13. J. M. Lundberg *et al.*, *Neuroscience* **4**, 1539 (1979).
14. I. Kupfermann and E. R. Kandel, *J. Neurophysiol.* **33**, 865 (1970).
15. N. J. Tublitz and J. W. Truman, *Soc. Neurosci. Abstr.* **7**, 253 (1981).
16. ______, *J. Exp. Biol.*, in press.
17. N. J. Tublitz, thesis, University of Washington, Seattle (1983).
18. N. J. Tublitz and J. W. Truman, *J. Exp. Biol.*, in press.
19. ______, *Soc. Neurosci. Abstr.* **9**, 19 (1983).
20. H. M. Taylor and J. W. Truman, *J. Exp. Biol.* **58**, 821 (1974).
21. The in vitro *Manduca* heart bioassay consisted of the abdominal portion of the pharate adult heart, which was isolated and placed in a 250-μl superfusion chamber and attached to a Bionix F-200 isotonic displacement transducer. The amplified signal was fed through a window discriminator and a digital-to-analog frequency monitor, which allowed for the measurement of instantaneous heart rate. An open perfusion system was used with the open point suspended 5 cm above the superfusion chamber. During each bioassay, saline flowed from the open point directly to the superfusion chamber. Samples (100 μl) were pulse-applied at the open point with a 100-μl gas-tight Hamilton syringe. Samples were applied only when the variability in the heart was ≤1 percent for a 15-minute period. In addition to the CAP's, octopamine and serotonin increase heart rate as measured on the in vitro *Manduca* heart bioassay; these biogenic amines can be separated from the CAP's by gel filtration or high-performance liquid chromatography, or both.
22. In these experiments, crude homogenates or partially purified $CAP_1$ or $CAP_2$ were incubated in the presence of Pronase which had been previously inactivated by boiling. The results show that inactivated Pronase neither interferes with the basal rate of the in vitro heart nor curtails the ability of the heart bioassay to respond to $CAP_1$ or $CAP_2$ (*16*).
23. J. P. Bacon and J. S. Altman, *Brain Res.* **138**, 359 (1977).
24. P. H. Taghert, thesis, University of Washington, Seattle (1981).
25. S. Miyazaki, *J. Comp. Physiol.* **140**, 43 (1980).
26. We thank J. Weeks for technical assistance and advice during the course of these experiments. We are grateful to S. H. P. Maddrell, P. K. Schofield, and J. E. Treherne for critical reviews of this manuscript. Supported by a National Science Foundation predoctoral fellowship and an National Institutes of Health traineeship to N.J.T. and by grants to J.W.T. from NIH, NSF, and the McKnight Foundation.
* Present address: Agricultural and Food Research Council Unit of Insect Neurophysiology and Pharmacology, Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, United Kingdom.

17 September 1984; accepted 20 December 1984

## Durability of the Accretion Disk of Millisecond Pulsars

Abstract. *Pulsars with pulsation periods in the millisecond range are thought to be neutron stars that have acquired an extraordinarily short spin period through the accretion of stellar material spiraling down onto the neutron star from a nearby companion. Nearly all the angular momentum and most of the mass of the companion star is transferred to the neutron star. During this process, wherein the neutron star consumes its companion, it is required that a disk of stellar material be formed around the neutron star. In conventional models it is supposed that the disk is somehow lost when the accretion phase is finished, so that only the rapidly spinning neutron star remains. However, it is possible that, after the accretion phase, a residual disk remains in stable orbit around the neutron star. The end result of such an accretion process is an object that looks much like a miniature (about 100 kilometers), heavy version of Saturn: a central object (the neutron star) surrounded by a durable disk.*

Spin-up of pulsars in a binary accretion scenario has been proposed by a number of investigators (*1*). We have argued that neutron stars formed in supernova events would be surrounded by a disk of material from the parent star (*2*, *3*). Most but not all of the stellar material from the supernova is either exploded to form a surrounding nebula or imploded to form a neutron star. We estimate that approximately $10^{-4}$ solar mass is left in orbit around the neutron star to form a disk. Dynamo currents between the remnant disk and the magnetized neutron star drive the observed pulsar emissions (*3–5*).

For millisecond pulsars (if they are formed by accretion events), a durable disk evolves from the accretion disk after the secondary object stops feeding the disk. Once the forced accretion stops, the portion of the disk inside the corotation distance continues to move inward and falls onto the neutron star. However, the portion outside the corotation distance moves away from the neutron star at a relatively slow rate because of the torque applied to it by dynamo currents between the disk and the star (*3*).

The viscous dissipation in the shrinking inner disk suggests that the disk would accrete entirely in a short time. However, some of the spin-down energy is pumped back into the disk and acts instead to eject it. We can calculate a critical viscosity $\nu_{crit}$ that dissipates energy in the disk faster than power is supplied by the central object as follows. The time derivative of the inward mass rate, $\dot{M}$, is $3\pi\nu\Sigma$ (*6*), where $\Sigma$ is the surface mass density of the disk (in grams per cubic centimeter). By equating the spin-down output $I\Omega\dot{\Omega}$ (where $I$ is the moment of inertia and $\Omega$ and $\dot{\Omega}$ are the spin rate and its time derivative, respectively) to the increased binding produced by a mass rate $G\dot{M}M/R_c$ [where $R_c$ is the corotation distance, $(GM/\Omega^2)^{1/3}$, and $G$ is the gravitation constant], we find $\nu_{crit}$ equal to $R_c I\Omega\dot{\Omega}/3\pi G\Sigma$. For a millisecond pulsar, $\Omega$ is about 4000 $sec^{-1}$, $\dot{\Omega}/\Omega$ is about $1.3 \times 10^{-19}$, $\Sigma$ is about $10^{12}$ g/cm$^2$, and $R_c$ is about $3 \times 10^6$ cm. With $I$ approximately $10^{45}$ g cm$^2$ as the moment of inertia of a typical neutron star, this gives a $\nu_{crit}$ of about 5 cm$^2$/sec. A value for $\nu$ of approximately 1 to 100 cm$^2$/sec has been calculated for matter at densities typical of white dwarfs (that is, essentially the disk) (*7*). The electron degenerate disks proposed here differ greatly from the nondegenerate disks proposed for pulsating x-ray sources, which are thought to have a viscosity $10^{14}$ times larger than that calculated by Flowers and Itoh (*7*).

The remnant of the companion star that provided the material for the disk and for spinning up the neutron star may be reasonably expected to form a degenerate dwarf (*8*). It has been argued that the companion star would spiral inward because of gravitational radiation and would eventually become tidally disrupted to add material to the disk (*8*). This scenario reinforces our proposal that a remnant disk is formed in the spin-up of the neutron star.

The only other suggestion for removing a disk is that such a disk could not survive if the companion star at a distance of only a few solar radii were to become a supernova (*9*). There are two mechanisms by which a disk might be dissipated in such a supernova event: (i) the gravitational impulse caused by the sudden passage of the ejected mass might shake the disk loose from the neutron star, and (ii) the direct impact of supernova ejecta might sweep the disk away.

The first mechanism cannot disrupt the disk. The neutron star and the disk are so close to each other that they receive almost identical gravitational impulses. The second mechanism, in which it is proposed that direct impact of supernova debris can blow away the disk of a neutron star, is also ineffective. To evaluate this possibility, we must make some assumptions that are dependent on our model. The disk is so stable that, even in the most unfavorable case, it can survive a nearby supernova explosion.

For example, we will suppose that an extremely energetic event propels the outer envelope of the exploding star outward with a velocity $V$ of $10^4$ km/sec and a peak mass density $\rho$ of the order of 1 g/cm$^3$. If the star undergoes a vigorous phase of mass loss just before detonation, smaller densities could be appropriate. In the most unfavorable case, the disk would be oriented face-on to the blast and not shielded by the neutron star magnetosphere. The column momentum impulse of the flow with an assumed depth of $10^{11}$ cm is $10^{20}$ g/cm sec, and the disk has a surface mass density $\Sigma$ of $10^{12}$ gm/cm$^2$. Thus the transfer of momentum from the impacting flow could impart a maximum velocity of about $10^3$ km/sec to the disk material. Comparison of this velocity with the escape speed from the disk location, which is approximately $10^5$ km/sec, indicates that the supernova wind would only buffet the disk and move on. Another way of stating the basic physical reason underlying the stability of the disk is that the flow speed of the supernova debris is comparable to the orbital speed of the disk material, whereas the mass density of the disk, because of tidal effects, exceeds that of the incoming material.

The face-on orientation considered above is too severe. According to the accretion hypothesis for the creation of a millisecond pulsar, material from a nearby star forms a disk that feeds material and angular momentum to the object that becomes the millisecond pulsar. The secondary object that feeds the accretion disk must lie in or near the plane of the disk. Because the remnant disk we propose is formed directly from the accretion disk or from the disruption of the companion, its plane should coincide closely with the plane of the accretion disk. Thus, when the secondary object becomes a supernova, its blast passes by a disk oriented edge on to the explosion, and the actual impulse delivered to the disk is considerably smaller than the most extreme case assumed above.

Finally, the disk could be protected by the magnetosphere of the neutron star. For example, if the magnetic field of a neutron star surrounded by a disk varied as $1/r^3$ from the star to the inner edge of the disk ($r$, distance from the center of the star) and as $1/r^2$ beyond that distance (*4*), the magnetic field of a $10^8$-gauss neutron star at $3 \times 10^8$ cm is $4 \times 10^4$ gauss. A magnetic field this strong would fully deflect a supernova plasma with a mass density of nearly 0.1 g/cm$^3$. Although we assumed a mass density of 1 g/cm$^3$ as an upper limit for our earlier example, a smaller mass density is likely. However, if the supernova plasma were dense enough to approach the disk closely, eddy currents would be induced in the disk so that the force of the supernova plasma would be transmitted to the disk by magnetic pressure rather than by direct impact (*10*). Thus we conclude that a durable pulsar disk remains around the neutron star after the accretion and possible supernova events that form a millisecond pulsar.

F. CURTIS MICHEL
*Department of Space Physics and Astronomy, Rice University, Houston, Texas 77251*

A. J. DESSLER
*Space Science Laboratory, NASA Marshall Space Flight Center, Huntsville, Alabama 35812*

**References and Notes**

1. M. A. Alpar, A. F. Cheng, M. A. Ruderman, J. Shaham, *Nature (London)* **300**, 728 (1982); P. C. Joss and S. A. Rappaport, *ibid.* **304**, 419 (1983); B. Paczynski, *ibid.*, p. 421; G. J. Savonije, *ibid.*, p. 422; D. J. Helfand, M. A. Ruderman, J. Shaham, *ibid.*, p. 423.
2. F. C. Michel and A. J. Dessler, *ibid.* **303**, 48 (1983).
3. ———, *Astrophys. J.* **251**, 654 (1981).
4. F. C. Michel, *ibid.* **266**, 188 (1983).
5. ———, *Rev. Mod. Phys.* **54**, 1 (1982).
6. J. E. Pringle, *Annu. Rev. Astron. Astrophys.* **19**, 137 (1981).
7. E. Flowers and N. Itoh, *Astrophys. J.* **206**, 218 (1976).
8. A. F. Cheng, *Ann. N.Y. Acad. Sci.* **422**, 182 (1984).
9. H. F. Henrichs and E. P. J. van den Heuvel, *Nature (London)* **303**, 213 (1983).
10. S. T. Suess and B. E. Goldstein, *J. Geophys. Res.* **84**, 3306 (1979).
11. We thank Dr. Ron Elsner and two referees for several helpful comments.

27 November 1984; accepted 4 March 1985

## Gravity, Drag, and Feeding Currents of Small Zooplankton

Strickler (*1*) concludes that, for copepods, "gravity helps set up a large feeding current." A copepod "uses its relative weight to create a strong feeding current and takes advantage of the double shear field to perceive its food" (*1*). However, Strickler does not provide any mechanism by which negative buoyancy sets up a large feeding current and enhances feeding. We suggest a general and testable hypothesis, namely that any retarding force, including gravity or drag, enhances feeding by small planktonic organisms.

Most zooplankters and planktonic larvae of benthic marine invertebrates live in a world dominated by viscosity rather than inertia (*2*). When viscosity is a dominant factor, there is a thick layer of water that moves with an animal or its appendages that deflects adjacent water with suspended food particles out of its path. Most small planktonic animals swim with cyclical movements of fibers, either appendages or cilia (*3*), that create a steep velocity gradient near the animal and bring particles within a distance that they may be perceived or contacted. Particles are captured by diverting and capturing the parcel of water containing suspended particles (*4*) or perhaps by filtering them from the surrounding water (*5*). If the fibers producing the current also serve as sensory structures or filters, then increasing flow around the fibers should enhance feeding (*6*). A restraining force should steepen the velocity gradient around the current-producing appendages (*7*). An increase in the movement of the appendages relative to the water will result in an increase of close encounters with particles, thereby enhancing feeding. Gravity can provide a retarding force on an upward swimming animal whose density is greater than that of seawater, and thereby create a steeper velocity gradient around the filtering (or water-parcel-capturing) fibers. Drag on a body can also provide an effective tether and operates in any direction the animal moves.

The relative effectiveness of increasing negative buoyancy or drag changes with swimming speed and animal size. At low Reynolds numbers ($Re \leq 1$), drag increases in proportion to body length ($L$) and swimming speed (*2*). Gravitational force increases with body volume or $L^3$. For small swimming animals (about 0.5 mm in length) drag may be a more effective tether than gravity. Let us consider an animal approximated by a prolate spheroid of width one third the length, an excess density relative to seawater of 0.03 g/cm$^3$ and a swimming speed of 1 mm/sec (*8*). For an animal 1 mm long, the drag is about $0.6 \times 10^{-8}$ newton and the gravitational force about $1.7 \times 10^{-8}$ newtons so the excess density has three times the effect of the drag (*9, 10*). An animal 0.6 mm long has a drag force equal to the gravitational force. Many zooplankters and invertebrate larvae are smaller than this.

Planktonic animals bear numerous structures that increase drag. Although these projecting or trailing structures may perform various functions, they also may enhance capture of food while decreasing swimming speed. These structures include mucous strands (*11*), egg masses, feces (*12*), and spines (*6*).

Arrangement of structures for moving water can also greatly increase or decrease drag on the whole animal (*13*) and also modify flow around structures for sensing or capturing food. For example, appendages and ciliated bands beating toward each other (*5, 6*) should produce steeper velocity gradients near food capturing or sensing structures.

In conclusion, negative buoyancy or drag could increase fluid motion near food collecting or sensory structures of many small planktonic animals. The effectiveness of increased weight or in-