and 'model-free' learning have not thus far been clearly revealed by human fMRI studies. Some of the main issues for future research on habits will be how executive control is devolved among structures during behavior and how flexible (or plastic) top-down control can avoid competition between the goal-directed and habit systems, to promote their optimal cooperation and integration in determining successful behavioral outputs.

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Context-dependent lateralized feeding strategies in blue whales

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Lateralized behaviors benefit individuals by increasing task efficiency 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 were 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°), conversely, occurred more often at shallower depths (<70 m) and were more likely to be performed anti-clockwise (left lateralized). More acrobatic rolls are typically used to target small, less dense krill patches 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). 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 ≤180° 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° 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 70 m of the water column (Figure 1C).

These rolls also have directionality, occurring when a whale initially rolls to the left or right. To assess whether rolls were lateralized at the population and individual levels, 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, there were significantly more right-lateralized individuals than left-lateralized individuals (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 S2B); 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 feeding occurred (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 krill 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 feeding depth. Our results show that this context-dependence is important to consider.
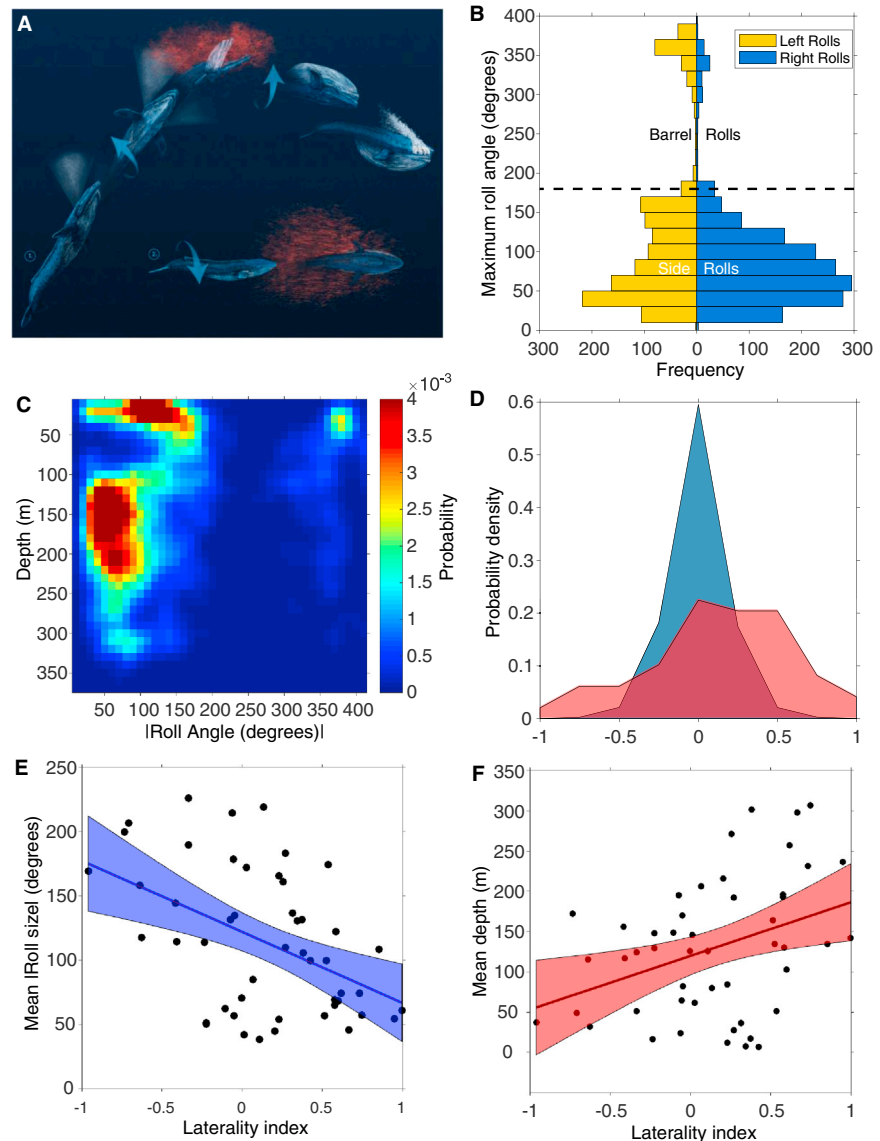

Figure 1. Lateralized feeding in blue whales.
(A) Artist rendition of the two types of lunge feeding strategies from side-on orientation (i.e. X–Z plane) — barrel and side-rolls. The top schematic (1) shows a left-sided barrel roll where the whale rotates a full 360° during prey capture. The bottom graphic (2) shows a right-sided roll, where the whale rotates less than 180° 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 is directed towards 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° represents the separation of classification of roll types (barrel rolls above, and side rolls below 180°, respectively). (C) Heat-plot showing the size of individual whales' 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° were excluded from (B) and (C) for clarity. (D) Distribution of the observed laterality indexes of individuals (red) (n = 49) and expected laterality indexes assuming no individual-level lateralisation (blue) (see Supplementary Information). These two distributions differ significantly from one another (χ^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.

SUPPLEMENTAL INFORMATION

Supplemental Information contains experimental procedures and 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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Emergent acoustic order in arrays of mosquitoes

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The yellow fever mosquito *Aedes aegypti* forms aerial swarms that serve as mating aggregations [1]. Despite lacking the remarkable collective order of other animal ensembles, such as fish and birds [2], the kinematic properties of these swarms bear the hallmarks of local interaction and global cohesion [3,4]. However, the mechanisms responsible for collective behaviour in mosquitoes are not well understood. Mosquitoes use their antennae as hearing organs to locate and interact with one another via the frequencies of sounds generated by their beating wings [5]. Acoustic detection and recognition are known to mediate copula formation in opposite-sex pairs [6], but have not been investigated in larger groups. By recording the flight tones of multiple, tethered, male *Ae. aegypti*, we test the hypothesis that acoustic signalling is a determinant of swarm morphology and present the first compelling evidence that flight tone interactions between males drive observed group coherence in the frequency domain. We find that group size critically affects collective and individual acoustic traits: cohesive acoustic behaviours emerge in groups of more than six male mosquitoes, occurring to a greater degree than predicted in the absence of interaction. Importantly, acoustic interactions between multiple males differ from those reported previously for same-sex pairs [7,8]. Our findings enable future research targeting key behavioural and reproductive aspects of the biology of mosquitoes of epidemiological importance.

We simultaneously recorded the individual flight tones of up to $N = 8$ tethered male *A. aegypti* in a linear arrangement using a custom-built microphone array (Figure 1A and Supplemental Information). Extraction of each mosquito's fundamental wing beat frequency was performed using Hilbert spectral analysis [9], yielding high-resolution spectra in both time and frequency (Figure 1B).

To test whether the mosquitoes' acoustic emissions changed with the number of males present, we calculated the differences between the flight tones of all pairs of males. Sorting these frequency differences for each male according to their closest, second closest, etc. flight tone match at each time point yielded a series of distributions that became progressively sharper, left-skewed and clearly separated with increasing group size (Figure 1C, left column and Figure S1A). Consequently, as groups became larger, individuals' wing-beat frequencies were more regularly spaced, and the average flight tone separation between them decreased (Figure 1D, black line). The instantaneous standard deviation of the group's collective wing-beat frequencies (the 'group spread', Supplemental Information) also varied with ensemble size. Small- and intermediate-sized groups exhibited a broader range of flight tone dispersals than larger arrays, for which the group spread was narrowly distributed (Figure 1C, right column, grey-shaded area). In larger groups ($N = 7–8$), individuals were tightly bound to the acoustic average: the median spread of flight tones in these arrays was comparable to the smallest ($N = 3$), and was much lower than at intermediate sizes ($N = 4–6$; Figure 1E, black line).

We hypothesise that acoustic interactions between males drive emergent phenomena in the frequency domain. To test this, we used permutation sampling to construct arrays of non-interacting individuals selected at random from recordings of different groups, or from recordings of males flying alone (labelled respectively 'random group' and 'random lone', detail in Supplemental Information). For all group sizes, both the median frequency separation and group spread were always lower for mosquitoes flown together than in the non-interactive arrays (Figure 1D,E), but only significantly so (in >95% permutations) in the largest groups ($N = 7–8$). The summary statistics of non-interactive groups also changed with their size: for combinations of lone males this relationship was roughly linear, whereas the properties of randomly sampled,