Luminous phenomena and earthquakes in southern Washington, *Experimentia* **42**, 991–999.
- Dolan, J. F., K. Sieh, T. K. Rockwell, R. S. Yeats, J. Shaw, J. Suppe, G. J. Huftile, and E. M. Gath (1995). Prospects for larger or more frequent earthquakes in the Los-Angeles metropolitan region, *Science* **267**, 199–205.
- Frankel, R. B., and R. P. Blakemore (1984). Precipitation of Fe<sub>3</sub>O<sub>4</sub> in magnetotactic bacteria, *Phil. Trans. R. Soc. Lond. B* **304**, 567–574.
- Fraser-Smith, A. C., A. Bernardi, P. R. McGill, M. E. Ladd, R. A. Helliwell, and O. G. Villard (1990). Low-frequency magnetic field measurements near the epicenter of the MS-7.1 Loma Prieta earthquake, *Geophys. Res. Lett.* **17**, 1465–1468.
- Gans, C. (1976). Can animals predict earthquakes? Overview and proposal, in EHRP conference I: *Abnormal Animal Behavior prior to Earthquakes, I*, Menlo Park, California, J. F. Evernden (Editor), U. S. Geological Survey, 272–282.
- Geller, R. J. (1991a). Shake-up for earthquake prediction, *Nature* **352**, 275–276.
- Geller, R. J. (1991b). Unpredictable earthquakes—reply, *Nature* **353**, 612.
- Geller, R. J., D. D. Jackson, Y. Y. Kagan, and F. Mulargia (1997a). Cannot earthquakes be predicted—responses, *Science* **278**, 488–490.
- Geller, R. J., D. D. Jackson, Y. Y. Kagan, and F. Mulargia (1997b). Geoscience—earthquakes cannot be predicted, *Science* **275**, 1616–1617.

- Gillespie, J. H. (1984). The molecular clock may be an episodic clock, *Proc. Natl. Acad. Sci. USA* **81**, 8009–8013.
- Gould, J. L. (1980). The case for magnetic sensitivity in birds and bees (such as it is), *Am. Scientist* **68**, 256–267.
- Gould, S. J., and E. S. Vrba (1982). Exaptation—a missing term in the science of form, *Paleobiology* **8**, 4–15.
- Gould, J. L., J. L. Kirschvink, and K. S. Deffeyes (1978). Bees have magnetic remanence, *Science* **201**, 1026–1028.
- Heaton, T. H., J. F. Hall, D. J. Wald, and M. W. Halling (1995). Response of highrise and base-isolated buildings to a hypothetical M(w) 7.0 blind thrust earthquake, *Science* **267**, 206–211.
- Hedervari, P., and Z. Noszticzius (1985). Recent results concerning earthquake lights, *Ann. Geophys.* **3**, 705–707.
- Johnston, A. C., and E. S. Schweig (1996). The enigma of the New-Madrid earthquakes of 1811–1812, *Annu. Rev. Earth Planet. Sci.* **24**, 339–384.
- Kalmijn, A. J. (1974). The detection of electric fields from inanimate and animate sources other than electric organs, in *Handbook of Sensory Physiology*, Vol. 9, A. Fessard (Editor), Springer-Verlag, Berlin, New York, 147–200.
- Kirschvink, J. L. (1989). Magnetite biomineralization and geomagnetic sensitivity in higher animals: an update and recommendations for future study, *Bioelectromagnetics* **10**, 239–259.
- Kirschvink, J. L. (1990). Geomagnetic sensitivity in cetaceans: an update with the U.S. live stranding records, in *Sensory Abilities of Cetaceans*, J. A. Thomas and R. Kastelein (Editors), Plenum, New York, 639–649.
- Kirschvink, J. L. (1997). Magnetoreception: homing in on vertebrates, *Nature* **390**, 339–340.
- Kirschvink, J. L., and J. L. Gould (1981). Biogenic magnetite as a basis for magnetic field sensitivity in animals, *Bio Systems* **13**, 181–201.
- Kirschvink, J. L., and A. Kobayashi-Kirschvink (1991). Is geomagnetic sensitivity real? Replication of the Walker-Bitterman conditioning experiment in honey bees, *Am. Zoologist* **31**, 169–185.
- Kirschvink, J. L., and M. M. Walker (1985). Particle-size considerations for magnetite-based magnetoreceptors, in *Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism*, Vol. 5, J. L. Kirschvink, D. S. Jones, and B. J. McFadden (Editors), Plenum, New York, 243–254.
- Kirschvink, J. L., D. S. Jones, and B. J. McFadden (Editors) (1985). Magnetite biomineralization and magnetoreception in organisms: a new biomagnetism, in *Topics in Geobiology*, Vol. 5, F. Stehli (Series Editor), Plenum, New York, 685 pp.
- Kirschvink, J. L., A. E. Dizon, and J. A. Westphal (1986). Evidence from strandings for geomagnetic sensitivity in Cetaceans, *J. Exp. Biol.* **120**, 1–24.
- Kirschvink, J. K., T. Kuwajima, S. Ueno, S. J. Kirschvink, J. C. Diaz-Ricci, A. Morales, S. Barwig, and K. Quinn (1992). Discrimination of low-frequency magnetic fields by honeybees: biophysics and experimental tests, in *Sensory Transduction, 45th Annual Symposium*, D. P. Corey and S. D. Roper (Editors), Society of General Physiologists, Rockefeller University Press, New York, 225–240.
- Kirschvink, J. L., S. Padmanabha, C. K. Boyce, and J. Oglesby (1997). Measurement of the threshold sensitivity of honeybees to weak, extremely low frequency magnetic fields, *J. Exp. Biol.* **200**, 1363–1368.
- Klinowska, M. (1985). Cetacean live stranding sites relate to geomagnetic topography, *Aquatic Mammals* **11**, 27–32.
- Kobayashi, A., and L. L. Kirschvink (1995). Magnetoreception and EME effects: sensory perception of the geomagnetic field in animals and humans, in *Electromagnetic Fields: Biological Interactions and Mechanisms*, M. Blank (Editor), American Chemical Society Books, Washington, D.C., 367–394.
- Lin, A. M. (1997). Instantaneous-shaking liquefaction induced by the M7.2 1995 Southern Hyogo prefecture earthquake, Japan, *Geology* **25**, 435–438.
- Lindauer, M. (1977). Recent advances in the orientation and learning of honeybees, Presented at the Proc. XV Int. Congr. Entomol., 1976, Washington, D.C., American Society of Entomology.
- Lindenlaub, T., H. Burda, and E. Nevo (1995). Convergent evolution of the vestibular organ in the subterranean mole-rats, *Cryptomys* and *Spalax*, as compared with the above ground rat, *Rattus*, *J. Morphol.* **224**, 303–311.
- Lockner, D. A., and J. D. Byerlee (1985). Complex resistivity of fault gouge and its significance for earthquake lights and induced polarization, *Geophys. Res. Lett.* **12**, 211–214.
- Lockner, D. A., M. J. S. Johnston, and J. D. Byerlee (1983). A mechanism to explain the generation of earthquake lights, *Nature* **302**, 28–33.
- Mann, S., N. H. C. Sparks, M. M. Walker, and J. L. Kirschvink (1988). Ultrastructure, morphology and organization of biogenic magnetite from sockeye salmon, *Oncorhynchus nerka*: implications for magnetoreception, *J. Exp. Biol.* **140**, 35–49.
- McIlroy, D., and G. R. Heys (1997). Paleobiological significance of *Plagiogmus arcuatus* from the lower Cambrian, *Alcheringa* **21**, 161–178.
- Mueller, R. J., and M. J. S. Johnston (1998). Review of magnetic field monitoring near active faults and volcanic calderas in California: 1974–1995, *Phys. Earth Planet. Interiors* **105**, 131–144.
- Ohta, T. (1996). The current significance and standing of neutral and nearly neutral theories, *Bioessays* **18**, 673–677.
- Ohta, T., and J. H. Gillespie (1996). Development of neutral and nearly neutral theories, *Theor. Pop. Biol.* **49**, 128–142.
- Ouellet, M. (1990). Earthquake lights and seismicity, *Nature* **348**, 492.
- Park, S. K. (1996). Precursors to earthquake—seismoelectromagnetic signals, *Surv. Geophys.* **17**, 493–516.
- Park, S. K., M. J. S. Johnston, T. R. Madden, F. D. Morgan, and H. F. Morrison (1993). Electromagnetic precursors to earthquakes in the ULF band: a review of observations and mechanisms, *Rev. Geophys.* **31**, 117–132.
- Pease, J. W., and T. D. Orourke (1997). Seismic response of liquefaction sites, *J. Geotech. Geoenviron. Eng.* **123**, 37–45.
- Phillips, J. B. (1996). Magnetic navigation, *J. Theor. Biol.* **180**, 309–319.
- Randall, J. A. (1997). Species-specific footdrumming in kangaroo rats—*Dipodomys ingens*, *D-deserti*, *D-spectabilis*, *Animal Behav.* **54**, 1167–1175.
- Randall, J. A., and E. R. Lewis (1997). Seismic communication between the burrows of kangaroo rats, *Dipodomys spectabilis*, *J. Comp. Physiol. A* **181**, 525–531.
- Randall, J. A., and M. D. Matocq (1997). Why do kangaroo rats (*Dipodomys spectabilis*) footdrum at snakes, *Behav. Ecol.* **8**, 404–413.
- Reiter, R. J. (1994). The pineal gland and melatonin synthesis: their responses to manipulations of static magnetic fields, in *Biological Effects of Electric and Magnetic Fields: Sources and Mechanisms*, Vol. 1, D. O. Carpenter and S. Ayrapetyan (Editors), Academic, New York, 261–286.
- Roeloffs, E., and J. Langbein (1994). The earthquake prediction experiment at Parkfield, California, *Rev. Geophys.* **32**, 314–336.
- Runnegar, B. (1982). A molecular-clock date for the origin of the animal phyla, *Lethaia* **15**, 199–205.
- Sayced, O., and S. Benzer (1996). Behavioral-genetics of thermosensation and hygrosensation in drosophila, *Proc. Natl. Acad. Sci. USA* **93**, 6079–6084.
- Semm, P., and R. C. Beason (1990). Responses to small magnetic variations by the trigeminal system of the bobolink, *Brain Res. Bull.* **25**, 735–740.
- Shapiro, V. A., and K. N. Abdullabekov (1982). Anomalous variations of the geomagnetic field in East Fregana—magnetic precursor of the Alay earthquake with M 7.0 (1978 November 21), *Geophys. J. R. Astr. Soc.* **68**, 1–5.
- Sieh, K. (1978). Central California foreshocks of the great 1857 earthquake, *Bull. Seism. Soc. Am.* **68**, 1731–1749.
- Sieh, K. (1996). The repetition of large earthquake ruptures, *Proc. Natl. Acad. Sci. USA* **93**, 3764–3771.
- Skiles, D. D. (1985). The geomagnetic field: its nature, history, and biological relevance, in *Magnetite Biomineralization and Magnetorecep-*

- tion in Organisms: A New Biomagnetism, Vol. 5, J. L. Kirschvink, D. S. Jones, and B. J. McFadden (Editors), Plenum, New York, 43–102.
- Smith, R. M. H., P. G. Eriksson, and W. J. Botha (1993). A review of the stratigraphy and sedimentary environments of the karoo-aged basins of Southern Africa, *J. African Earth Sci. Middle East* **16**, 143–169.
- Tichy, H., and R. Loftus (1996). Hygroreceptors in insects and a spider—humidity transduction models, *Naturwissenschaften* **83**, 255–263.
- Torres de Araujo, F. F., M. A. Pires, R. B. Frankel, and C. E. M. Bicudo (1985). Magnetite and magnetotaxis in algae, *Biophys. J.* **50**, 375–378.
- Tributsch, H. (1982). *When the Snakes Awake: Animals and Earthquake Prediction*, MIT Press, Cambridge, Massachusetts, 248 pp.
- Vanderwall, S. B. (1993). Seed water-content and the vulnerability of buried seeds to foraging rodents, *Am. Midland Naturalist* **129**, 272–281.
- Walcott, C. (1978). Anomalies in the earth's magnetic field increase the scatter of pigeon's vanishing bearings, in *Animal Migration, Navigation and Homing*, K. Schmidt-Koenig and W. T. Keeton (Editors), Springer-Verlag, Berlin, 143–151.
- Walcott, C., J. L. Gould, and J. L. Kirschvink (1979). Pigeons have magnets, *Science* **205**, 1027–1029.
- Walker, M. M., and M. E. Bitterman (1985). Conditioned responding to magnetic fields by honeybees, *J. Comp. Physiol. A* **157**, 67–73.
- Walker, M. M., and M. E. Bitterman (1989). Honeybees can be trained to respond to very small changes in geomagnetic field intensity, *J. Exp. Biol.* **145**, 489–494.
- Walker, M. M., J. L. Kirschvink, S.-B. R. Chang, and A. E. Dizon (1984). A candidate magnetic sense organ in the Yellowfin Tuna *Thunnus albacares*, *Science* **224**, 751–753.
- Walker, M. M., J. L. Kirschvink, A. E. Dizon, and G. Ahmed (1992). Evidence that fin whales respond to the geomagnetic field during migration, *J. Exp. Biol.* **171**, 67–78.
- Walker, M. M., C. E. Diebel, C. V. Haugh, P. M. Pankhurst, J. C. Montgomery, and C. R. Green (1997). Structure and function of the vertebrate magnetic sense, *Nature* **390**, 371–376.
- Westphal, J. A., M. A. Carr, W. F. Miller, and D. Dzurisin (1983). Expandable bubble tiltmeter for geophysical monitoring, *Rev. Sci. Instruments*, **54**, 415–418.
- Wiltshcko, R., and W. Wiltshcko (1995). Magnetic orientation in animals, in *Zoophysiology*, Vol. 33, Springer, Berlin, 297 pp.
- Wray, G. A., J. S. Levinton, and L. H. Shapiro (1996). Molecular evidence for deep Precambrian divergences among metazoan phyla, *Science* **274**, 568–573.
- Wyss, M. (1991). Evaluation of proposed earthquake precursors, in *IASPEI Sub-commission on Earthquake Prediction*, American Geophysical Union, Washington, D.C., 94 pp.
- Wyss, M. (1997). 2nd round of evaluations of proposed earthquake precursors, *Pure Appl. Geophys.* **149**, 3–16.
- Wyss, M., and D. C. Booth (1997). The IASPEI procedure for the evaluation of earthquake precursors, *Geophys. J. Int.* **131**, 423–424.

Division of Geological and Planetary Sciences  
 California Institute of Technology 170-25  
 Pasadena, California 91125  
 kirschvink@caltech.edu

Manuscript received 13 July 1998.