Intermittency, fluctuations and maximal chaos in an emergent universal state of active turbulence

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The phenomenon of active turbulence, a complex organization of matter driven at the scale of its constituent agents, is puzzling. Specifically, the lack of scale-separation in low-Reynolds-number active flows breaks away from the familiar notions of the energy cascade and approximate scale-invariance of inertial turbulence. Here, using a generalized hydrodynamic model developed for bacterial turbulence, we provide compelling analytical and numerical evidence that, beyond a critical drive, active turbulence indeed attains universality akin to inertial turbulence. In this asymptotic state, the energy spectrum scales as $k^{-3/2}$, reminiscent of some classes of inertial turbulence. The flow also exhibits spatio-temporal intermittency beyond the transition, as seen from non-Gaussian fluctuations in velocity differences. With these tell-tale fingerprints, active turbulence is placed closer in phenomenology to inertial turbulence than previously held. We show, however, that as a consequence of a finite range of scales, the degree of chaoticity and hence mixing efficiency saturates to a maximum in the asymptotic regime, unlike unbounded chaos in inertial turbulence. We conclude that active turbulence, depending on the level of drive, can switch between fundamentally distinct non-universal and universal states.

The emergent fluid behaviour of a dense suspension of motile bacteria 1–4 is susceptible to a wide range of dynamical phases 5–7. This makes such systems and their characterization quite distinct from our more accustomed understanding of (classical) inertial fluids, which typically undergo a laminar–turbulence transition at moderately large Reynolds numbers 8. Among the different dynamical phases, the ‘active turbulence’ regime is arguably the most vexing 4,9. Although the suspensions have a decidedly low Reynolds number, this phase displays features that seem to suggest that an analogy with inertial, high-Reynolds-number turbulent flows is not entirely out of place 1. Yet, the question of whether low-Reynolds-number active flows can truly be considered turbulent and if, indeed, the physics is universal for such systems remains to be fully answered. These are, of course, important questions, not only from the point of view of theoretical, non-equilibrium physics, but also from a biological perspective. The underlying reasons for why nature allows such complex, emergent flows in a suspension of active agents, with reasonably simple rules of interactions and motion, ought to be intrinsically related to optimal strategies for evasion and foraging 10,11. Recent studies have shown the effects of anomalous superdiffusion in Lagrangian measurements, underlining a key distinction between these two classes of turbulence, the origin of which perhaps lies in what is best for the microorganisms...
that constitute such flows\textsuperscript{12,13}. These theoretical studies\textsuperscript{6,13} in fact, were a first hint (albeit from a Lagrangian perspective) that the active turbulence phase may fundamentally change depending on the level of activity. What has remained elusive is whether, in this phase, there is a limiting behavior upon increasing activity and thus a universal state similar to inertial turbulence\textsuperscript{4,5} with the Reynolds number going to infinity? In particular, are the tell-tale signatures of inertial turbulence, namely (approximate) scale-invariance with a universal spectral scaling exponent, fluctuations, intermittency and chaos, replicated in active turbulence?\textsuperscript{5}

In this Article we address these questions and show that, for values of activity beyond a critical threshold, which are nevertheless consistent with velocities in experimentally realizable bacterial flows\textsuperscript{1,16}, fluctuations of the velocity field are intermittent (non-Gaussian) and accompanied by a scale-invariant distribution of kinetic energy across Fourier modes with a universal scaling exponent. The existence of such a critical activity—at which a universal, turbulent and maximally chaotic state emerges—has paradoxically no counterpart in the analogous Reynolds-number parameter for the most generic case of statistically homogeneous, isotropic inertial turbulence.

### Generalized hydrodynamics model

We perform detailed direct numerical simulations (Methods) of the evolution equation

\[
\partial_t \mathbf{u} + \mathbf{u} \cdot \nabla \mathbf{u} = -\nabla p + \partial_i \partial_j \mathbf{u}^i - \partial_j \mathbf{u}^j - (\alpha + \beta |\mathbf{u}|^2 \mathbf{u})
\]

(1)

for the incompressible, coarse-grained velocity field \( \mathbf{u}(x, t) \) of an active, bacterial suspension\textsuperscript{1}. This is a minimal, dry active turbulence model leading to self-sustaining flows, ignoring hydrodynamic interactions with the solvent fluid, and thereby constrained to being valid in the high bacterial density limit\textsuperscript{6}, which is the regime in which we are interested. The nature—pusher or puller—of the constituent bacterium is determined by the sign of \( \lambda \). Our study focuses on pushers with \( \lambda = 3.5 \). In the Toner–Tu driving term\textsuperscript{17,18}, \( \beta > 0 \) for stability and \( \alpha < 0 \) ensures an active injection of energy at scales \( 1/\sqrt{|\beta|} \).

The coefficients \( \Gamma_0 \) and \( \Gamma_1 \) lead to length \( \Gamma_{\text{r}} = \sqrt{\Gamma_0 \Gamma_1} / \Gamma_0 \) and time \( \tau_{\text{r}} = \Gamma_1 \Gamma_0^2 \), which arise from linear instabilities. We choose parameters consistent with experiments\textsuperscript{1,4,20}: \( \Gamma_0 = 0.045 \), \( \Gamma_1 = 1.03 \), \( \beta = 0.5 \), and \( -8 \leq \alpha \leq -1 \), approximating flows with bacterial velocities in the range of 25–75 \( \mu m \text{s}^{-1} \).

### Intermittency and fluctuations

Taking our cue from high-Reynolds-number turbulence, we begin by investigating signatures of intermittency, with increasing activity. Figure 1a,b presents vortex trails as a temporal superposition of regions with vorticity magnitude \( \omega \) greater than multiples of their respective root-mean-square vorticity \( \omega_{\text{rms}} \). Low-threshold vortex trails are equally prevalent for mildly (\( \alpha = -1 \)) and highly (\( \alpha = -6 \)) active suspensions. At higher thresholds \( \langle |\omega| \rangle \gtrsim \omega_{\text{rms}} \), mildly active suspensions appear quiescent, whereas highly active suspensions continue to show strong deviations in \( \omega \). We quantify this behaviour by considering the distribution of (longitudinal) velocity increments \( \delta \mathbf{v} = [\mathbf{u}(x + r) - \mathbf{u}(x)] \cdot \frac{\mathbf{r}}{|\mathbf{r}|} \).

In fully developed turbulence, the analogue of such measurements in the so-called inertial range shows a strong departure from a Gaussian distribution, and the fat tails suggest that velocity increments are intermittent, with bursts of extreme values\textsuperscript{1}. For low activities, the distributions of the increments, as well as the velocity gradients, are Gaussian, as also noted in previous studies\textsuperscript{4,12,13}. However, we find (Fig. 1c) that as \( \alpha \lesssim -5 \), the distributions become distinctly non-Gaussian, reminiscent of high-Reynolds-number turbulence\textsuperscript{4,13}.

This departure from a Gaussian is a sign of intermittency and is quantified by measuring the kurtosis \( \kappa = \langle |\delta \mathbf{v}|^4 \rangle / \langle |\delta \mathbf{v}|^2 \rangle^2 \) as a function of \( r \), as shown in the inset of Fig. 1d. Although for mild levels of activity (\( \alpha = -1 \)) we see a scale-independent \( \kappa \approx 3 \), as it should be for Gaussian distributions, when \( \alpha \lesssim -5 \), clear evidence of intermittency appears as \( \kappa > 3 \) over a wide range of \( r \). Fixing on a single (representative) value of \( r = 1.0 \), we see (Fig. 1d) a clear rise in \( \kappa \) from the Gaussian limit as soon as \( \alpha \lesssim -5 \). Experiments on swarming Bacillus subtilis have also shown non-Gaussian velocity gradient statistics\textsuperscript{21} that may well be the first signs of intermittency. This emergent intermittency suggests that active suspensions may have asymptotic (in activity) states that have more in common with inertial turbulence than previously appreciated.

### Non-universal spectral scaling at low activity

The transition from non-intermittent to intermittent flow has important consequences for scale-invariance in such suspensions. A useful probe for this is the energy spectrum, \( E(k) \), characterizing the (self-similar) distribution of kinetic energy across Fourier modes\textsuperscript{8}. The scaling form for the energy spectrum is easy to obtain dimensionally from the (advective) energy flux \( f(k) \) (Methods) and the local (scale-dependent) turnover timescale \( \tau_{\text{tot}}(k) \) via \( \tau_{\text{tot}}(k) f(k) \cdot k E(k) \). At high activity, velocity increments are Gaussian and the effective timescale, \( \tau_{\text{eff}}(k) \), is a constant, independent of \( k \), as shown by others\textsuperscript{22}. By using this argument in the spectral equation, we obtain \( E(k) \approx K^{-2} \) with, unlike in inertial turbulence, an activity-dependent, non-universal scaling exponent \( \delta \), which suggests a change in the nature of the flow as \( \alpha \to \alpha_c \), to a possibly universal state. Naively, setting \( \delta = 0 \), we obtain \( \alpha_c = 2/\tau_{\text{eff}} - 2\tau_{\text{tot}} \) (for \( \beta = 0.5 \)). This, of course, makes the strong assumption that \( \tau_{\text{tot}} \) is strictly scale-independent all the way up to \( \delta = 0 \).

We know that \( \tau_{\text{tot}} \) itself is a function of \( \alpha \) and, empirically, as long as \( \alpha > \alpha_c \), the root-mean-squared velocity is \( u_{\text{rms}} = \sqrt{2 \tau_{\text{tot}} \sim c \sqrt{\alpha_c + 2} \text{, where} c_1 < 0 \text{ and } c_2 > 0 \text{ are constants}\textsuperscript{22,23} \).

By using this expression, and solving the resultant quadratic equation, we obtain \( \alpha_c = -10 \). The change in flow behaviour at \( \alpha = -5 \) (Fig. 1d and in the following) occurs well before this theoretical prediction. This hints that the assumption of a constant \( \tau_{\text{eff}} \) becomes weak and indeed breaks down as \( \alpha \to \alpha_c \) from above.

### Universal spectral scaling beyond critical activity

Assuming a scaling form \( E(k) \sim k^\delta \), the local turnover timescale \( \tau_{\text{edd}} \sim \sqrt{k E(k)} \) can no longer be ignored as larger scales become more energetic when \( \delta \lesssim 0 \). Furthermore, the flow reorganization seen in earlier studies of highly active turbulence \( (\alpha \lesssim \alpha_c) \) suggests an additional source of ‘noise’ that accentuates non-local interactions in Fourier space. We conjecture a simple self-similar timescale \( \tau_\alpha \sim 1/k \) for this noise, which may emerge from a constant-activity-induced velocity \( v_\alpha = \sqrt{|\alpha|/\beta} \) acting across scales, leading to an ansatz

\[
\tau_{\text{eff}}(k) = (\tau_{\text{edd}}(k) \tau_\alpha)^{1/2} \sim k^{-(\frac{\alpha+\delta}{2})}
\]

of a scale-dependent, effective energy transfer timescale for \( \alpha \lesssim \alpha_c \).

In principle, although more complex forms of \( \tau_{\text{eff}} \) may be proposed, we posit our definition given its simplicity and sound physical motivation for both \( \tau_{\text{tot}} \) and \( \tau_{\text{edd}} \). Although it is not possible to independently measure \( \tau_{\text{tot}} \), we test our conjecture in Fig. 2, showing log–log plots of \( \tau_{\text{eff}} = \frac{\mu k^2}{U_{\text{tot}}} \) versus \( k \) for \( \alpha \) values on either side of \( \alpha_c \). Reproducing the phenomenology of active turbulence at \( \alpha \gtrsim \alpha_c \), this effective timescale is indeed a constant and independent of \( k \) (ref. 22).

However, as soon as \( \alpha \lesssim \alpha_c \), a clear power-law \( \tau_{\text{eff}} \sim k^\delta \) emerges.
with large values of ω, the highly active suspension shows spatio-temporal intermittency, of each separated by Δt with vorticity above increasing thresholds, superimposed over 20 snapshots, α for mildly (~) k, k argument, that E(α) = −3/2 as δ → 0 as α → ac, the spectral exponent δ ≳ α eff for a scale-dependent flux |δu||/σ for different values of α, extracted from plots such as those shown in the inset. We find a sharp transition from a linear (non-universal) dependence of the energy spectrum on activity, consistent with earlier measurements, to a constant, universal asymptotic state δ = −3/2 as α ≤ ac = −5. Here we highlight that the crossover value of ac does not vary with system size, provided the largest vortices are well-resolved within the simulation domain, which we rigorously ensured.

Although we show a simple transition in active turbulence to an asymptotic, universal intermittent state (Fig. 1) with a scale-dependent timescale (Fig. 2) and a constant spectral exponent (Fig. 3), the precise form of the flux is not consistent with the theoretical conjecture.

The heuristic argument outlined above is physically appealing. Nevertheless, a more rigorous, analytic way to show the transition at α ≤ ac is by using the (approximate) equation of motion (assuming closure at the level of the fourth moment) for E(k) (ref. 20). As detailed in the Methods,
one can then show that $\xi \neq 0$ leads inevitably to an $\alpha$-independent $\delta$. Furthermore, a solution of this spectral equation yields an energy spectrum $E(k) \sim k^{-5/3}$ with an $\alpha$-dependent exponential tail. The agreement between the analytical and phenomenological approaches, along with the compelling numerical evidence, leaves little doubt about the existence and robustness of this critical activity parameter.

Eulerian chaos in active turbulence

Although the lack of a constant flux is in sharp contrast to high-Reynolds-number turbulent flows, the emergent state seems to share more in common with inertial turbulence: intermittency, non-Gaussianity and a universal scaling of the energy spectrum. Inertial turbulence has another important attribute, namely, the dependence of chaos—quantified by a positive Lyapunov exponent $\Lambda$—on the Reynolds number of the flow. This is particularly interesting, because the lack of a true inertial range (characterized by constant energy flux across scales) in active turbulence results in no appreciable widening of the range of scales, with increasing activity, over which the spectral scaling $k^{-5/3}$ holds. Thus, from this point of view, increasing the level of activity is not analogous to an increasing Reynolds number in inertial turbulence.

To test these ideas, we set up perturbed twin simulations that allow tracking of the evolution of a controlled initial (white noise) perturbation (Methods), and thus a measure of Eulerian chaos. The divergence between the unperturbed A and perturbed B solutions is quantified by the difference vorticity $\Delta \omega(x, t) = \omega^B(x, t) - \omega^A(x, t)$ and difference velocity $\Delta u(x, t) = u^B(x, t) - u^A(x, t)$ fields, and the evolution of the perturbation is governed by the time-dependence of the decorrelator $\Phi(t) \equiv \langle \Delta u(x, t) \Delta u(x, t') \rangle$ (where $\langle \rangle$ denotes spatial and ensemble-averaging).

Understandably, at long times, systems A and B decorrelate and hence $\Phi(t)$ saturates to $2E_{\text{tot}}$. At short times, however, we expect an exponential growth $\Phi(t) \sim \exp \delta t$ indicative of the chaotic nature of these suspensions. Figure 4c confirms these two behaviours for different $\alpha$, from which we extract the Lyapunov exponent $\Lambda$—a measure of the level of chaos in the system—and examine its dependence on activity (Fig. 4c, inset, left axis). Interestingly, and perhaps unsurprisingly, $\Lambda$ increases monotonically with activity and achieves a maximum as $\alpha \to \alpha_c$ (from above) and then plateaus. Thus, active suspensions are indeed maximally chaotic, and remain so, as $\alpha \leq \alpha_c$ (indicated by the vertical blue bar). The importance of these maximally chaotic states is best understood by normalizing $\Lambda$ with the root-mean-square vorticity $\omega_{\text{rms}}$. A plot of this normalized Lyapunov exponent (Fig. 4c, inset, right axis) reveals that the perturbation growth timescale in fact becomes smaller in comparison to the vortex timescale when $\alpha \leq \alpha_c$. In other words, the chaoticity of the suspension increases fundamentally when $\alpha$ goes beyond $\alpha_c$, and not as a consequence of more vigorous advection.

A visual impression of how these systems decorrelate is best obtained by introducing a localized perturbation. In Fig. 4a,b we show representative pseudo-colour plots of $\Delta \omega$ for $\alpha = -1$ and $\alpha = -6 < \alpha_c$, respectively, over time. The initially $(t = 0)$ localized Gaussian ($\sigma = 0.02L$) perturbation spreads rather quickly in a self-similar manner until the $\Delta \omega$ field itself becomes indistinguishable from the corresponding vorticity fields (Methods). (The Lyapunov exponents measured from such spatially localized perturbations are consistent with those shown in Fig. 4c, and these results are qualitatively insensitive to the exact nature and amplitude of the perturbation.)

Finally, we examine the spectral growth of the perturbation energy by tracking the energy spectrum $\Delta E(k)$ of the difference vorticity $\Delta \omega$. Figure 4d shows that, for $\alpha = -1$, the initial perturbation rapidly assumes a self-similar spectral shape that grows at a constant exponential rate (equidistant curves along the vertical log scale) until saturation, revealing a single dominant Lyapunov exponent, because the mildly active flow has a single vortex scale. At $\alpha = -6$, the flow becomes truly multiscale, which is reflected in Fig. 4e, where the initial perturbation first assumes a self-similar shape until saturation of the high wavenumbers, followed by a successive (and slower) saturation of the low wavenumbers. We highlight that this behaviour is reminiscent of inertial turbulence, where the growth of perturbation energy slows down as successively larger scales saturate, according to Lorenz.
or the so-called ‘permanence of large eddies’\(^6\). However, the saturation of \(\Lambda\) with increasing activity is unlike the unbounded growth of \(\Lambda\) with Reynolds number in inertial turbulence\(^{20-22}\).

**Discussion and conclusions**

We show that low-Reynolds-number active flows, beyond a critical threshold of activity \(\alpha_c\), are universal in a manner similar to inertial turbulence. Interestingly, unlike the case of inertial, homogeneous and isotropic turbulence, where the estimate of a critical Reynolds number is moot, active suspensions seem to allow a critical value of activity when a truly turbulent and universal phase emerges. This is summarized in terms of a transition, most dramatically seen in the activity when a truly turbulent and universal phase emerges. This is

\[
\delta = \frac{\text{cell}(2\alpha + 4\beta_{\text{tot}})}{4} - 1 \geq 0 \quad \alpha \geq \alpha_c
\]

\[
\delta \leq -3/2 \quad \alpha \leq \alpha_c
\]

Although the evidence for this transition at \(\alpha_c = -5\) leaves little room for doubt, the form of the scaling is reminiscent of several classes of turbulent flows where \(\delta = -3/2\). The most well-known example of this is perhaps magnetohydrodynamic turbulence\(^{31,32}\), but other instances are known in the area of wave turbulence\(^{33}\)—such as acoustic turbulence\(^4\), active binary fluid turbulence\(^{34}\), as well as more unrelated examples like the Burgers equation on a fractally disordered (Fourier) lattice\(^{35}\). It is important in future work to understand whether active turbulence in the \(\alpha \leq \alpha_c\) regime can be described in terms of the formalisms developed in these areas.

We note that universal spectral scaling has also been observed in a minimal model for active nematic flows with \(k^3\) at small wavenumbers\(^{36}\). Sparse systems, like active swimmers\(^{37}\) or self-assembling magnetic spinners\(^{38}\), may also exhibit Kolmogorov statistics with \(k^5\) spectra, but these systems without any collective motion are fundamentally different and not exactly comparable to our dense bacterial suspensions. Recent numerical work on inertial active nematics has shown energy spectra that may be compatible with both \(-3/2\) or \(-5/3\), while experiments on cell-division- and apoptosis-driven epithelial turbulence\(^{39}\) display scaling with an exponent in the range of \(-1.58\) (experiments) \(\leq \delta \leq -1.40\) (simulations); in both cases the authors suggest this is close to \(-5/3\). Within the uncertainty of measurements, \(-3/2\)
and $-5/3$ can in fact be indistinguishable. Experiments on different active systems, moreover, have often yielded different exponents, but most have yet to tread into higher activity regimes. Our work, robustly revealing an emergent universal, asymptotic state, now provides a fresh impetus for such an enterprise. The fact that, very recently, studies of the Lagrangian properties of active turbulence in the $\alpha < \alpha_c$ regime theoretically showed $^{12,13}$, for the first time, similar signatures of anomalous superdiffusion and Lévy walks as experiments $^{12}$, together with experiments showing non-Gaussian gradients $^{12}$ that may be signs of intermittency, bolsters hope of experimentally exploring active turbulence with increasing activity into states that may also exhibit asymptotic universality. We believe that experiments on extremely active suspensions, for instance involving bacteria that swim an order of magnitude faster $^{36}$, would shed more light on the precise nature of the turbulence displayed in such asymptotic states. We should underline, however, that the existence of a crossover activity $\alpha_c$ is independent of the precise form in which the energy spectrum scales.

Furthermore, the emergence of a maximally chaotic state shows that the phenomenology of active turbulence is rich and riddled with surprising nuances, which at times bridge the analogy with inertial turbulence, and at others break them. Broad-brushed parallels with inertial turbulence may thus obfuscate biologically relevant strategies for survival and growth.

**Online content**

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41567-023-01990-z.

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Spectral analysis, critical activity and universal scaling exponent

Each term in equation (1) can be decomposed into its Fourier series, where, for instance, the velocity, ignoring time-dependence, becomes

\[ u(r) = \sum_k u(k)e^{ik\cdot r} \]  

(3)

where \( k \) has components \( k_x, k_y, k_z \) that are integer multiples, \([1, 2, ..., n]\), of \( 2\pi/L \), where \( L \) is the physical system size along one direction and \( n = N_x/2 \), where \( N_x \) is the number of collocation points along one direction. The Fourier coefficients are given as

\[ u(k) = \frac{1}{L^3} \int_0^L \int_0^L \int_0^L u(r)e^{-ik\cdot r} \, dx \, dy \]  

(4)

Furthermore, the energy spectrum over the scalar wavenumber \( k \) is defined as

\[ E(k) = \frac{1}{k^2} \sum_{k' = -k/2}^{k + k/2} \langle u(k') \cdot u(k') \rangle \]  

(5)

where \( k = \sqrt{k_x^2 + k_y^2 + k_z^2} \) and \( \langle \cdot \rangle \) denotes ensemble-averaging. Similarly, taking the Fourier transform of the terms of equation (1), multiplying the resultant equation with \( u^*(k) \) (which is the complex conjugate of \( u(k) \)) and taking the shell-sum as in equation (5), gives the energy spectrum equation \(^{20,22}\) as

\[ \frac{\partial E(k)}{\partial t} = 2\gamma p(kE(k)) - \lambda T^{adv}(k) + T^{cub}(k) \]  

(6)

where \( T^{adv}(k) \) and \( T^{cub}(k) \) are the advective and cubic terms, respectively, and \( T^{adv}(k) \) appears with a pre-factor \( \lambda \) due to the generalized nonlinear term in equation (1). Here, \( \gamma(p) \) is the spectral form of the linear terms in equation (1) and is given as \( \gamma(k) = -\alpha + \Gamma_0 k^2 - \Gamma_2 k^4 \). Furthermore, the energy flux is defined as \( \Pi(k) = -\int_0^k T^{adv}(p)dp \), which can be dimensionally related to the energy spectrum, using a scale-dependent effective timescale \( \tau_{eff} \) as

\[ \tau_{eff} \Pi(k) \equiv \lambda k E(k) \]  

(7)

Using a general form of \( \tau_{eff} = k/\epsilon \) (where \( \epsilon \) is some dimensional constant), the flux can be rewritten as

\[ \Pi(k) \equiv c\lambda k^{1-\alpha} E(k) \]  

(8)

Following ref. \(^{20}\), we use the quasi-normal approximation \( T^{adv}(k) = -8\beta \epsilon E(k) \), where \( \epsilon = \epsilon_{\text{crit}} \) which, for a statistically stationary state, reduces equation (6) to

\[ -2(\alpha + 4\beta E_{\text{tot}} - \Gamma_0 k^2 + \Gamma_2 k^4)E(k) + \frac{d\Pi(k)}{dk} = 0 \]  

(9)

At mild levels of activity, where \( \tau_{eff} = \text{const.} (\xi = 0) \) in equation (7), one simply gets \( \Pi(k) \equiv \lambda k E(k)/\tau_{eff} \) and, ignoring the \( \Gamma_2 \) term (because we focus on the scaling at low \( k \)), \( \Gamma_0 \) is dominant at high \( k \), equation (9) can be solved to obtain the energy spectrum scaling \(^{20}\) as

\[ E(k) = E_0 k^\xi \exp \left( - \frac{\Gamma_0 \tau_{eff}}{\lambda} - k^2 \right) \]  

(10)

where \( \delta = (2\alpha + 8\beta E_{\text{tot}})\tau_{eff}/\lambda - 1 \), with \( E_0 \), a constant of integration. The spectral slope in this mildly active regime, where \( \tau_{eff} = \text{const.} (\xi = 0) \), varies with \( \alpha \), as also observed in the simulations.

However, for highly active suspensions, with a scale-dependent \( \tau_{eff} \), \( k/\epsilon \) (\( \xi \neq 0 \) for the reasons explained in the main text) we retain the general form of \( \Pi(k) \equiv c\lambda k^{1-\alpha} E(k) \). By using this, equation (9) leads to (again, ignoring the \( \Gamma_2 \) term at low \( k \))

\[ -2(\alpha + 4\beta E_{\text{tot}} - \Gamma_0 k^2)E(k) + c(1 - \xi)k^{-\xi}E(k) + c\lambda k^{1-\alpha} \frac{d\Pi(k)}{dk} = 0 \]  

(11)

which we rearrange as

\[ \frac{d\Pi(k)}{E(k)} = \frac{2(\alpha + 4\beta E_{\text{tot}})k^\xi}{c\lambda} k^{-\xi}dk - \frac{2\Gamma_0}{c\lambda} k^{1+\xi}dk - (1 - \xi)k^{-\xi}dk \]  

Equation (12) can be solved to obtain the energy spectrum as

\[ E(k) = E_0 k^{\xi - 3/2} \exp \left( \frac{2(\alpha + 4\beta E_{\text{tot}})k^\xi - 2\Gamma_0}{c\lambda} k^{1+\xi} - (1 - \xi)k^{-\xi} \right) \]  

(13)

Importantly, when \( \xi > 0 \) (that is, when \( \tau_{eff} \) becomes scale-dependent), the theoretical energy spectral scaling also becomes \( \alpha \)-independent at low \( k \) (because the first term on the right-hand side of equation (12) integrates to algebraic instead of logarithmic as in the case of \( \xi = 0 \)), hence consistent with the empirical observation of an \( \alpha \)-independent asymptotic universal scaling in the numerical simulations. By using the observed scaling of \( \tau_{eff} \sim k^{-7/8} \), we get

\[ E(k) = E_0 k^{-\xi - 3/8} \exp \left( \frac{2(\alpha + 4\beta E_{\text{tot}})k^{\xi - 7/8}}{-7c\lambda/8} - \frac{2\Gamma_0 k^{1+\xi}}{-9c\lambda/8} \right) \]  

(14)

Finally, \( E_0 \) is still undetermined. In the analogous calculation for classical, inertial turbulence, because \( \tau_{eff} = \epsilon^{-1} k^{-4} \), where \( \epsilon \) is the (constant) rate of energy dissipation, it can be shown that \( E_0 = \epsilon^{-1/2} \) (see also ref. \(^{20}\)). However, in active turbulence, with a scale-dependent flux and no real scale-separation, such a straightforward calculation is difficult. Nevertheless, we can show by comparing the non-exponential part of equation (14) to the flux and energy spectrum relation of equation (7) (with \( \xi = -7/8 \)) that \( \Pi(k) = c\lambda k^{1/8} E_0 k^{-5/8} \), or \( E_0 = \Pi(k)/c\lambda \). Because \( \Pi(k) \) is shown to have a weak scale-invariance \( \Pi(k) \sim k^{3/8} \), the spectral analysis yields (ignoring the exponential tail)

\[ E(k) \sim k^{-3/2} \]  

(15)

consistent with the numerically observed and phenomenologically explained (main text) \( \alpha \)-independent scaling of the energy spectrum as \( \alpha \leq \alpha_c \).

Twin simulations

We choose an arbitrary realization of the statistically steady vorticity field \( \omega_0 = \omega_0 \) from the numerical solutions of equation (1) for a given set of parameters, and obtain \( \omega_0 = \omega_0^\text{obs} + \delta \omega_0 \eta \). The two vorticity fields, denoted by superscripts A and B, are thus nearly identical up to a small perturbation \( \delta \omega_0 \eta \) introduced at each grid point at \( t = 0 \). We fix the amplitude \( \delta \omega_0 = 10^{-5} \), and \( \eta \in [-1, 1] \) is a uniformly distributed random
noise. We use \( \omega^A_0 \) and \( \omega^B_0 \) as initial conditions for simultaneous simulations of systems A and B and measure, pointwise, the difference vorticity \( \Delta \omega(x, t) = \omega^B(x, t) - \omega^A(x, t) \) and difference velocity \( \Delta u(x, t) = u^B(x, t) - u^A(x, t) \) fields as a function of space and time. The decorrelator \( \Phi(t) \equiv \langle \frac{1}{2} |\Delta u(x, t)|^2 \rangle \) is obtained by ensemble-averaging over space, as well as over ten independent twin simulations. For visualization alone, we perform separate twin simulations with spatially localized Gaussian perturbations as shown in this Article and in the Supplementary Video (see also https://www.youtube.com/watch?v=t0cLEbuuxY).

Data availability
Energy spectra and their scaling exponents, as well as twin-simulation decorrelators, have been shared in a public repository on Open Science Framework, which may be accessed at https://osf.io/tcsyw/ with https://doi.org/10.17605/OSF.IO/TCSYW. Field data, which are large-sized, are available from the corresponding author upon request.

Code availability
Simulations were performed using our in-house codes, which are available from the corresponding author upon request.

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Author contributions
S.S.R. and S.M. designed the research. S.M. performed the simulations and analysis. S.M., R.K.S., M.J. and S.S.R. contributed to interpretation of the results and writing the manuscript.

Competing interests
The authors declare no competing interests.

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