produced a rich literature describing the behavioral changes, computational principles and neural structures that underlie this learning. Applying this mechanistic insight of perceptual learning has substantial potential to promote more effective training for those striving to improve their perceptual skills. While to date our knowledge of perceptual learning is substantial, research in the field is active with many unresolved questions and much knowledge still to be gained.

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A hydrodynamically active flipper-stroke in humpback whales

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A central paradigm of aquatic locomotion is that cetaceans use fluke strokes to power their swimming while relying on lift and torque generated by the flippers to perform maneuvers such as rolls, pitch changes and turns [1]. Compared to other cetaceans, humpback whales (*Megaptera novaeangliae*) have disproportionately large flippers with added structural features to aid in hydrodynamic performance [2,3]. Humpbacks use acrobatic lunging maneuvers to attack dense aggregations of krill or small fish, and their large flippers are thought to increase their maneuverability and thus their ability to capture prey. Immediately before opening their mouths, humpbacks will often rapidly move their flippers, and it has been hypothesized that this movement is used to corral prey [4,5] or to generate an upward pitching moment to counteract the torque caused by rapid water engulfment [6]. Here, we demonstrate an additional function for the rapid flipper movement during lunge feeding: the flippers are flapped using a complex, hydrodynamically active stroke to generate lift and increase propulsive thrust. We estimate that humpback flipper-strokes are capable of producing large forward oriented forces, which may be used to enhance lunge feeding performance. This behavior is the first observation of a lift-generating flipper-stroke for propulsion cetaceans and provides an additional function for the uniquely shaped humpback whale flipper.

We deployed suction-cup attached digital recording tags outfitted with high-resolution cameras [7] on krill-feeding humpback whales gathered in large aggregations off the coast of South Africa. We recorded two instances of hydrodynamically active flipper-strokes, performed by different humpback whales (Figure 1A–J; Movie S1, Movie S2). For a flipper-stroke to be hydrodynamically active, it must generate lift and lift-induced drag as a result of its flapping motion and we used the following visual cues to identify these strokes: both flippers moved symmetrically; the flippers were angled into the path of the stroke; the stroke was oriented perpendicular to the body and not aligned with the direction of travel; there was a clearly visible flipper tip reversal between upstroke and downstroke; and the flipper-stroke occurred rapidly. We chose these criteria because they suggest the flippers are producing lift as a result of the stroke. Specifically, a rapidly revolving hydrofoil angled into the path of motion produces lift, and the orientation of the stroke suggests the lift is directed anteriorly [8]. Also, the symmetrical strokes indicate that the flippers are not being used to perform rolling or turning maneuvers, and the tip reversal suggests that the upstroke is hydrodynamically active and is not the type of recovery stroke that characterizes rowing motions. Finally, the rapid upstroke and downstroke further distinguish our observations from previously documented, drag-based rowing and sculling behaviors [5]. A flipper-stroke does not need to meet all of these criteria to produce lift and drag, and it is possible that further kinematic analysis of common flipper movements will reveal that they also generate hydrodynamic forces. To estimate the forces generated by both flapping humpback whale flippers we used a simple hydrodynamic model based on the blade element theory for flapping appendages (Figure 1K; Supplemental information; [8]). The model assumes that a flapping hydrofoil acts like a propeller blade, revolving in a flat plane with a uniform angle of attack and no translational velocity (Figure 1L).

Our first example of a lift-generating flipper-stroke shows a humpback whale performing a feeding lunge while swimming past the tagged animal (Figure 1A–J, Movie S1). Both the upstroke and the downstroke took 0.8 seconds and had a stroke amplitude of approximately 90° (Figure 1K). The flipper-stroke was oriented perpendicularly to the body. Assuming the flipper is 4.16 m long [3], the average velocity of the flipper tip is calculated as 8.2 m/s. The radius of gyration of the humpback flipper is 2.26 m, and the average translational velocity at this radius is 4.4 m/s. Across a range of plausible angles of attack [2], two flapping flippers are capable of producing

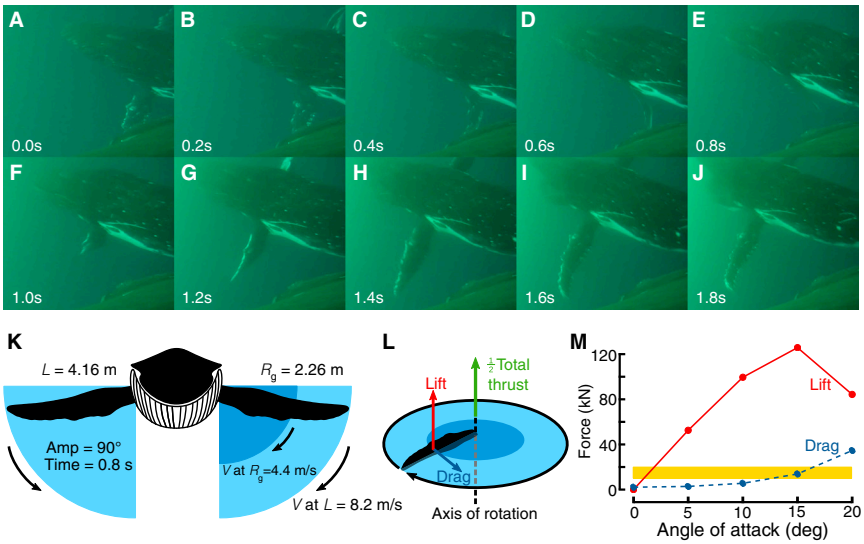

Figure 1. A humpback whale performs a hydrodynamically active flipper-stroke during a feeding lunge.

(A) The flippers begin in an abducted position and extended laterally. (B) As the stroke begins, the flippers symmetrically rotate downwards while starting their rapid adduction. (C, D) The downstroke path is roughly perpendicular to the body, with the leading edge of the flipper angled into the stroke. (E) The downstroke has an amplitude of approximately 90 degrees and takes 0.8 seconds. (F) As the upstroke begins, the flipper rotates medially around the long axis so that the leading edge is oriented with the path of the upstroke. (G, H, I) Like the downstroke, the upstroke is also roughly perpendicular to the body, has an amplitude of approximately 90 degrees, and takes 0.8 seconds. The mouth begins to open during the upstroke, between panels G and H. (J) At the end of the upstroke, the reversed flipper returns to a fully abducted and laterally extended position with the leading edge oriented into the direction of travel. By this time the buccal cavity is beginning to expand. During the course of the stroke the whale moves forward but does not change its heading or roll, and pitch does not seem to be affected by the movement of the flippers. (K) A quasi-steady hydrodynamic model suggests that a humpback flipper-stroke can produce high propulsive forces. A humpback whale with a 4.16 m flipper performs a downstroke with an amplitude of 90 degrees in 0.8 seconds. At the radius of gyration (R_g = 2.26 m) the velocity of the flipper (V) is 4.4 m/s. The upstroke is similar. (L) A propeller based model is used to calculate the hydrodynamic force produced by a spinning flipper. The lift is oriented perpendicularly to the stroke plane and drag resists the motion of the flipper. Because the flipper stroke is oriented perpendicular to the body, the lift generated by both flippers is used as forward thrust. Full details of the model are found in Supplemental information. (M) The estimated lift and drag produced by two humpback flippers performing a flipper-stroke across a range of average angles of attack. The yellow band represents the estimated contractile force produced by the musculature of the tail (from [9]).

a substantial amount of forward force (Figure 1M; maximum: 125.8 kN at a 15° angle of attack). However, at high angles of attack, rapid flipper-strokes induce large drag forces acting on long lever arms (up to 13.8 kN acting at the 2.26 m radius of gyration). The drag forces oppose the movement of the flippers and must be overcome by contraction of the adductor and abductor muscles. Even assuming that the whale flaps with a lower average angle of attack, the rapidly moving flippers are still capable of generating high levels of forward force (52.5 kN lift and 2.8 kN drag at a 5° angle of attack). Our second example shows a different individual performing a flapping stroke (Movie S2). This flipper-stroke was slower than the first example (2.6 s for the downstroke), and as a result the downstroke would generate approximately one tenth of the force. As a comparison, estimates of the maximum contractile force generated by humpback tail muscles are approximately 15 kN [9]. Our analysis suggests that the rapid, lift-generating flipper-strokes are capable of producing large, forward oriented forces, which may be used to enhance lunge feeding performance.

Although other aquatic animals, such as penguins and sea-lions, flap their forelimbs to generate lift and power locomotion [10], hydrodynamically active flipper-strokes have never been documented in cetaceans. The flipper stroke of the humpback whale and its kinematic similarity to the forelimb powered swimming strokes of these unrelated taxa is a powerful example of evolutionary convergence. It is possible that humpbacks are the only cetaceans performing lift-generating flipper-strokes because other species cannot attain high flapping velocities with their shorter flippers. If this is true, the ability to generate lift through flapping flipper-strokes could provide an additional mechanism for the evolution of the uniquely shaped humpback whale flipper.

SUPPLEMENTAL INFORMATION

Supplemental information including acknowledgements, two movies, experimental procedures and two tables can be found with this article online at http://dx.doi.org/10.1016/j.cub.2017.05.063.

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