this pattern: (i) If a female is in her natal group and a male who was reproductively active when the female was born is still in the group, the female does not breed. (ii) Once a female disperses, she breeds. (iii) Birds disperse alone or in unisexual units only.

That these rules may also be sufficient to account for the pattern of inbreeding avoidance is suggested by two types of rare anomalies which have led to possible inbreeding. First, by rule (i) above group offspring are inhibited from reproduction by their parent of the opposite sex. But siblings may inbreed if the parents of a bisexual set of offspring both die at about the same time (observed once). Second, by rules (ii) and (iii), the probability of relatives of both sexes moving to new groups and breeding together outside their natal territory is reduced. But, individuals of common group origin have been observed to immigrate separately to the same group and subsequently to breed together (observed twice). A mating between siblings is presumably as deleterious as that of parent-offspring incest (both result in an equivalent degree of inbreeding). However, the conditions leading to the former are apparently so unusual that no mechanism has evolved to avoid it on the rare occasions when the opportunity arises.

Another consequence of the acorn woodpecker's mating system is that group offspring are frequently not full siblings, even when all have fledged from the same nest. This will be the case whenever communal nesting occurs, even if the females themselves are closely related. This diminution of relatedness between siblings will be further accentuated if more than one male breeds in a group. Such promiscuity within groups means that nonbreeding nest helpers (group offspring still in their natal group) are *less* closely related to subsequent siblings whom they help to feed than a hypothetical helper in a permanently territorial monogamous species, where siblings more often share both parents even when born in successive broods (*13*). Similarly, individuals in unisexual sibling units of the acorn woodpecker who immigrate together and ultimately nest communally are likely to share fewer of their genes than siblings in monogamous societies. Thus, our data reveal mechanisms that lower the genetic relatedness between cooperating individuals by promoting multiple parentage of nest helpers, a phenomenon not previously predicted to occur among cooperative breeders (*14*).

These results support the findings of others in pointing out some of the complexities underlying social organizations that superficially seem to entail considerably reduced gene flow and low effective population sizes (*15*). In the case of the acorn woodpecker, the apparent stability of family groups is deceiving; specific behavioral mechanisms, detectable only in long-term study of banded individuals, act to reduce inbreeding. Genetic heterogeneity within social units is thus maintained despite their communality in nesting.

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1. See, for example, S. L. Vehrencamp, *Science* **197**, 403 (1977) and references cited therein.
2. M. H. MacRoberts and B. R. MacRoberts, *Ornithol. Monogr.* **21**, 1 (1976).
3. W. D. Koenig, thesis, University of California, Berkeley (1978). Birds were individually color-banded and many were fitted with plastic wing streamers. Histories of 477 birds have been followed since 1971, when banding was begun. Our work, based on 68 nest histories, was conducted between July 1974 and September 1978. Some data were also drawn from 24 earlier such histories (*2*). Hastings Reservation is located 30 miles southeast of Monterey in central coastal California.
4. In birds, the minimum interval between eggs laid by a single female is 1 day [D. Lack, *Ecological Adaptations for Breeding in Birds* (Methuen, London, 1968), p. 187].
5. The latter is significantly larger (Mann-Whitney U test, $n_1 = 17$, $n_2 = 3$, U = 0, $P < .01$).
6. Mann-Whitney U test, $n_1 = 17$, $n_2 = 12$, U = 66, $P > .10$.
7. Mann-Whitney U test, $n_1 = 17$, $n_2 = 2$, U = 0, $P < .05$.
8. Mann-Whitney U test, $n_1 = 12$, $n_2 = 2$, U = 0, $P < .05$.
9. We also have evidence that male group offspring may suffer reproductive inhibition in the presence of their mothers.
10. Intrasexual subordinance has been implicated as being responsible for reproductive inhibition in the Australian magpie *Gymnorhina tibicen* [R. Carrick, *U.S. Dep. Inter. Wildl. Res. Rep.* **2**, 41 (1972)], and has been shown to result in inhibition of sexual maturation in other natural populations of vertebrates [R. Borowsky, *Science* **201**, 933 (1978)].
11. Mann-Whitney U test, $n_1 = 17$, $n_2 = 5$, U = 0, $P < .001$.
12. See Y. Yom-Tov, G. M. Dunnet, A. Anderson, *Ibis* **116**, 87 (1974).
13. W. D. Koenig and F. A. Pitelka, in *Natural Selection and Social Behavior: Recent Research and New Theory*, R. D. Alexander and D. W. Tinkle, Eds. (Chiron Press, New York, in press).
14. R. E. Ricklefs, *Ibis* **117**, 531 (1975); J. L. Brown, *Annu. Rev. Ecol. Syst.* **9**, 123 (1978).
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16. We thank A. B. Clark, J. Davis, J. R. Griffin, W. J. Hamilton III, T. Kaehler, R. L. Mumme, J. P. Myers, J. L. Patton, P. W. Sherman, S. L. Vehrencamp, and P. L. Williams for comments and assistance. M. H. MacRoberts and B. R. MacRoberts provided help getting our work started. Supported in part by an NSF predoctoral fellowship, an NSF aid-to-dissertation grant, and NSF grant DEB 78-08764.

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Parabolic Flight: Loss of Sense of Orientation

Abstract. *On the earth, or in level flight, a blindfolded subject being rotated at constant velocity about his recumbent long body axis experiences illusory orbital motion of his body in the opposite direction. By contrast, during comparable rotation in the free-fall phase of parabolic flight, no body motion is perceived and all sense of external orientation may be lost; when touch and pressure stimulation is applied to the body surface, a sense of orientation is reestablished immediately. The increased gravitoinertial force period of a parabola produces an exaggeration of the orbital motion experienced in level flight. These observations reveal an important influence of touch, pressure, and kinesthetic information on spatial orientation and provide a basis for understanding many of the postural illusions reported by astronauts in space flight.*

Many sensory channels provide information about body orientation. Normally, these representations are concordant and specify the same relations of the body to the environment. We describe here the dynamic sensory interactions that determine apparent posture when the body is exposed to increases and decreases in gravitoinertial force while horizontal and being rotated about its long body axis, the *Z* axis. These observations indicate that when touch and pressure stimulation and vision are denied during exposure to free fall, all sense of orientation to the environment may be lost. They also provide a basis for understanding many of the postural and sensory illusions experienced by astronauts and cosmonauts during orbital space flight.

Several receptor systems transduce information about acceleration. The semicircular canals respond to angular accelerations and are activated minimally or not at all when one is rotated at constant velocity about his horizontal *Z* axis. The otolith organs respond to linear acceleration and are dynamically active during horizontal *Z*-axis rotation under normal gravitational conditions, because they are being continually reoriented in relation to the gravitoinertial force vector. The pressure on the surface of the body also changes systematically during rotation as a consequence of the contact forces of support provided by the me-

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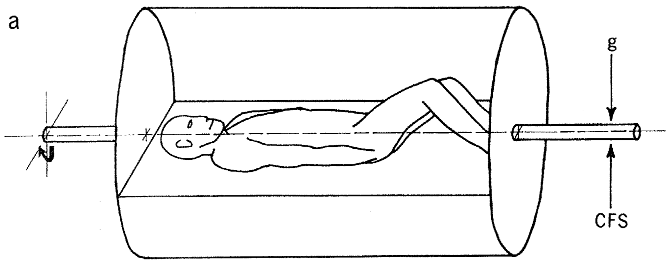

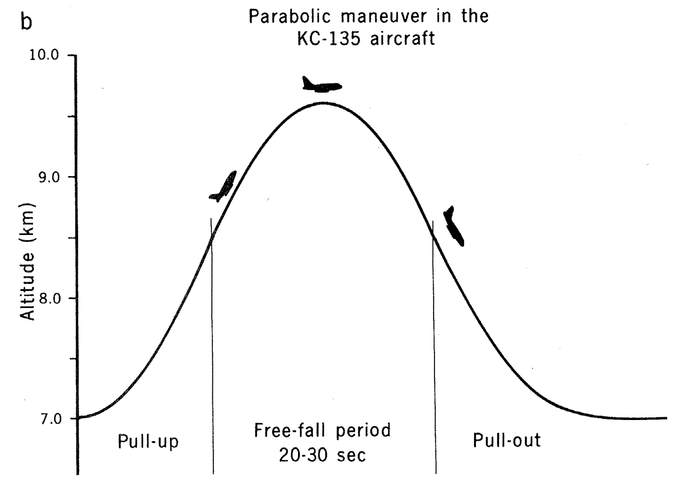

Fig. 1. (a) Schematic illustration of the forces acting on the subject's body during rotation at constant velocity about his horizontal Z axis. The force of gravity (g) is opposed by the contact forces of support (*CFS*) provided by the body mold (not illustrated) in which the subject is encased and restrained. (b) Flight profile of the KC-135 aircraft during a parabolic maneuver to generate periods of free fall (zero gravity).

chanical apparatus in opposing the action of gravity and thereby preventing the body from being accelerated to the ground as it rotates. Figure 1a illustrates the experimental situation.

During clockwise rotation about the horizontal Z axis, the pattern of pressure on the body surface changes in a counterclockwise direction in relation to the body; simultaneously, the otolith organs signal clockwise rotation of the body about the Z axis. At angular velocities less than 6 to 10 rev/min, a blindfolded subject's apparent orientation is determined largely by the otolith signals and he experiences clockwise rotation of his body. However, at higher angular velocities, his apparent posture is determined by the patterns of pressure cues and he experiences counterclockwise orbital motion without rotation of his body. The changing contact forces on the subject's body are perceived as preserving his orbit and preventing him from being thrown out of the apparatus (*1*). The subject experiences one complete circuit of his apparent orbit each time his body actually rotates once. As he goes through his apparent counterclockwise orbit, if there is a continuous sound source that is stationary in the test chamber and just lateral to his head, he will hear the sound as circling his head in a counterclockwise orbit (*2*). If the subject changes the pressure on his body surface by bracing himself in the apparatus, he usually experiences a change in his apparent orientation; for example, pushing down with his feet may make him feel upright as he goes through his counterclockwise orbit. When unrestricted vision is permitted during rotation, sounds are localized correctly and the body is experienced as turning over completely in the true direction of rotation although it feels displaced somewhat from the center of rotation (*3*). Figure 2a shows the relationship between the subject's true and experienced motion during Z-axis rotation.

The foregoing observations were made during the course of experimental studies of motion sickness. As part of this program we had the experimental apparatus, the Z-axis recumbent rotator (ZARR) (*4*), aboard the Johnson Space Center's KC-135 aircraft while it performed parabolic flight maneuvers to generate alternate periods of "zero gravity" (free fall) and "supragravity" (≈ 1.8 g) (*5*). The flight profile is illustrated in Fig. 1b. Four individuals rode the ZARR during these flights, including one of the authors, who rode it three times; each flight involved 40 maneuvers.

Before the parabolic maneuvers, during straight and level flight, the subject was positioned in the ZARR, blindfolded, and accelerated to a clockwise angular velocity of 30 rev/min, which was maintained throughout the flight. At this time, the subject experienced counterclockwise orbital motion with his head and body always facing the same direction; his eyes also exhibited the periodically reversing nystagmus that is present during ground-based rotation (*6*).

As the aircraft entered a parabola and the gravitoinertial force began to increase, each subject experienced his counterclockwise orbit as expanding until it reached its maximum size during the peak force load of approximately 1.8 g. Each subject estimated that the diameter of his orbit had about doubled and that his orbital velocity had also doubled. One complete revolution of the body in 1.8 g corresponded to a complete traverse of the apparent orbit, just as on the ground. Eye movement recordings indicated that both the frequency and the amplitude of nystagmus increased during supra-g. A sound source that was stationary in the aircraft and lateral to the subject's head as he rotated was heard as moving in a counterclockwise orbit around his head; the diameter of this orbit did not change when the subject's own apparent orbit doubled during 1.8 g.

When the force load began to decrease from 1.8 to 0 g the diameter of the subject's apparent orbit diminished, until at ≈ 0.2 g he no longer experienced any motion at all; moreover, for the entire weightless (free fall) period, the subject felt absolutely stationary. He generally could not tell whether he was upright, horizontal, or upside down; his position in relation to the aircraft (and the ground) often seemed indeterminate. Occasionally, a subject would feel oriented in the direction last experienced during his apparent orbital motion; for example, if in > 0.2 g he had experienced a counterclockwise orbital motion of his horizontal body with his head facing down, then in < 0.2 g he might feel stationary, horizontal, and facing down. Subjects either felt that they were in the orientation in which they had last traversed their apparent orbit in > 0.2 g, or they had no sense of orientation at all. However, by bracing themselves within the body mold in the ZARR and putting pressure on a part of their body, they could immediately elicit a sense of orientation; for example, by pushing with the top of their head they could make themselves feel upside down. Whenever there was a pattern of imposed pressure on the body, a definite orientation was experienced. The subject, during zero gravity, heard a sound source stationary in the airplane cabin as going through a counterclockwise orbit about his (apparently stationary) head. The diameter of the apparent orbit of the sound source remained constant throughout all variations in force loading, as did the position of the sound orbit in relation to the subject's head.

During the transition to 0 g, nystagmoid movements of the eyes rapidly diminished. It is rare during parabolic flight that a perfect 0 g is obtained for the full 20 to 30 seconds of the "zero gravity phase" of the parabola; there is an occasional ripple of 0.1 to 0.2 g about 0; however, despite such fluctuations, a subject's eyes often remained totally stationary in his head for periods of 5 to 10 seconds and occasionally for most of the free-fall phase of the parabola. Representative recordings from one subject for three consecutive parabolas are presented in Fig. 2b.

In the transition out of the 0-g phase of the parabola, all subjects first reported their bodies again in motion when the force load reached ≈ 0.2 to $0.3\ g$. The sensation of motion always returned as an apparent spiral expansion into a counterclockwise orbit. The head was experienced as facing in the same direction during the spiraling out.

Several subjects, including one of the authors, rode the ZARR without a blindfold during parabolic flight. In this situation, with eyes closed, the patterns experienced were those just described for the 0-, 1-, and 1.8-g phases of flight. With the eyes open during 1 g, clockwise motion of the body is experienced but with the body displaced 7 to 15 cm from the center of rotation; sounds are veridically localized. During 1.8 g, the body seems to turn over clockwise and simultaneously to undergo counterclockwise orbital motion with an orbit diameter of 15 to 30 cm: for each revolution of the ZARR the body is felt to rotate once and simultaneously to achieve one complete circuit of the illusory counterclockwise orbit. The orbital motion is five or six times smaller than that experienced when blindfolded or with the eyes closed. Sounds are localized veridically. In both 1 and 1.8 g, it was possible by simply opening and closing the eyes to switch back and forth between the motions just described and the counterclockwise orbits characteristic of the eyes-closed situations; the transition from one state to the other takes 1 or 2 seconds at most.

During 0 g, with the eyes open, the visual world is seen as moving leftward with respect to one's self. The subject is aware that he is turning clockwise at 30 rev/min in relation to the aircraft; however, he has no sensation of movement and feels completely stationary. He can intellectually ascribe the visual motion to the aircraft rotating around him, to himself moving with respect to the aircraft, or to both moving in relation to each other; nonetheless, he feels stationary. It is possible, however, that visually induced apparent self-rotation would result if the 0-g phase of each parabola were longer than 20 seconds. With the eyes open, sounds were correctly localized.

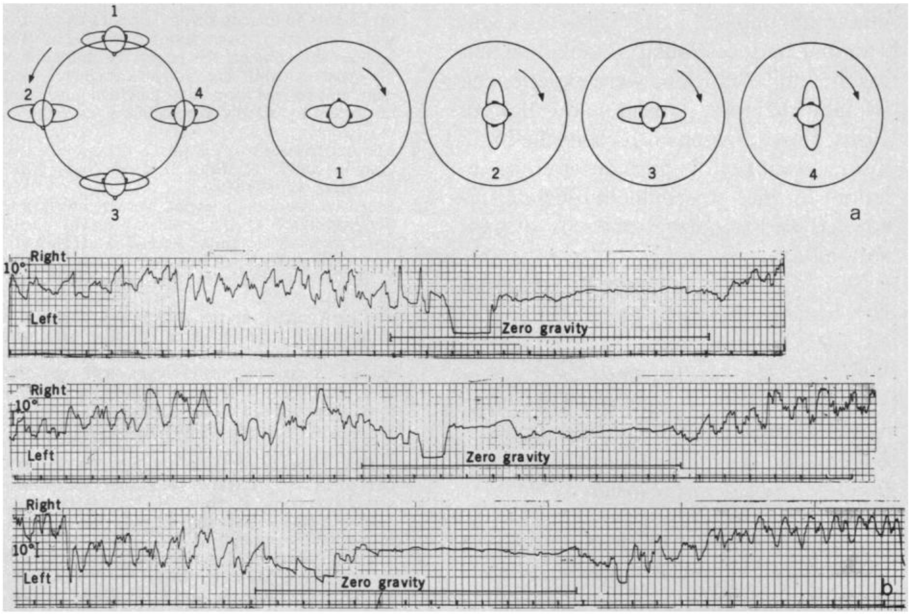

Fig. 2. (a) The leftmost illustration depicts a subject who is experiencing face-down orbital motion. The numbered illustrations to the right are keyed to the orbit numbers and show the subject's true orientation for different experienced orbital positions. (b) Eye movement record of a horizontal, blindfolded subject rotating at 30 rev/min about his Z axis during parabolic flight maneuvers. The zero-gravity or free-fall phase of three consecutive parabolas is illustrated. Shortly after entering the 0-g phase of the parabola, the subject loses all sense of body motion and his nystagmoid eye movements abate until he again experiences motion on transition out of the free-fall period. The time axis at the bottom of the records is divided into 2-second intervals.

The observations described indicate that in the absence of other imposed linear accelerations the otolithic and touch-pressure receptor systems no longer yield effective orientational information when the gravitoinertial force level is less than $\approx 0.2\ g$. Consequently, if the subject is blindfolded, he has no information about his orientation other than that provided by auditory stimulation. In this situation, if he applies pressure to part of his body and thereby creates a pressure pattern that under ground-based conditions is associated with a particular orientation relative to gravity, he immediately gains a "postural reading" and feels that he is in that orientation. During the transition from zero to higher levels of gravitoinertial force, when the blindfolded subject again begins to feel motion, the motion is primarily determined by the pattern of somatosensory stimulation of his body. The character of his nystagmus also mirrors the experienced motion of his body as determined by the pattern of somatosensory stimulation. The dependence of the subject's nystagmus pattern on his subjective posture hence represents an overriding of the vestibular influence on oculomotor activity (*6*). It is notable that when a subject's eyes were open during rotation, the visual cues largely supplanted the somatosensory ones in determining apparent orientation at 1 g, but during exposure to 1.8 g there was a coalescence of the visual and somatosensory contributions and the subject simultaneously experienced clockwise body rotation and counterclockwise orbital motion.

The complex sensory interactions that influence apparent posture during exposure to increased and decreased levels of gravitoinertial force reflect the activity of spatial-constancy mechanisms (*7*). These mechanisms normally allow us to determine accurately our orientation in space and to discriminate between changes in sensory stimulation that are contingent on movements of or within the environment and changes that are contingent on our own movements. It is clear that these mechanisms do not employ an elaborate spatial memory but make continuous use of visual, vestibular, proprioceptive, and somatosensory information in determining the body's apparent orientation. If some of these information sources are eliminated, reliance is placed on remaining ones; if they are in conflict, one overrides the others or there is a coalescence of their effect on apparent posture; if all are eliminated, no apparent orientation can be determined and there is awareness only of the relative configuration of the body and not of body orientation in relation to the external environment.

Astronauts and cosmonauts in orbital flight often experience postural illusions with "lifting" of the gravitational force vector (*8*). Such illusions are probably due to the unusual patterns of touch and pressure and vestibular stimulation that result; similar illusions were experienced by subjects in the present study. In both cases, these illusions represent the organism's attempt to impose order on its relation to the environment despite restricted and abnormal patterns of sensory afflux.

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References and Notes

1. The contact forces provide a consistent representation of apparent posture but one that is alternative to that provided by the vestibular input [J. R. Lackner and A. Graybiel, *Aviat. Space Environ. Med.* **49**, 484 (1978); *ibid.*, p. 798].
2. The relationship between the subject's apparent posture and sound localization is predictable from the classical studies of auditory localizatior → H. Wallach [*J. Exp. Psychol.* **27**, 339 (1940)].
3. With eyes closed, different subjects' apparent orbits vary in diameter from about 45 to 180 cm; with eyes open, from about 8 to 32 cm. The heavier the subject, the larger the diameter of his apparent orbit. The subject can switch from experiencing one form of motion to experiencing the other by simply having his eyes open or closed.
4. The experimental apparatus is described in A. Graybiel and E. F. Miller, II, *Aviat. Space Environ. Med.* **47**, 893 (1976).
5. When we mention *g* levels, we are referring to the magnitude of the resultant gravitoinertial force vector in G^* units [see J. L. Patterson and A. Graybiel, in *Environmental Physiology*, N. S. Balfour, Ed. (Mosby, St. Louis, 1974), pp. 163–275].
6. The slow phase of the subject's nystagmus is compensatory for the direction of experienced motion; for example, when the subject experiences leftward motion his eyes drift right and beat left. The amplitude and frequency of the nystagmus depend on the subject's experienced velocity in his orbit, not on his true rotary velocity.
7. Further aspects of these mechanisms are discussed by J. R. Lackner [in *Handbook of Sensory Physiology*, R. Held, H. Leibowitz, H.-L. Teuber, Eds. (Springer-Verlag, New York, 1978), vol. 8, pp. 805–845].
8. These illusions are described in A. Graybiel and R. S. Kellog [*Aerosp. Med.* **38**, 1099 (1967)] and in R. S. Johnston and L. F. Dietlein, Eds. [*Biomedical Results from Skylab* (SP-377, NASA, Washington, D.C., 1977)].
9. Supported by NASA contracts NAS9-15147 and T-5904B. We thank C. Diamond, L. Lamolinara, and G. E. Tanner for technical assistance and D. Griggs, crew chief of the Johnson Space Center's KC-135 aircraft.

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Fluorine Is a Major Constituent of the Marine Sponge *Halichondria moorei*

Abstract. *Fluorine constitutes about 10 percent of the dry weight of the marine sponge* Halichondria moorei. *The fluorine occurs as potassium fluorosilicate, which is a potent anti-inflammatory agent. A closely related sponge living in the same habitat does not contain any fluorine. The habitat was found to be free of fluorine except for the small amount naturally present in seawater.*

Many marine organisms accumulate iodine, bromine, and chlorine (*1*, *2*). Reports of fluorine accumulation by marine organisms are rare and mostly confined to its occurrence as fluorite (CaF_2) or fluorapatite [$Ca_5(PO_4)_3F$] in calcareous skeletal tissue. Some mollusks and brachiopods, such as the gastropod *Archidoris britannica*, are known to contain up to 3 percent (dry weight) fluorine (*1*, *3*), probably in the form of fluorite spicules (*4*). However, until now there has apparently been only one report of fluorine incorporation by sponges, that of Bowen and Sutton (*5*), who noted its presence in *Dysidea crawshayi* or in its symbionts without detailing its concentration or form. We report that specimens of the marine sponge *Halichondria moorei* Bergquist found off Auckland, New Zealand, contain fluorine at remarkably high concentrations (up to 11.5 percent of dry weight).

Interest was first aroused when an extract of *H. moorei* was shown to have potent anti-inflammatory activity. The active constituent was isolated and identified as potassium fluorosilicate (K_2SiF_6), also known as the mineral hieratite. (These findings were especially interesting in light of a report that the Maoris believed that the application of this sponge to wounds promoted healing.) Examination of *H. moorei* extracts for anti-inflammatory activity was carried out by inducing edema in rat paws with carrageenan (*6*). This test was used as a guide to fractionation during the isolation of the anti-inflammatory constituent. Upon being collected, the sponge was frozen and ground cryogenically. The pulverized organism was extracted sequentially with aqueous ethanol, water, and dilute ammonia, and each extract was separated from the insoluble material by centrifugation (32,000*g*). Each of the extracts displayed some anti-inflammatory activity, but the extract with ammonia was the most potent and, because of its low salt content, the most easily fractionated. Highly purified active material (0.83 percent of dry weight) was separated from this extract by successive diafiltration (Amicon UM05 membrane, with a 500-dalton cutoff), gel permeation chromatography (Sephadex G10), and high-pressure liquid chromatography on octadecyl silica. Powder x-ray diffraction analysis of this material, supported by atomic absorption and emission spectroscopy data, revealed that it contained about 33 percent potassium fluorosilicate. By comparison with an authentic sample, potassium fluorosilicate was established as the anti-inflammatory constituent of *H. moorei*.

Studies on the mechanism of action of potassium fluorosilicate (*7*) have shown that the compound probably exerts its anti-inflammatory activity by means of some counterirritant mechanism (*8*). Intraperitoneal administration of potassium fluorosilicate (50 mg/kg) causes mice to writhe.

Subsequently a more comprehensive study of the occurrence of fluorine in *H. moorei* and its habitat was recently undertaken. Fresh samples of *H. moorei* were collected near Auckland from Westmere Reef in Waitemata Harbour and at Takapuna. Potassium fluorosilicate was readily identified by x-ray diffraction as a major constituent of freeze-dried *H. moorei* from both locations. No other fluorine-containing substance was identified in the samples by this technique. The sponges were shown to contain 11.5 percent (Westmere Reef sample) and 9.7 percent (Takapuna sample) fluorine (equivalent to 22.2 and 18.7 percent potassium fluorosilicate), respectively, on a dry weight basis by analysis with a fluoride ion-specific electrode (detection limit, 0.1 percent) of extracts made with 1 percent sodium carbonate solution. Analysis of both the suspended and bottom sediments of the Westmere habitat detected no fluorine.

A second sponge, *Hymeniacidon perleve* Montagu, collected from Westmere Reef and from nearby Mill Bay in Manakau Harbour, was subjected to the same forms of analysis, but no fluorine or potassium fluorosilicate was detected. This sponge has a comparable growth pattern, occupies a similar habitat, and belongs to the same taxonomic order (Halichondrida) as *H. moorei*.

Since electron microscopy studies of *H. moorei* have shown it to be free of algal and bacterial symbionts (*9*), and since there are no unusual fluorine sources such as volcanic activity and industrial pollution in the immediate vicinity of the collection sites, it must be concluded that the fluorine in *H. moorei* is obtained from the low concentration (1.3 μg/ml) naturally present in seawater (*10*).

It is apparent that most sponges require little or no fluorine for their life

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