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Context-dependent lateralized feeding strategies in blue whales

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Lateralized behaviors benefit individuals by increasing task efficiency, providing indirect fitness benefits in foraging and anti-predator behaviors [1–4]. The conventional lateralization paradigm suggests individuals are left or right lateralized, although the direction of this laterality can vary for different tasks (e.g. foraging or predator inspection/avoidance). By fitting tri-axial movement sensors to blue whales (*Balaenoptera musculus*), and by recording the direction and size of their rolls during lunge feeding events, we show how these animals differ from such a paradigm. The strength and direction of individuals' lateralization was related to where and how the whales were feeding in the water column. Smaller rolls (≤ 180°) predominantly occurred at depth (> 70 m), with whales being more likely to rotate clockwise around their longest axis (right lateralized). Larger rolls (> 180°), on the other hand, occurred more often at shallower depths (< 70 m) and were more likely to be performed anti-clockwise around their longest axis (left lateralized). More acrobatic rolls are typically used to target small, less dense patches of krill near the water's surface [5,6], and we posit that the specialization of lateralized feeding strategies may enhance foraging efficiency in environments with heterogeneous prey distributions.

Blue whales (n = 63 individuals) exhibited stereotyped maneuvers during lunge feeding events (n = 2,863 lunges in total; 45 ± 5.3 (mean ± SE) lunges from each individual, Figure S1A in Supplemental Information, published with this article online).

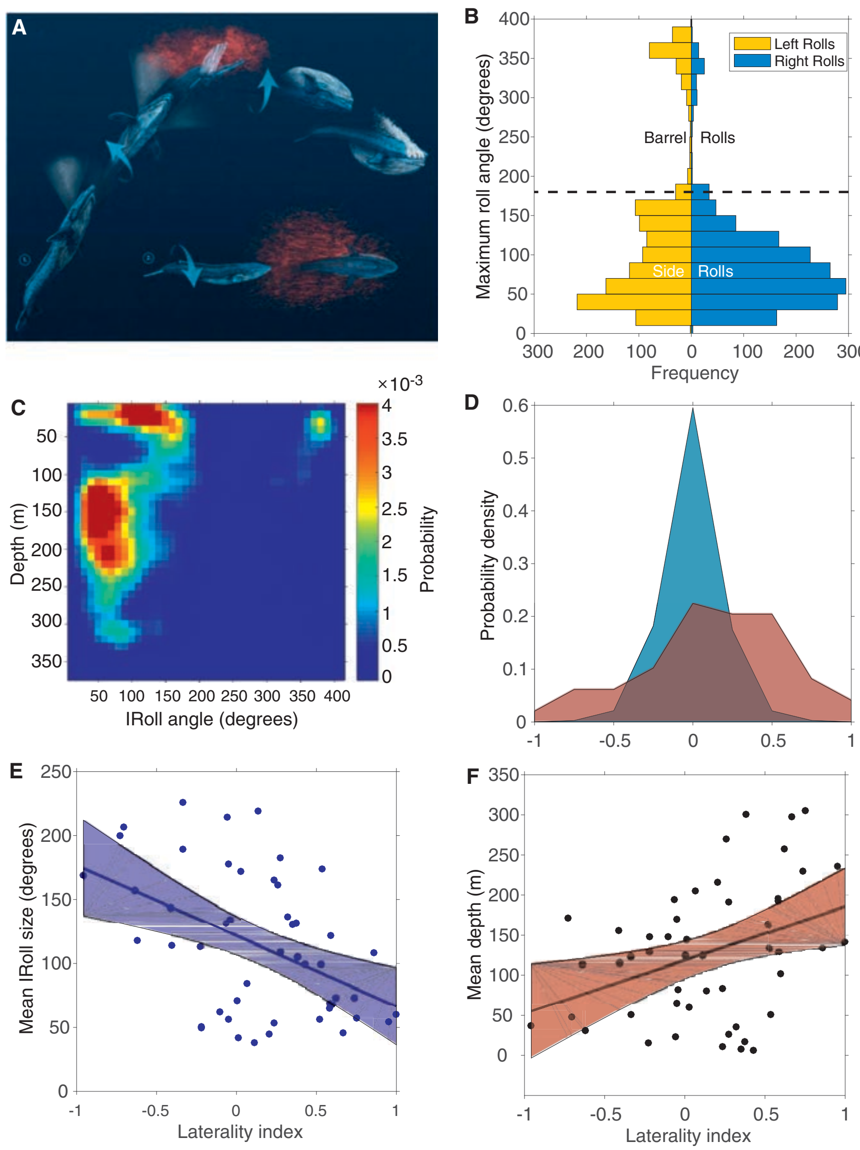

Figure 1. Lateralized feeding in blue whales.
(A) Artist rendition of the two types of lunge feeding strategies from side-on orientation (i.e. X-Z plane) — barrel and side rolls. The top schematic shows a left-sided barrel roll where the whale rotates a full 360 degrees during prey capture. The bottom graphic shows a right-sided roll, where whale rotates less than 180 degrees during the feeding event. The estimated angle of visual range is shown as a white cone and demonstrates that during the left-side roll, the whale's right eye maintains visual contact (or direction) with the prey until the lunge (mouth opening) is initiated. (B) Distributions of the maximum rolls angles for left (yellow) and right (blue) roll directions. The dashed line at 180 degrees represents the separation of classification of roll types (barrel rolls above, and side rolls below 180 degrees respectively). (C) Heat-plot showing the size of an individual whale's rolls as a function of depth. The majority of side rolls (< 180 degrees) are performed deeper than 70 m, whereas larger barrel rolls usually occur in the top 70 meters of the water column. Three rolls greater than 400 degrees were excluded from (B) and (C) for clarity. Distribution of the observed laterality indices of individuals (red) (n = 49) and what would be expected by chance (blue) based on the number of times we observed whales perform rolls (D). These two distributions differ significantly from one another ($\chi^2 = 38.9$, df = 1, $p < 0.001$). (E) Relationship between the laterality index of an individual and the mean size of its rolls. The larger the size of an individual's rolls, the more likely it was to be left lateralized. (F) Relationship between the mean depth an individual was feeding at and its laterality index. Individuals feeding at shallower depths were more likely to be left lateralized. In E and F, shaded regions represent the 95% confidence intervals for the fitted regression lines.

Immediately before a whale opened its mouth to capture prey, it made a rolling movement around its longest axis (Figure 1A). Two types of rolling behavior were associated with these lunges — 'side-rolls' and 'barrel rolls'. Smaller side-rolls consisted of the whale rotating less than or equal to 180-degrees in one direction during the feeding lunge, followed by a rotation in the opposite direction to its initial rotation (i.e. non-complete rotation) (Figure 1A). In contrast, larger, more acrobatic 'barrel-rolls' consisted of a uni-directional roll past the horizontal (i.e > 180 degree rotation) (Figure 1A,B). While the majority of side-rolls were performed deeper than 70 m, the majority of barrel-rolls were performed in the upper 70m of the water column (Figure 1C).

These rolls also have directionality, and can either occur when a whale initially rolls to the left or right around its longest axis. To assess whether these rolls were lateralized at the population and individual level, we calculated a laterality index (*LI*) for each individual that made 10 or more rolls (n = 49 individuals). The *LI* of each individual was calculated as: $LI = \frac{R_r - L_r}{R_r + L_r}$, where R_r and L_r are the numbers of rolls that an individual made to the right and left respectively. At the population level, the distribution of laterality indices differed significantly from what would have been expected assuming no individual-level lateralization ($\chi^2 = 38.9$, df = 1, $p < 0.001$; Figure 1D). There were both more individuals that were left and right lateralized in the population than would be expected by chance (Figure 1D). At the individual level, 28 of the 49 individuals we measured had absolute laterality indices that differed significantly from chance (Figure S2). Of these individuals, there were significantly more right-lateralized individuals than left-lateralized individuals in the population (Binomial Test, n = 21, N =28, P = 0.006) (Figure 1D).

Individuals were consistent in the size of their rolls to the left or right (Spearman Rank Correlation: $r_s = 0.78$, n = 55, $p < 0.001$; Figure S3 **(Au: references to supplemental figures need to be revised in the light of the new supplement)**; some whales made consistently larger rolls whereas some made consistently smaller rolls. Individuals that made larger rolls were more likely to be left lateralized, whereas individuals that made smaller rolls were more likely to be right lateralized (Spearman Correlation, $r_s = -0.40$, n = 49, p = 0.005; Figure 1E). Further, individuals' laterality indexes were related to the mean depth at which they were feeding (Pearson Correlation, R = 0.37, n = 49, p = 0.009; Figure 1F). The shallower the depth at which individuals fed, the more likely individuals were to have a negative laterality index. There was no evidence, however, that individual whales made consistently the same sized rolls above or below 70 m (see Supplemental Information).

Why should individuals show different lateralized feeding strategies depending on where and how that behavior is performed? Blue whales feed exclusively on krill and the abundance and distribution of this resource influences their foraging behavior [6,7].

Krill patches are generally smaller and less dense near the water's surface, and more acrobatic maneuvers, such as barrel rolls, may be required to capture these evasive prey [6,7]. Blue whales' eyes are laterally positioned, and thus rolling maneuvers may be required in order to see prey above them. At shallow depths, whales lunged at steeper pitch angles and rolled more often to the left, providing visual input of the prey to the whale's right eye (Figure 1A). In vertebrates, the optic nerves innervate the brain's hemispheres contra-laterally, and the left hemisphere of the brain controls kinematic coordination, predictive motor control and the ability to plan and coordinate actions [8]. Using these types of movements may be important at this body size where movements take considerably longer to complete due to mechanical scaling effects and physical limitations of sensory transduction. Acrobatic, albeit stereotypical movements, coordinated through the brain's left hemisphere, may be required to target small patches of prey that are easily visible, and hence manifest as a left-sided rolling behavior. It is unclear, however, why whales predominantly show right-sided lateralized feeding behavior at depth, making it important for these findings to be compared across other populations of blue whales and other species of whale. While fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*), for example, appear to only exhibit lateralized behaviors in one direction [9,10], these studies did not account for the depth at which feeding events took place, and our results show that this context dependence is important to consider. ~~Although lateralized feeding behaviors have been demonstrated in a number of systems, our results represent a previously unrecognized context-dependent lateralization that depends on where and how animals perform stereotypical behaviors in their natural environment.~~

SUPPLEMENTAL INFORMATION

Supplemental Information contains experimental procedures, two figures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2017.10.023.

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