lost during the processing of some infant formulations[10], thus some bottle-fed infants may be receiving a diet marginally deficient in biotin.

The findings do not suggest that SIDS results from biotin deficiency alone, but, by analogy with chickens, we postulate that biotin insufficiency may leave the infant in a condition in which SIDS can be triggered by mild stress, for example infection, a missed meal, excessive heat or cold, or a changed environment. The evidence to date is circumstantial and it would be difficult to provide 'unequivocal proof' linking biotin, or for that matter any nutrient, with SIDS because of the difficulties in undertaking biochemical studies with experimental and control subjects.

Epidemiological techniques will have to be used and if our recommendation to supplement infant formulas with biotin[10] is implemented, the subsequent trends in the incidence of SIDS may enable the existence of any association to be evaluated more effectively.

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The role of gastropod pedal mucus in locomotion

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Gastropods move using a single appendage—the foot. For many gastropods the power for locomotion is provided by muscular waves moving along the ventral surface of the foot[1–3], the force of these waves being coupled to the substratum by a thin layer of pedal mucus. This mucus acts as a glue, allowing the animal to adhere to the substratum on which it crawls[2,3]. This adhesive ability is advantageous, particularly to animals (such as limpets and certain snails) which live in intertidal or arboreal habitats where the forces of waves and gravity must be resisted while the animal forages. However, the adhesiveness of the pedal mucus presents the animal with a problem. How can an animal with only one foot walk on glue? This question was studied using as an example the terrestrial pulmonate slug, *Ariolimax columbianus*, and locomotion is found to depend on the unusual mechanical properties of the pedal mucus.

The pedal mucus of *A. columbianus* is 96–97% water and dissolved salts[4]. The relevant mechanical properties of the material are determined by the remaining 3–4% which is a high molecular weight glycoprotein. The glycoprotein, a polyelectrolyte, is highly expanded in water, and individual molecules are crosslinked to form a gel network[4]. The presence of this crosslinked network accounts for any elasticity shown by the mucus[5,6]. The nature of the crosslinks was determined by examining the material's solubility. The glycoprotein network is not readily soluble in water, but is soluble in 1% 2-mercaptoethanol and in 8 M urea or 8 M guanidine HCl. Solubility in 1% 2-mercaptoethanol indicates the presence of disulphide bonds as network crosslinks[7], formed between the cysteine molecules which comprise 3% of the amino acids of the protein chains. Solubility in 8 M urea or 8 M guanidine HCl is evidence of the presence of a second form of network crosslink—hydrogen bonds and/or hydrophobic interactions between carbodydrate chains[7].

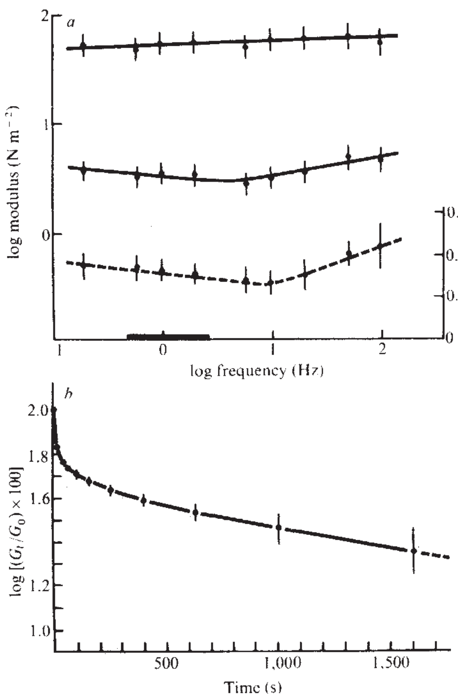

Fig. 1 Network properties of pedal mucus. [Stress is force divided by area (Nm^{-2}); shear strain is shear deformation divided by sample thickness[6].] *a*, The dynamic stiffness of *A. columbianus* pedal mucus at small strains. Results shown are the average from six samples tested in air at 100% relative humidity, 22–23 °C. The bars are 95% confidence intervals. Tests are performed by applying a sinusoidal strain ($\gamma = 0.2$ to 0.5) and measuring the resulting stress. Stress amplitude/strain amplitude is G^*, the complex modulus, a measure of the material's stiffness at a given frequency[6]. The phase shift between strain and stress (δ) is a measure of the relative viscous and elastic contribution to $G^*: G'$, the storage modulus, $=G^* \cos\delta$, and is a measure of elastic stiffness. G'', the loss modulus, $=G^* \sin\delta$, and is a measure of viscous stiffness. The ratio G''/G' is $\tan\delta$. The parallel plate dynamic apparatus (from ref. 8), was modified to test samples in shear rather than in tension. The bar on the abscissa shows the approximate range of frequencies at which the mucus is deformed under a crawling slug. *b*, The stress relaxation behaviour of *A. columbianus* pedal mucus. In the relaxation tests a sample is quickly deformed to a set strain and the force required to maintain that strain is followed with time. The curve shown is the average of 10 tests carried out in air at high relative humidities, 21–23 °C. The bars are 95% confidence intervals. Values on the ordinate are the ratio of the shear modulus at time $t(G_t)$ to the shear modulus at the start of the test (G_0), plotted as the logarithm. No small set of relaxation times adequately describes this relaxation behaviour.

The mechanical properties of the mucus at small shear strains, γ, (Fig. 1 legend) were measured in a parallel plate dynamic testing apparatus (modified from Gosline[8]). This apparatus allows the elastic (G') and viscous (G'') components of the material's dynamic stiffness (G^*) to be measured as a function of the frequency of deformation. At small deformations ($\gamma < 5$) the pedal mucus shows the properties of a soft, primarily elastic solid (Fig. 1*a*). G' is 100 N m^{-2} (10^{-4} times the stiffness of rubber) and G'' is about 8 Nm^{-2}. Both values are virtually constant from 0.1

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to 100 Hz. The stress relaxation properties of the mucus were measured at small strains ($\gamma < 5$) with a cone and plate apparatus in which the mucus is held between a small angle acrylic plastic cone and a coaxial aluminium plate. Rotation of the plate by an electric motor shears the mucus, and the consequent force is measured by monitoring (with a linearly variable differential transformer) the torsion of the bar supporting the cone. The theory of this apparatus is described by Ferry[6]. The gel stress relaxes without reaching equilibrium (Fig. 1*b*), indicating[6] that the network crosslinks, while stable over short times encountered during dynamic testing (milliseconds to seconds), are labile under stresses applied for long periods (minutes to hours).

These mechanical properties, although representative of the mucus at small strains, will not necessarily apply if higher strains are encountered during locomotion. The thickness of the mucus layer (measured by a method similar to that used by Lissman[9] for slugs crawling on aluminium foil) is typically 10–20 μm. The surface of the foot of *A. columbianus* moves forward about 1 mm with each wave; and the strain is thus 50–100, considerably higher than that used in the tests described above.

The properties of the pedal mucus at large strains were measured with the cone and plate apparatus. At $\gamma = 5$ to 6 the mucus network is disrupted and the material yields (Fig. 2*a*). With further extension the mucus shows the properties of a viscous liquid. The magnitudes of the yield stress (σ_y) and the

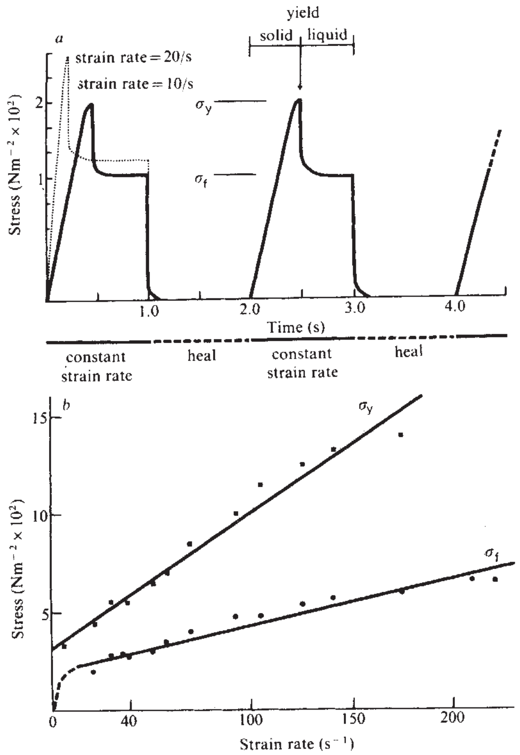

Fig. 2 Properties of pedal mucus under simulated natural conditions. *a*, Mechanical properties of *A. columbianus* pedal mucus at high strains. The abscissa is calibrated in seconds, where for alternate periods the mucus is sheared at a constant strain rate and held stationary. The mucus is thus exposed to conditions analogous to those found under a crawling slug. When first sheared, stress is proportional to strain, indicating that the mucus is an elastic solid. At a strain of 5–6 (stress = σ_y) the mucus yields. With further strain stress is proportional to strain rate, that is, the mucus behaves as a liquid. When shearing is stopped the mucus begins to heal. The healing period of 1 s represents the time the mucus is unsheared beneath an interwave during locomotion. Yield stress and flow stress both increase with increasing strain rate; yield strain is constant. *b*, A representative plot of yield stress (σ_y) and flow stress (σ_f) as a function of strain rate. The range of strain rates is approximately that found under crawling slugs. While σ_f is linearly related to strain rate at the rates measured, it is assumed to have a nonlinear behaviour (shown by the dashed line) at strain rates below those measured in these tests. [σ_y: $y = 6.9x + 313$; $r = 0.986$. σ_f: $y = 2.3x + 199$; $r = 0.971$]

flow stress (σ_f) increase with increasing strain rate (Fig. 2*b*), while the yield strain does not vary with strain rate. If, after the mucus has yielded, the material is allowed to stand unstressed, the mucus will 'heal' that is, as the mucus stands the gel network reforms, and the material again shows the properties of an elastic solid. The mucus can be shown[4] to regain appreciable solidity in times as short as 0.1 s. This 'yield–heal' cycle can be repeated 20 to 30 times without change in either σ_y or σ_f. The precise mechanism of the healing process is not known, though it seems likely that it involves the easily reformed hydrogen and/or hydrophobic bonds of the gel network rather than the covalent disulphide bonds.

The yield–heal characteristics of this mucus are ideally suited to the locomotion of *A. columbianus*. During locomotion 12 to 17 muscular waves are present on the slug's foot; each wave being an area of forward motion, initiated at the posterior end of the animal as the tail is pulled forward. A wave is translated anteriorly until it reaches the head of the animal where it is dissipated as the head moves forward. In a small area (50–100 μm long anterio-posteriorly) at the leading edge of a wave the mucus is stressed to yielding; consequently most of the wave area moves over mucus in its liquid form. This liquid offers little resistance to movement. The waves alternate with interwaves, these being stationary relative to the ground. The mucus beneath the leading edge of the interwave quickly heals, and most of the interwave rests on mucus in its solid form. If the shear strength of the solid mucus (σ_y) is sufficient to resist the forces produced by the movement of the waves, the animal will be able to crawl forward. The mechanical properties reported here can be combined with precise measurements (from video tapes) of foot movements and areas to produce a model of the forces operating under a moving slug. The model predicts that the mucus beneath the interwaves is indeed capable of resisting wave forces, and these predictions prove accurate when compared to those forces actually measured under *A. columbianus* crawling horizontally[10]. Thus the yield–heal cycle of the pedal mucus allows it to act as a material ratchet, facilitating forward movement, but resisting backward movement. The result is effective adhesive locomotion.

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Inhibitory effect of prolactin on ovulation in the *in vitro* perfused rabbit ovary

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Prolactin is best known for its effects on the breast, promoting mammary growth and lactation. In some species, including rat, mouse, hamster, sheep and rabbit, prolactin is necessary for the maintenance of the corpus luteum[1–5]. Further, a relationship has

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