life cycle of *Drosophila*. Emergence in *Drosophila*, a nonperiodic event, is controlled by a circadian clock (*21*) localized in the head region (*22*). It is possible that components of the same clock regulating emergence also function in the Malpighian tubules to control the time of appearance of urate oxidase activity in the tubules.

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23. A 5-μl sample of the reaction mixture was removed at 2 minutes and again at 6 minutes after initiation of the reaction with 2-[^{14}C]urate. The amount of [^{14}C]allantoin formed per minute of reaction time was calculated from the difference in disintegrations per minute between the two 5-μl samples.
24. We thank M. Wing for expert technical assistance, and E. Goudsmit, P. Ketchum, and P. Friedman for helpful discussions. This work was supported by funds from the Oakland University Research Committee, an Oakland University Alumni Association undergraduate research grant to D.H.J., and NIH Biomedical Science Support grant 5-07-RR07131.

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Compressional and Surface Waves in Sand: Used by Desert Scorpions to Locate Prey

Abstract. *Loose sand conducts compressional and surface (Rayleigh) waves at relatively low velocities (95 to 120 meters per second and 40 to 50 meters per second, respectively) compared to other natural substrates. For frequencies between 1 and 5 kilohertz, the specific attenuation factor,* Q, *for sand is 18. Compound slit sensilla on basitarsal leg segments of sand-dwelling scorpions respond to surface waves generated by movements of insects as far as 50 centimeters away, and tarsal sensory hairs respond to higher-frequency (mostly compressional-wave) components of the signal.*

The nocturnal sand scorpion *Paruroctonus mesaensis* captures prey with its pedipalps after an abrupt turn and forward movement toward small disturbances of the substrate nearby (*1*). For cricket-sized insects walking on the surface of the sand less than 20 cm away, the scorpion can determine both direction and distance of the prey's location with enough accuracy to consistently place its pedipalps within a few centimeters of the target in a single movement. Two or more movements are usually required to locate prey farther than 20 cm away. The range, accuracy, and speed of localization are such that in three or four orientation movements, lasting about 1 second each, the scorpion can position itself over a burrowing cockroach (*Arenivaga investigata*) that was initially 50 cm away. Thereafter, movements of the cockroach provoke a fast digging behavior from the scorpion that uncovers the prey. Fast and accurate localization of the cockroaches is essential for successful hunting, because these burrowers are also highly sensitive to disturbances of the substrate and respond to a scorpion's approach by burrowing deep into the sand.

Behavioral experiments with scorpions (*1, 2*) have shown that they use information propagated through sand to locate their prey. Natural solids are not considered important avenues of information transfer, since they are generally heterogeneous and inelastic, or the conduction velocity and wavelength of the signals they conduct are too large to convey biologically useful information other than to warn of a disturbing force nearby (*3*). To determine the direction and distance of disturbances several decimeters away, however, the scorpion must sense small changes in some feature (for example, time of arrival, intensity, or frequency) of the signal that activates its spatially separated sense organs.

To identify the signals detected by the scorpion, I measured some of the physical properties of substrate vibrations in desert sand. The results show that, in this medium, biologically useful signals are transmitted as low-velocity surface (Rayleigh) waves (*4, 5*) and compressional body (*P*) waves. Each type of wave is detected by a different sense organ on the legs of the scorpion, and input from one of these receptors is used to determine the direction of the wave source.

Standard techniques for three-dimensional seismic modeling were used to determine the types of waves propagated through sand and the extent to which sand acts as an elastic medium at biologically important frequencies. The model was a Styrofoam box (30 by 50 by 40 cm deep) filled with loosely packed desert sand. Substrate displacement pulses were generated with a piezoelectric crystal on the sand surface, and another piezoelectric transducer (*6*) was used as a receiver.

Two separate waves were distinguished in the seismogram recorded from sand (Fig. 1A) when the receiver was placed at the surface with its movement-sensitive axis oriented radially with respect to the vibration source. The first wave to arrive at the receiver had a short period (about 0.5 msec). It was followed by a slower surface wave of longer period (1.2 to 1.5 msec). The amplitude of the fast wave was diminished and the amplitude of the slow wave was increased when the movement-sensitive axis of the receiver was oriented perpendicular to the surface. When the receiver was oriented so as to be sensitive to transverse displacements, neither wave was recorded. If an absorbant object (for example, my hand or a rubber brick) was placed on the surface between the source and receiver, the slow wave diminished in amplitude or disappeared without change in the fast wave. The amplitude of the slow wave progressively diminished to zero as the receiver was placed at increasing depths (down to 3 cm) below the surface.

These characteristics of the fast and slow waves suggest they are, respectively, the analogs of *P*- and Rayleigh waves observed in other solid materials (*5*). I did not observe waves with the properties of shear and Love waves when I used these source-receiver geometries.

The conduction velocities of *P*- and Rayleigh waves in loose sand are about one-tenth their values in other natural substrates. The *P*-wave velocity varied between 95 and 120 m/sec at the surface depending on the degree of compaction, and 120 to 150 m/sec at various depths to 30 cm below the surface (*7*). The velocity of the Rayleigh wave was measured at 40 m/sec, on the basis of the migration of reproducible peaks in the receiver output as the source-to-receiver distance was varied (*8*). In lightly tamped sand the velocity increased to about 50 m/sec.

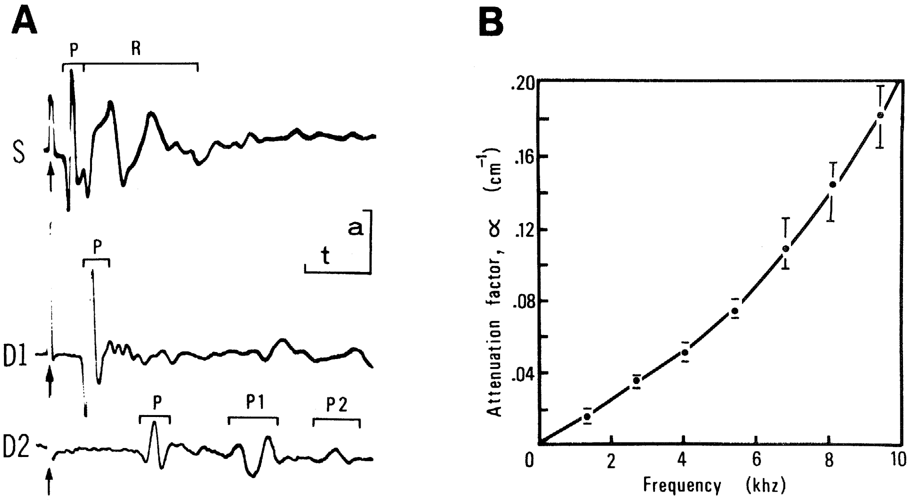

Fig. 1. Propagation of compressional (*P*) and Rayleigh (*R*) waves in sand. (A) A displacement pulse from a piezoelectric transducer on the surface generated waves that were detected by a receiver on the surface 5 cm away (*S*), and at depths of 6 cm (*D1*) and 19.5 cm (*D2*) in the sand directly below the source. For the surface recording (*S*), the source displacement was generated by a square voltage pulse of 50 volts for 100 μsec. The electromagnetic artifact (arrow) from the source pulse was followed by a fast, short-period *P*-wave and slower, longer-period surface waves (*R*). In the recordings from receivers below the surface, the electromagnetic artifact was followed only by the *P*-wave and its reflections. The *P*-wave was delayed (conduction velocity, 138 m/sec) and attenuated by the 13.5 cm of sand between the subsurface receivers at *D1* and *D2*. In *D2*, spreading of the *P*-wave was evident in its first reflection (*P1*) from the bottom of the model and the second reflection (*P2*) from the sand surface. The displacement pulse in *D1* and *D2* was generated by a pulse (150 volt, 10 μsec) applied to the transducer. Time (*t*) calibration: *S*, 2 msec; *D1*, *D2*, 1 msec. Amplitude (*a*) calibration: *S* and *D1*, 400 μv; *D2*, 200 μv. (B) Frequency-dependence of the attenuation coefficient α. At each measured frequency the best estimate of α was plotted as a dot with the range of possible values represented by vertical bars. As frequency increased to 5 khz, α increased linearly (Q = 18).

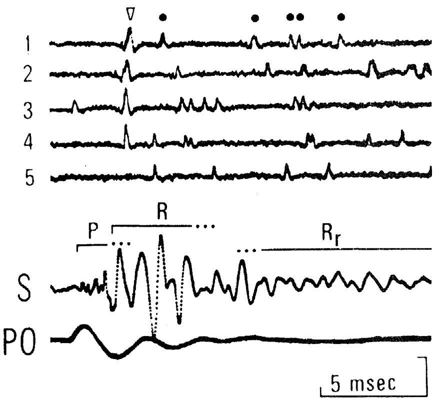

Fig. 2. Response of the scorpion's tarsal mechanoreceptors to waves in sand. The voltage output of a photocell (*PO*) monitored movements of an electromagnetically driven probe used to disturb the sand. The waves produced by the disturbance were recorded by a piezoelectric receiver (*S*) (displacement-sensitive axis perpendicular to surface) on the surface of the sand 10 cm from the vibration source. The tarsal segment of the leg also rested on the sand 10 cm from the source. At this distance, both the tarsal hairs and the compound slit sensillum responded to the waves. In differential recordings from platinum wires (25 μm diameter) implanted through the leg cuticle 1 mm proximal (negative input to the amplifier) and 1 mm distal (positive input) to the slit sensillum, action potentials from the tarsal hairs were recorded as large triphasic potentials (∇) and action potentials from the slit sensillum appeared as small monophasic potentials (•). Traces 1 to 5 are successive responses to repetition of the stimulus. In trace 3, a spontaneous slit sensillum potential preceded the stimulus. Most of the 2-msec delay between the front of the *P*-wave complex (*P*) and the first neural response is lag time between the displacement of the tarsus and the appearance of action potentials at the recording electrodes. Abbreviations: *R*, Rayleigh wave complex; R_r, Rayleigh waves reflected from the sides of the model. Amplitude calibration: *S*, 500 μv; *PO*, 20 μm.

The low conduction velocity of *P*- and Rayleigh waves enable sand-dwelling animals to determine the direction of a vibration source from the time delay between arrival of the waves at widely spaced sense organs. In *P. mesaensis* the critical sense organs for detection of substrate vibrations are on the distal segments of their legs. For an adult scorpion in a hunting stance, the contact points of the distal segments with the substrate form a stereotyped circular array 5 cm in diameter (*1*). For this distance, the time delay between the arrival of the surface wave at near and far tarsi (relative to the source) is about 1 msec, regardless of source direction, and about 0.4 to 0.5 msec for the compressional wave delay. When the arrival time of a signal at opposed legs was controlled with vibration sources on opposite sides of a scorpion, it responded appropriately to delays of 0.2 msec but was most sensitive to delays of 0.8 to 1.5 msec (*1*). Thus, the direction of a wave source can be determined from the temporal pattern of leg stimulation by either wave, although other results (below) suggest that the slower surface wave is critical.

For biologically useful signals to be conducted through sand for any distance, the attenuation of frequencies in the 0.1- to 5-khz band must be small, as this is the range of greatest sensitivity for most mechanoreceptors (*3*). In homogeneous media the amplitude of a propagated signal decreases as a result of (i) geometric spreading, $G(d)$, and (ii) frequency-dependent absorption and scatter by the medium. The latter value is expressed as an exponential of the attenuation function, $\alpha(\omega)$, where ω is angular frequency. The amplitude spectrum $A(d,\omega)$ of a signal at distance d from its source is the product of these two loss factors and the amplitude excitation spectrum at the source, $A(0,\omega)$:

$$A(d,\omega) = A(0,\omega)G(d)e^{-\alpha(\omega)d}$$

For compressional waves in an elastic medium such as air, α is effectively zero at frequencies below 5 khz, so all signal attenuation is attributable to spreading of the wave (for example, at distances greater than a few wavelengths, $G(d) = d^{-1}$ for spherically diverging sound waves in air).

To determine the compressional wave attenuation factor for sand, I performed a spectral analysis of *P*-wave pulses recorded at various depths (6 to 30 cm, at 3-cm intervals) beneath a wave source located on the surface (*9*). Subsurface recordings were chosen to reduce noise and to avoid interference from surface waves. The oscillograms of the *P*-wave pulses were digitized and subjected to numerical Fourier analysis. The normalized amplitude spectrum for each pulse was multiplied by distance to correct for loss resulting from spherical geometric spreading, and the corrected amplitudes of the various frequency components of the pulses were plotted semilogarithmically against distance. The values of α obtained from the slopes of these plots were replotted against frequency (Fig. 1B).

The attenuation factor for sand increases linearly with frequency between 1 and 5 khz. In this band the specific attenuation factor (*10*), Q, for sand was 18 (that is, $Q = \omega/2\alpha c$, where $c = 140$ m/sec). At frequencies above 5 khz, there was a progressive nonlinear increase in α that can be attributed to scatter (*10*), since the wavelengths at these frequencies ($\lambda_{5\text{khz}} = 23$ mm) had decreased to about ten times the diameter of sand grains (1.5 to 3.0 mm) used for the model. Because scattering of the signal by the medium occurs outside the range of greatest mechanoreceptor sensitivity, it should not seriously limit conduction of information through sand. Below 5 khz, frequency-dependent absorption by the medium is sufficiently small (less than 1 db/cm) that most of the attenuation of signals conducted a few decimeters from their source is due to the geometric spreading factor as in highly elastic media.

Thus, for vibration-sensitive animals on the surface, the Rayleigh wave should become the only detectable energy with increased distance from a wave source, inasmuch as $G(d)$ is less for cylindrically spreading surface waves [where $G(d) = d^{-1/2}$] than for spherically spreading compressional waves [$G(d) = d^{-1}$] (*11*). This is particularly true for disturbances at the surface of the sand, since most of the vibrational energy at the source of these signals propagates away as a surface wave (*12*).

Evidence to support this hypothesis was provided by electrophysiological experiments with the scorpion. Two types of mechanoreceptors located at the end of each walking leg of the scorpion respond to the waves that propagate through sand. These sense organs are the hairs that support the tarsus on the surface of the sand and a group of eight slit sensilla (the basitarsal compound slit sensillum) (*13*) located on the cuticle that forms the socket of the last leg joint. In electrical recordings from platinum wires permanently implanted in the tarsal leg segments, each sense organ had a characteristic action potential which I identified by selective stimulation, ablation of the critical sense organ, and by locating the origin of the extracellular field potential for each type of spike. It was possible, therefore, to simultaneously record waves produced by disturbances of the sand and the neural responses these waves evoked from each type of receptor.

Waves from a uniform source of substrate vibrations were recorded by a receiver on the surface of the sand 10 cm away (Fig. 2). The form and intensity of the disturbance were adjusted to simulate components of the vibration generated by the burrowing cockroach (*14*). When a scorpion was positioned near the receiver so that a tarsus with implanted electrodes also rested on the sand 10 cm away, both sense organs responded to the stimulus (Fig. 2, traces 1 to 5). Action potentials from the tarsal hairs appeared first in the neural records and were associated with the arrival of compressional waves at the receiver. These were followed by action potentials from the basitarsal compound slit sensillum which were excited by surface waves.

Both sense organs were strongly activated by the simulated cockroach disturbance when it was presented 5 cm from the tarsus. At 10 cm distance the tarsal hairs occasionally failed to respond (Fig. 2, trace 5), and from 20 cm away they were never excited. Over the same distance, however, the intensity of the slit sensillum response to the surface wave was relatively constant, with some slits being excited from as far as 50 cm. The surface wave, therefore, is the only signal detected by the scorpion at long distances from the vibration source.

In their natural environment, scorpions determined the direction of burrowing cockroaches from 50 cm away. The slit sensilla were the only sense organs activated by the simulated cockroach disturbance at 20 to 50 cm distance, so their input must be used to determine direction of the vibration source. The critical role of the slit sensilla in locating the direction of the source is supported by behavioral observations of scorpions with ablated sense organs (*1*). A single pin hole 250 μm in diameter through the cuticle of the basitarsal slits on some or all of the eight legs systematically altered the accuracy of the orientation response to local disturbances of the substrate, whereas removal of tarsal sensory hairs had no effect (*15*).

The role of the tarsal hairs in localization remains unresolved. The sensitivity of the hairs to compressional waves might enable scorpions to determine distance of a wave source, however, since two waves with different conduction velocities are detected by separate sense organs. Thus, as the distance of the source from the scorpion increases, so should the time delay between the tarsal hair response to the early-arriving *P*-wave and the slit sensillum response to the late-arriving Rayleigh waves.

Sand is a solid medium that favors transmission of biologically useful information. These experiments with scorpions and some other behavioral observations (*1*) of insects (burrowing cockroach; larval antlion, *Paranthoclisus sp.*; sand-treader cricket, *Macrobaenetes valgum*) suggest that sand-dwelling arthropods may commonly use this source of information. Other granular and consolidated substrates are acoustically similar to sand, and many organisms, particularly arthropods, are sensitive to 1- to 100-Å displacements at the frequencies transmitted by these substrates (*3*). In view of this sensitivity of mechanoreceptors and other results reported, the possibility that critical information is transferred through the substrate should be considered in behavioral studies of animals in contact with solid substrate.

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6. Lead/zirconium/titanate disk (1 by .01 inch, Gulton Industries, model G1500).
7. These values are comparable to earlier measurements of the velocity of the *P*-wave in sand with small static loads applied to the surface [E. Matsukawa and A. Hunter, *Proc. Phys. Soc. London Sect. B* **69**, 847 (1956)].
8. Such a measurement assumes that velocity dispersion of the Rayleigh wave was negligible, that is, that the body-wave velocities do not vary significantly in the depth range of Rayleigh-wave penetration. I estimate this penetration to be about 2 cm before the amplitude diminishes to 10 percent of its surface value. As the *P*-wave velocity was constant down to 4 cm depth, dispersion of the Rayleigh wave was probably negligible.
9. Attenuation of the Rayleigh wave with distance could not be measured as a result of the inconstancy of the receiver-model coupling at the surface, and interference from the *P*-wave and its reflections.
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14. All surface disturbances of the sand (a single pulse from a piezoelectric transducer and walking and burrowing movements of insects) produced one or a series of wave pulses. Each pulse contained a burst of early-arriving, short-period *P*-waves followed by late-arriving, longer-period Rayleigh waves (Figs. 1 and 2).
15. These ablations did not alter normal ambulatory movements or the accuracy of the turning response to direct tactile stimulation of the tarsi. Thus, it is unlikely they interfered with motor control mechanisms for turning.
16. I thank Drs. R. Farley and F. Schwab for assistance in design and execution of this work. I also thank them and Drs. H. Shorey and S. Beihler for critical reading of manuscripts. An Environmental Sciences predoctoral fellowship partially supported this research.

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Childhood IQ's as Predictors of Adult Educational and Occupational Status

Abstract. *IQ's between 3 and 18 years of age were used to predict attained education and occupational status after 26 years of age. By the second grade these predictive correlations approached those that have been obtained with contemporaneous adult IQ's, especially for occupational status. However, they were not high enough for practical purposes requiring long-term prediction for individual normal children.*

Many uses of intelligence tests scores (IQ's) are based on the assumption that children's IQ's reveal something of their adult potential for educational and occupational success. But do the tests predict well enough to be used in that way? Jencks and his colleagues (*1*) recently reviewed the sparse evidence on the predictive validity of IQ tests and found that the correlations between school-age IQ and indices of adult educational and occupational success rarely exceed .60, not high enough for practical purposes requiring long-term prediction. Below we examine evidence on this issue from the Fels Longitudinal Study.

While many of the correlations reviewed by Jencks were based on large samples representing a wide spectrum of socioeconomic classes, often only dichotomous indices of educational or occupational attainment were used (for instance, blue versus white collar), the tests typically had been given at only one age during childhood, and data were often available only for males. The Fels sample contains families from the top 85 percent of the socioeconomic scale and is somewhat skewed to the right in educational attainment, but it has the advantage that parents and children of both sexes were assessed, over a wide age range, with more accurate procedures than has been typical of many previous reports. An important result of the research reported here is its general consistency with the data reviewed by Jencks.

All Fels subjects who had reached at least 26 years of age, about whom sufficient information was available to determine a Hollingshead scaled score for attained adult education and occupation (*2*), and who had had at least one IQ determination between 3 and 18 years of age were included in the sample. There were 94 males and 96 females who qualified, and correlations with later attainment could be determined from childhood IQ's at each of 16 ages, based upon 46 to 90 subjects of each sex.

These subjects were born between 1930 and 1943. They scored somewhat above average in IQ (mean of 117, varying somewhat with age) but with average variability (S.D. = 15.9). Of the females, 3 percent had not graduated from high school, 31 percent had gone through high school but not beyond, and 34 percent graduated from college. The comparable figures for males were 1 percent, 22 percent, and 56 percent. Further details of this subject population are given elsewhere (*3, 4*).

The mental test data available included Pinneau corrected Stanford-Binet IQ (1937) scores at 3, 3½, 4, 4½, 5, 5½, 6, 7, 8, 9, 10, 11, and 12 years (forms L and M were given at alternate ages), Wechsler-Bellevue full-scale IQ at 13 and 16 years, and the total scores from the Primary Mental Abilities (PMA) test at 18 years. Cross-age correlations indicated that the Binet and the Wechsler tests were quite similar to each other but somewhat different from the 18-year PMA, though the PMA is probably as faithful a measure of

Fig. 1. Correlations of childhood IQ at various ages with attained adult educational and occupational status (Fels sample) and with IQ at age 40 years (Child Guidance sample). Also, correlation of fathers' and mothers' education with offsprings' adult occupational (open square) and adult educational (filled circle) status.