

Wave-Making by Whirligig Beetles (Gyrinidae)

Abstract. *Swimming whirligig beetles (Dineutes carolinus) either make no waves at all or make conspicuous circular or vee-shaped patterns of capillary waves. The beetle's swimming speed can be determined from these wave patterns (or lack of them). Capillary waves precede the beetle for several body lengths, and their reflections may help the beetle avoid solid objects by echolocation. The gravity waves produced by a beetle are always longer than the beetle's hull length. Hence the waves do not interact with the hull to impose an upper limit on speed as they do with conventional ships. Although the beetles swim at high speeds, they apparently do not hydroplane.*

Swimming whirligig beetles often make conspicuous wave patterns on the surfaces of ponds and quiet streams. The beetles apparently use the reflections of the waves to detect objects at a distance (1); hence they, and some noctuid moths, are the only insects thought to use some form of echolocation (2). Some of the waves have wavelengths several times longer than the beetle's body length. This fact is curious, because conventional ships cannot make waves of such great relative length. The waves have characteristic patterns that are explained by hydrodynamic theory and provide a means for estimating the swimming speed of the beetle.

I photographed the wave patterns

made by whirligig beetles (*Dineutes carolinus*) swimming on a pond and in an aquarium in the laboratory. I also photographed the waves produced by a dead beetle mounted on a wire and oriented in a lifelike manner on the surface of a smoothly flowing stream. All the beetles had the same body length (0.0106 m) with a mean weight of 452 mg (six beetles; standard deviation, 46).

On the pond, undisturbed beetles usually were in constant, jerky motion and were surrounded by concentric circles of about a dozen waves (Fig. 1). There were prominent bow and stern waves. When the beetles moved slowly, they made no waves at all. Occasionally, a beetle would put on a burst of speed and leave a vee-shaped trail of waves behind it for several tens of body lengths. Vee-shaped patterns were photographed in the laboratory by disturbing beetles in an aquarium (Fig. 2). They also were produced by the dead beetle mounted on the surface of the stream (cover). Except for the stern wave, all of the conspicuous waves made by a beetle formed in front of the head and preceded the beetle for a dozen or more wavelengths (cover).

Hydrodynamic theory (3) describes two general types of surface waves, one influenced by gravitational forces, the other by surface tension forces. Both types have wavelengths (λ) that are functionally related to wave speed (c). The speed of waves influenced solely by gravity is given by the equation

$$c = [g\lambda/(2\pi)]^{1/2} \quad (1)$$

For waves influenced solely by surface tension, the corresponding equation is

$$c = [2\pi T/(\lambda d)]^{1/2} \quad (2)$$

At 25°C, T is surface tension (0.072 newton/m), d is density of water (997 kg/m³), and g is the acceleration due to gravity (9.8 m/sec²).

The speed of an actual wave (Fig. 3) is influenced to some extent by both gravitational and surface tension forces so that

$$c = [g\lambda/(2\pi) + 2\pi T/(\lambda d)]^{1/2} \quad (3)$$

The minimum speed below which waves cannot propagate (c_m , 0.23 m/sec) is attained at a wavelength of 0.017 m. Longer waves (gravity waves) are influenced primarily by gravitational forces, and their wavelengths increase with speed. Shorter waves (capillary waves) are influenced primarily by surface tension forces and their wavelengths decrease with speed.

A relevant property of both gravity and capillary waves is group velocity. If an isolated group of waves of a given wavelength advances over the water, in general the speed of the whole group will differ from that of the individual waves composing it. For example, when group velocity is less than wave speed, a particular wave forms at the back of the group, advances through the group, and dies out at the front. The opposite occurs if group velocity is greater than wave speed.

In deep water (several wavelengths), gravity waves have group velocities that are less than wave speed, and the opposite is true for capillary waves. Thus,



Fig. 1 (left). Whirligig beetle swimming toward the right in a jerky manner on the surface of a pond. Four sets of circular capillary waves can be seen, each with its center at a different point along the beetle's path. Fig. 2 (above). Whirligig beetle producing a vee-shaped wake of capillary waves in an aquarium. Bow and stern waves are conspicuous. The angle of the vee and the wavelengths of the waves both indicate a swimming speed of 0.47 m/sec. Gravity waves traveling at this speed would have a wavelength 13 times as long as the beetle.

a group of capillary waves moves ahead of an object moving through the water, and a group of gravity waves falls behind. Group velocities for both types of waves can be determined from Fig. 3 by drawing a tangent to the curve at the wavelength of interest. The group velocity for that wavelength is the value where the tangent line intersects the vertical axis.

The pressure disturbances that initiate the waves accompanying a swimming beetle can be explained by Bernoulli's equation, which states that the sum of kinetic and potential energy of an ideal fluid is constant. Taking the beetle as a reference point, water approaching the beetle's head slows down from free stream velocity and loses kinetic energy. The hump of water that forms in front of the beetle reflects a gain of potential energy at the expense of kinetic energy. As the water flows around the bulging sides of the beetle, it speeds up, then slows down to free stream velocity again as it converges at the tail. Thus, the beetle swims in a trough bounded by a bow and stern wave corresponding to the conversions between kinetic and potential energy.

The above relations explain the wave patterns made by a swimming beetle. At speeds below 0.23 m/sec, waves cannot propagate, so no wave pattern forms. A beetle swimming steadily at higher speeds produces a stationary pattern (relative to the beetle) of both capillary and gravity waves. The latter are not visible in my photographs because of their long wavelength and low amplitude, but a group of them is left behind the beetle and can be seen occasionally on the water. The bow wave is the first of this group. The bow wave also is the most posterior of a group of capillary waves propagating forward faster than the water is moving. These waves are conspicuous, and in some photographs more than 14 waves are visible extending 6.5 body lengths ahead of the beetle.

Circular wave patterns are generated by the jerky swimming motions of the beetle. An abrupt acceleration causes a local pressure disturbance that initiates an expanding ring of capillary waves. The beetle swims forward following the innermost wave as it expands outward. The beetle may accelerate abruptly again after swimming a few body lengths and may generate a new pattern of expanding waves. Some of my photographs show beetles within four circles of waves, each with its center at a different point along the beetle's path (Fig. 1).

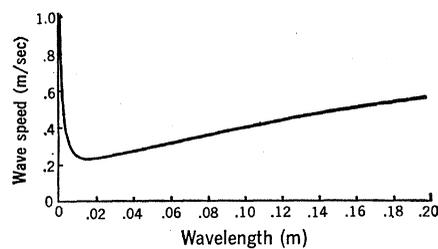


Fig. 3. The relation between wavelength and speed for capillary waves and gravity waves less than 0.2 m long.

Vee-shaped capillary wave patterns are produced when the beetle swims faster than 0.3 to 0.4 m/sec, which is about the speed of an expanding group of capillary waves. The angle (θ) between lines asymptotic to the arms of the vee is functionally related to swimming speed (V) by the equation

$$V = 2 c_m / \sin \theta \quad (4)$$

Since the bow wave of an object moving through the water generates a group of gravity waves that are left behind, these waves can interact with the object and can have a profound effect on the power required to move it through the water. Because of this interaction the maximum speed of a conventional ship is set by its waterline length. When a ship moves slowly, its length spans several gravity waves along its sides in the group that is being generated at the bow. As the ship moves faster, the wavelengths of these waves increase. At a particular speed (hull speed), the wavelength has increased to approximately waterline length, and the second wave crest in the group formed at the bow reinforces the wave crest formed at the stern. The ship now is settled in a trough between its bow and stern waves. The amount of power required to sail faster is too large to be practical for commercial vessels (4).

Some light and powerful boats avoid the speed limitations of wave-making by generating hydrodynamic lift and partially rising out of the water. The boat is no longer supported solely by buoyancy forces resulting from the displacement of water but skims along the surface at greater than hull speed, supported by hydrodynamic forces. Boats that hydroplane in this manner make relatively small waves that may have lengths several times that of the boat's waterline (5).

The whirligig beetles in this study escape the limitation of hull speed, for they form gravity waves that may be over ten times longer than their waterline length, yet they apparently do not

hydroplane. Part of the explanation lies in the size of the beetle. Since the beetles are shorter than the shortest gravity wave, the gravity waves being generated at the bow cannot possibly reinforce the stern wave.

It is interesting that almost all gyrenids are shorter than the shortest gravity wave. The largest North American species is 0.016 m long, and most species worldwide are less than 0.010 m long (6). However, the largest known gyrenid (*Porrhorynchus landani* from the torrential mountain streams of Southeast Asia) is 0.027 m long (7).

Evidence that the beetles in this study do not hydroplane comes from morphology and from the wave patterns produced at high swimming speeds. First, the shape of the beetle's hull is not appropriate for hydroplaning. Below the waterline in longitudinal section the beetle's body is convex, whereas a hull that can hydroplane has virtually straight and parallel lines. The reason for this is apparent from Bernoulli's equation. Since water flows around the bottom of a convex hull at a higher speed than free stream velocity, a low pressure region develops beneath the hull, which is sucked deeper into the water as it goes faster. In contrast, a hull with straight and parallel lines can develop high pressure beneath it as speed increases, and as a result it rises partially out of the water (5).

Second, the wave patterns produced at high speed do not indicate that the beetles are hydroplaning. Even at high speed the beetles generate a bow wave anterior to the head and a stern wave, and they swim in the trough between (Fig. 2). If the beetles were hydroplaning, the bow wave would move posteriorly and the stern wave and trough would disappear as the beetle rises out of the water.

Even though the beetles do not hydroplane, their bodies displace only about half their weight of water at rest. The remainder of the supportive force is provided by the surface film of the water, which is conspicuously depressed around a resting beetle.

There is some evidence that whirligig beetles can detect reflections of the waves they produce and by this form of echolocation avoid solid objects in their paths (1). These authors did not mention that capillary waves form far ahead of the beetle. They apparently thought that the beetle could echolocate only by swimming in small circles and awaiting the return of reflections from its waves. This study shows that a beetle swimming steadily in a straight line also may

produce waves that could be used for echolocation. Since capillary waves extend at least 6.5 body lengths ahead of the beetle, their reflections might be perceptible from an object directly ahead at a distance of perhaps three body lengths. In addition, the jerky swimming pattern may aid echolocation by producing waves as pulses (8). Pulsed waves help to avoid confusion between outgoing and incoming signals and carry away less energy than continuous waves. They usually are used in echolocating devices such as radar and sonar and also are characteristic of the echolocating sounds of animals (9).

Two different measures of a beetle's swimming speed may be obtained from wave patterns. One of these is calculated (with Eq. 3) from the wavelength of capillary waves moving at the same speed as the beetle. This condition is met in the region where the waves cross the line along which the beetle is moving. The other measure is calculated (with Eq. 4) from the angle of the vee-shaped wake. A third measure of swimming speed could have been obtained from the wavelength of gravity waves had they been visible in the photographs.

The means of the wavelength method and the wake method are in excellent agreement (0.41 and 0.40 m/sec, respectively) for the 17 beetle photographs to which both methods can be applied. The mean difference between the two estimates for each beetle is 0.04 m/sec. My highest estimate of swimming speed was 0.53 m/sec, although speeds up to 1 m/sec have been measured (10). This is a remarkably high speed for so small an animal, and probably few nonflying insects are faster.

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Antiparkinsonian Drugs: Inhibition of Dopamine Uptake in the Corpus Striatum as a Possible Mechanism of Action

Abstract. A variety of antiparkinsonian drugs are potent, noncompetitive inhibitors of dopamine uptake into synaptosomes in homogenates of rat corpus striatum. Inhibition of dopamine uptake may potentiate the synaptic actions of dopamine in the striatum and could explain the antiparkinsonian effects of these drugs. This hypothesis accounts for several clinical features of Parkinson's disease and predicts compounds which may be new therapeutic agents.

A variety of drugs are useful in the treatment of Parkinson's disease, including anticholinergic agents, antihistamines, phenothiazines, and sympathomimetics. We report here that several of these drugs are potent inhibitors of dopamine uptake in the corpus striatum.

In most regions of the brain, dopamine serves as a precursor for norepinephrine, but in the corpus striatum (caudate nucleus and putamen), it is the predominant catecholamine and occurs in concentrations 100 times higher than norepinephrine (1). Recent evidence suggests a role for striatal dopamine in the pathophysiology of Parkinson's disease. The major neuropathological change in the brains of patients with Parkinson's disease is a degeneration of the substantia nigra, a region which contains the cell bodies of the dopamine-containing neurons that terminate in the corpus striatum (2). There is a marked decrease in the striatal dopamine content in brains of pa-

tients with Parkinson's disease (2). Moreover, recent reports indicate that L-dopa (L-dihydroxyphenylalanine), the metabolic precursor of dopamine, ameliorates the major symptoms of Parkinson's disease (3).

Catecholamines can be accumulated into brain tissue by a neuronal membrane transport system as well as by reserpine-sensitive retention in storage granules. The membrane uptake system appears to account for the physiologic inactivation of norepinephrine released at peripheral sympathetic synapses and may play a similar role in terminating synaptic activity of norepinephrine and dopamine in the brain (4). The neuronal membrane uptake of catecholamines in the brain can be demonstrated in vivo and in vitro in brain slices, homogenates, and synaptosomes (sheared-off nerve endings) (5). Catecholamine uptake in the striatum differs from that in other areas of the brain in its resistance to inhibition by desmethylimipramine (6), a potent inhibitor of

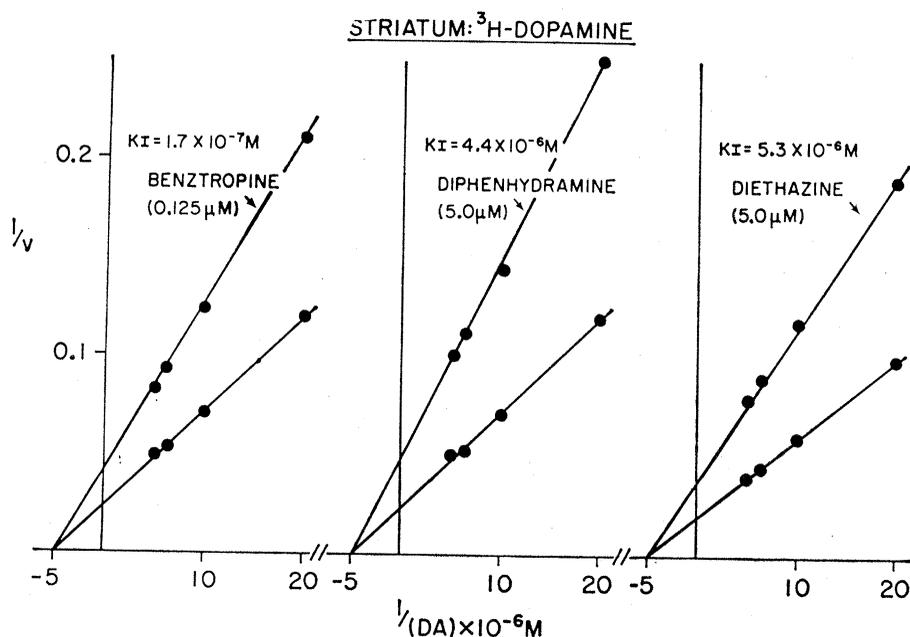


Fig. 1. A graphic analysis of the kinetics of inhibition by benztropine, diphenhydramine, and diethazine of ^3H -dopamine uptake into striatal synaptosomes according to the method of Lineweaver and Burk (8). Homogenates were incubated in triplicate with concentrations of ^3H -dopamine ranging from 0.05 to 0.2 μM and a constant concentration of drug.