

**Figure 4 | Angled hairs break reflection symmetry, both in geometry as well as in drag response.** **a**, Schematic of straight hairs, cantilevered perpendicularly to the base. This configuration is invariant to reflections about hair axes (dashed line). **b**, Schematic of hairs anchored at an angle  $\theta_0$  with respect to the surface normal, which break reflection symmetry. **c**, Photograph of elastomer hairs with  $\theta_0 = 30^\circ$ . **d**, Schematic of angled hairs bending down in response to flow with the grain. **e**, For flow against the grain, hairs bend up and decrease the gap through which fluid flows. This results in an impedance ( $Z_-$ ) that is larger than for flow with the grain ( $Z_+$ ). **f**, Impedance ratio  $Z_-/Z_+$  as a function of the rescaled velocity  $\tilde{v} = (4\eta L^2 \nu / E \phi a^2 H)(1 - (L/H) \cos \theta_0)^{-3/2}$ . Larger values of  $Z_-/Z_+$  correspond to increased rectification. Experimental results (symbols) and numerical results (lines) for hair beds of different anchoring angles  $\theta_0$  (legend, top left). Hair dimensions satisfy  $L \cos \theta_0 / H = 0.47$ .

Here, because of Nature's formatting, the results were interpreted earlier, and the discussion section doubles as the conclusion

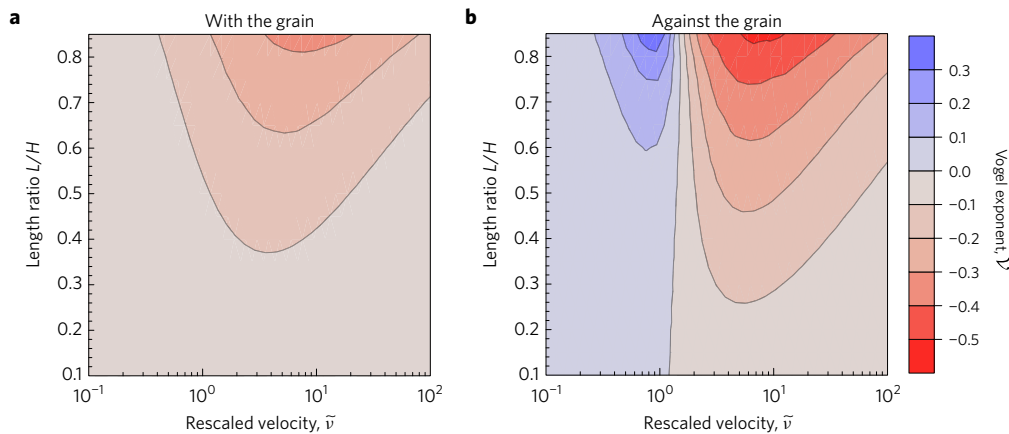
The authors restate their claims, as well as the key insights/techniques that enabled their results

Then, they place their results within the broader body of relevant literature, indicating how the new results provide new insights into other fields.

Finally, they address how their results can be built upon in valuable future work (here, to enable new technologies)

### Discussion

To summarize, we have shown that beds of deformable hairs can reconfigure in response to fluid flows. We identified a dimensionless, elastoviscous parameter  $\tilde{v}$ , which defines different response regimes. When  $\tilde{v}$  is of order one, hair reconfiguration results in a nonlinear response. When hairs are straight, or when fluid flows with the grain of angled hairs, we find a drag-reducing nonlinear response, characterized by a negative Vogel exponent  $\mathcal{V}$ . In contrast, drag-increasing response and positive  $\mathcal{V}$  occur when fluid flows against the grain of angled hairs. We were able to



**Figure 5 | The reconfiguration regime of angled hairs is characterized by a Vogel exponent that can attain positive values when flow is against the grain.** **a**, Numerically computed contour plot of the Vogel exponent  $\mathcal{V}$  as a function of the length ratio  $L/H$  and rescaled velocity  $\tilde{v} = (4\eta L^2 \nu / E\phi a^2 H)(1 - (L/H)\cos\theta_0)^{-3/2}$  for hairs with  $\theta_0 = 30^\circ$  and flow with the grain. **b**,  $\mathcal{V}$  for flow against the grain. Blue areas denote a positive Vogel exponent.

probe these nonlinear responses by assuming that shear stress is concentrated at the hair tip. This simplifying assumption dispenses with the need to integrate stresses over the entire hair surface, and allows us to probe beyond the linear regime<sup>35</sup>.

The drag-reducing response of straight hairs, which we described with the rescaled impedance  $\tilde{Z}$  (see Fig. 2c), provides experimental evidence that hairy surfaces reconfigure to reduce the shear stress experienced by the anchoring surface. Hair beds such as the hyaluronan brushes of blood vessels<sup>11,13</sup> or brush-border microvilli of kidney tubules<sup>7</sup> have been implicated in mechanotransduction, in analogy to experimental systems where hair deflection is used to sense fluid forces<sup>36–41</sup>. Our work raises the hypothesis that the drag-reducing nonlinearity of biological hair beds protects sensitive mechanotransductive mechanisms from excessive stresses.

Additionally, the drag-reducing and drag-increasing response of angled hairs amounts to rectification, or an axially asymmetric flow response, which we express by the impedance ratio  $Z_-/Z_+$  (see Fig. 4f). Prior studies have shown that control over a rectification response can lead to the development of diverse microfluidic components, such as pumps and diodes<sup>42–44</sup>. Typically, rectification at low Re is challenging to attain because the governing Stokes equations are linear and time-reversible. Existing designs have overcome this difficulty by employing viscoelastic fluids<sup>42</sup> or anisotropic surface-wetting properties<sup>43,44</sup>. The rectification response we report here instead relies on a geometric nonlinearity, whose operating range can be controlled by the geometric factors embedded in  $\tilde{v}$ . The rectification nonlinearity of angled hairs holds at arbitrarily low Reynolds number and is compatible with Newtonian fluids and conventional surfaces. Future work could lead to the design of integrated microfluidic components such as diodes and pumps.