The role of mechanical resonance in the neural control of swimming in fishes[☆]

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ABSTRACT

The bodies of many fishes are flexible, elastic structures; if you bend them, they spring back. Therefore, they should have a resonant frequency: a bending frequency at which the output amplitude is maximized for a particular input. Previous groups have hypothesized that swimming at this resonant frequency could maximize efficiency, and that a neural circuit called the central pattern generator might be able to entrain to a mechanical resonance. However, fishes swim in water, which may potentially damp out many resonant effects. Additionally, their bodies are elongated, which means that bending can occur in complicated ways along the length of the body. We review previous studies of the mechanical properties of fish bodies, and then present new data that demonstrate complex bending properties of elongated fish bodies. Resonant peaks in amplitude exist, but there may be many of them depending on the body wavelength. Additionally, they may not correspond to the maximum swimming speed. Next, we describe experiments using a closed-loop preparation of the lamprey, in which a preparation of the spinal cord is linked to a real-time simulation of the muscle and body properties, allowing us to examine resonance entrainment as we vary the simulated resonant frequency. We find that resonance entrainment does occur, but is rare. Gain had a significant, though weak, effect, and a nonlinear muscle model produced resonance entrainment more often than a linear filter. We speculate that resonance may not be a critical effect for efficient swimming in elongate, anguilliform swimmers, though it may be more important for stiffer carangiform and thunniform fishes.

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1. Introduction

Nearly all objects that bend or flex have a natural frequency: a frequency at which they naturally tend to oscillate. At the natural frequency, a minimal force input produces a maximum motion output. For example, a clock pendulum relies on the natural frequency of the clock's spring to keep swinging back and forth. Arms and legs are also like pendulums, and humans will spontaneously swing their arms at the natural frequency of their shoulder joints (Hatsopoulos and Warren, 1996), potentially reducing the energy required for locomotion (Ahlborn et al., 2006; Goodman et al., 2000; Verdaasdonk et al., 2006). Can fishes, whose body and appendages are not like pendulums, benefit from similar energy savings?

The natural frequency is a simple consequence of a mechanical system that has a restoring and damping force (Hartog, 1985; Hatsopoulos and Warren, 1996). For example, for a pendulum or a swinging arm or leg, the restoring force is gravity: the higher the angle of the pendulum away from vertical, the stronger the component of the gravitational force that pushes it back toward vertical. Springs also tend to exhibit resonance: the more they are compressed, the stronger they push back. If a spring is compressed by an object with mass m, the restoring force F_{rest} is proportional to the displacement x: $F_{rest} = kx$, where k is a spring constant. The damping force, in turn, is proportional to the velocity $\dot{x}$: $F_{damp} = b\dot{x}$, where a dot represents a time derivative and b is a damping constant. Thus, the total force balance on the object is

$$m\ddot{x} + b\dot{x} + kx = f_{in}, \qquad (1)$$

where $\ddot{x}$ is the acceleration and F_{in} is an input force. Dividing by the mass m, this equation is normally written

$$\ddot{x} + 2\zeta\omega_r\dot{x} + \omega_r^2 x = \frac{F_{in}}{m}, \qquad (2)$$

where $\omega_r = \sqrt{k/m}$ is the undamped natural frequency and $\zeta = b/(2\sqrt{mk})$ is the damping ratio. When ζ is less than 1, the system is called underdamped, and if the input force is periodic with a frequency near ω_r, the output oscillations in x can be very large (a resonant peak): much larger than if the input has a frequency below

or above ω_r. The location of the resonant peak shifts lower as damping increases. If ζ is greater than 1, the system is overdamped, and does not have a resonant peak. Regardless of the damping, close to the resonant frequency the motion will be 90° out of phase with the input force, another indication of resonance.

Therefore, swinging a pendulum-like arm or leg should require minimal energy input at the resonant frequency, provided the damping is low. Previous studies have shown that animals do tend to walk or run near the resonant frequency of their limbs (Hatsopoulos and Warren, 1996; Williamson, 1998) and that this may contribute to energy savings (Pelc et al., 2008; Verdaasdonk et al., 2006). Moreover, a swinging limb near its resonant frequency is more predictable and simpler to stabilize (Goodman et al., 2000).

For efficient locomotion, it would make sense that the nervous systems of animals could have evolved to take advantage of resonance. The properties of a neural circuit for locomotion, called a central pattern generator (CPG), may allow it to detect a resonant peak and match the resonant frequency. CPG circuits are found in both vertebrates and invertebrates and produce the basic muscle activation patterns for locomotion (Orlovsky et al., 1999; Grillner, 2003; Mullins et al., 2011); they also respond to sensory inputs during the locomotory cycle (Rossignol et al., 2006). A number of studies have indicated that simple CPGs, when connected in a feedback loop with a mechanical system, can converge on the mechanical resonant frequency, a phenomenon called "resonance entrainment" (Hatsopoulos, 1996; Iwasaki and Zheng, 2006; Williams and DeWeerth, 2007), potentially resulting in more efficient and stable locomotion.

Can aquatic organisms benefit from the same savings? Fishes and other organisms do not have pendulum-like limbs, and the water introduces fluid dynamic forces, but their bodies and fins are elastic, and so they might benefit from resonance.

The present study is divided into two parts. In the first, we address the question of whether fish bodies might have a mechanical resonance and what form that resonance might take, presenting data from a computational model of lamprey (*Ichthyomyzon unicuspis*) swimming. In the second part, we consider resonance entrainment, summarizing results from several computational and experimental studies, and then present data from a closed-loop preparation of the lamprey CPG.

2. Is there resonance underwater?

Fish bodies are elastic (Aleyev, 1977; Long et al., 2002a), but internal damping (Long et al., 2002b) and the fluid around them may contribute substantial damping forces. Somewhat surprisingly, given the complex internal anatomy of fishes, almost all previous results have indicated that they bend like a homogeneous elastic beam (Katz et al., 1999; Long et al., 2002a). Thus, as a first approximation we can treat a section of a fish's body as a damped harmonic oscillator (like Eq. (2)), with a nonlinear term introduced by the fluid:

$$\ddot{x} + \underbrace{2\zeta\omega_r\dot{x}}_{internal} + \underbrace{C\dot{x}^2}_{drag} + \omega_r^2 x = \frac{F_{in}}{m}, \tag{3}$$

where C is a parameter that represents the scaling of the side-to-side drag force on a segment of the body:

$$C = \frac{1}{2}\frac{\rho S C_D}{m}, \tag{4}$$

and ρ is the fluid density, S is an area (in this case, usually the lateral projected area or the wetted surface area), and C_D is a drag coefficient. This model represents bending at a single "joint" along the fish's body, and so it neglects many important features of an elongated swimmer, but it is used to illustrate the importance of
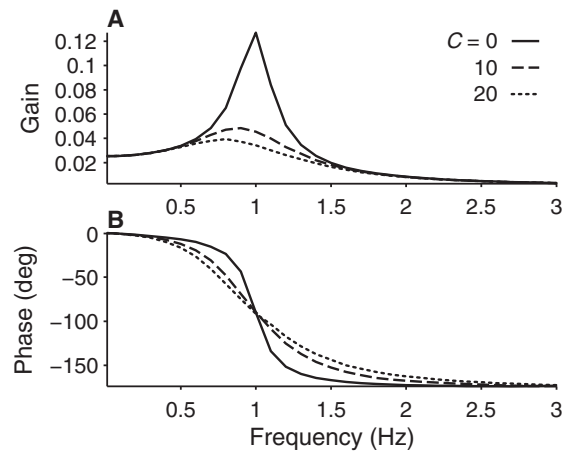

Fig. 1. Hydrodynamic damping can eliminate a resonant peak. Plots show the gain and phase for an underdamped harmonic oscillator ($\zeta = 0.1$) with fluid forces. (A) Gain of the output position with respect to the input force for three different values of the hydrodynamic damping coefficient C (solid line: $C = 0$; dashed: $C = 10$; dotted: $C = 0.1$). (B) Phase of the output position relative to the input force.

fluid damping. A more sophisticated model (Ramananarivo et al., 2011) found similar effects when they included a nonlinear drag force.

If the damping is large, either internally or due to drag, a system like that in Eq. (3) will not have a resonant peak. For a fish that has about the same density as water, $m = \rho V$, where V is a volume, and C_D is between 1 and 2 (for side-to-side oscillations) (Hoerner, 1965). The "fluid dynamic damping" is therefore of the order S/V, and it will only be large if the volume is relatively small compared to the area, which is not true for a cylinder or sphere, but is true for a flat plate – or a fish's tail fin – moving from side to side. Thus, even if fish bodies are elastic and not heavily damped internally, fluid drag may damp out any resonant peak.

Fig. 1 shows an example simulation of such a system (Eq. (3)) with $\zeta = 0.1$ and $f_r = \omega_r/2\pi = 1$ Hz, for a range of fluid damping values. For a sinusoidal forcing, the nonlinear damping term means that the output is not necessarily sinusoidal, but we can still estimate the gain (the ratio of the output amplitude to the input amplitude) and the phase offset between the output and input (Fig. 1). Even the medium fluid damping (dashed line) nearly eliminates the resonant peak. Ramananarivo et al. (2011) found a similar lack of resonance for flapping wings as long as they included the nonlinear effects of drag.

3. Do fish bodies have a useful mechanical resonance?

Consistent with the idea that fish bodies may be overdamped due to fluid effects, McHenry et al. (1995) found no clear resonant effects in a silicone model of a pumpkinseed sunfish (*Lepomis gibbosus*). They cast elastomer models with the same shape as a sunfish and a range of stiffnesses close to that of the fish, and oscillated the models back and forth near the head. The tail amplitude decreased monotonically as frequency increased from 2 Hz to 4 Hz, regardless of stiffness (McHenry et al., 1995).

Although the impact of resonance was not clear in that study, further studies by Long and colleagues demonstrated that body stiffness and damping clearly have an effect on swimming (Long et al., 1996, 2002b; Long and Nipper, 1996; Long, 1998). They hypothesized that fish might stiffen their bodies to swim faster. Long and Nipper (1996) and Long (1998) then developed a device to bend the whole bodies of fish and measure the stiffness, both passively and when the muscles were stimulated to produce force. Indeed, they found that the effective passive stiffness could increase