Rapid worldwide depletion of predatory fish communities

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Serious concerns have been raised about the ecological effects of industrialized fishing[1–3], spurring a United Nations resolution on restoring fisheries and marine ecosystems to healthy levels[4]. However, a prerequisite for restoration is a general understanding of the composition and abundance of unexploited fish communities, relative to contemporary ones. We constructed trajectories of community biomass and composition of large predatory fishes in four continental shelf and nine oceanic systems, using all available data from the beginning of exploitation. Industrialized fisheries typically reduced community biomass by 80% within 15 years of exploitation. Compensatory increases in fast-growing species were observed, but often reversed within a decade. Using a meta-analytic approach, we estimate that large predatory fish biomass today is only about 10% of pre-industrial levels. We conclude that declines of large predators in coastal regions[5] have extended throughout the global ocean, with potentially serious consequences for ecosystems[5–7]. Our analysis suggests that management based on recent data alone may be misleading, and provides minimum estimates for unexploited communities, which could serve as the 'missing baseline'[8] needed for future restoration efforts.

Ecological communities on continental shelves and in the open ocean contribute almost half of the planet's primary production[9], and sustain three-quarters of global fishery yields[1]. The widespread decline and collapse of major fish stocks has sparked concerns about the effects of overfishing on these communities. Historical data from coastal ecosystems suggest that losses of large predatory fishes, as well as mammals and reptiles, were especially pronounced, and precipitated marked changes in coastal ecosystem structure and function[5]. Such baseline information is scarce for shelf and oceanic ecosystems. Although there is an understanding of the magnitude of the decline in single stocks[10], it is an open question how entire communities have responded to large-scale exploitation. In this paper, we examine the trajectories of entire communities, and estimate global rates of decline for large predatory fishes in shelf and oceanic ecosystems.

We attempted to compile all data from which relative biomass at the beginning of industrialized exploitation could be reliably estimated. For shelf ecosystems, we used standardized research trawl surveys in the northwest Atlantic Ocean, the Gulf of Thailand and the Antarctic Ocean off South Georgia, which were designed to estimate the biomass of large demersal fish such as codfishes (Gadidae), flatfishes (Pleuronectidae), skates and rays (Rajiidae), among others (see Supplementary Information for detailed species information). In all other shelf areas for which we could obtain data, industrialized trawl fisheries occurred before research surveys took place. For oceanic ecosystems, we used Japanese pelagic longlining data, which represent the complete catch-rate data for tuna (Thunnini), billfishes (Istiophoridae) and swordfish (Xiphiidae) aggregated in monthly intervals, from 1952 to 1999, across a global $5° \times 5°$ grid. Pelagic longlines are the most widespread fishing gear, and the Japanese fleet the most widespread longline operation, covering all oceans except the circumpolar seas. Longlines, which resemble long, baited transects, catch a wide range of species in a consistent way and over vast spatial scales. We had to restrict our analysis of longlining data to the equatorial and southern oceans, because industrialized exploitation was already underway in much of the Northern Hemisphere before these data were recorded[11,12]. Longlining data were separated into temperate, subtropical and tropical communities (see Methods).

For each shelf and oceanic community, i, we estimated

$$N_i(t) = N_i(0)[(1 - \delta_i)\,e^{-r_i t} + \delta_i] \quad (1)$$

where $N_i(t)$ is the biomass at time t, $N_i(0)$ is the initial biomass

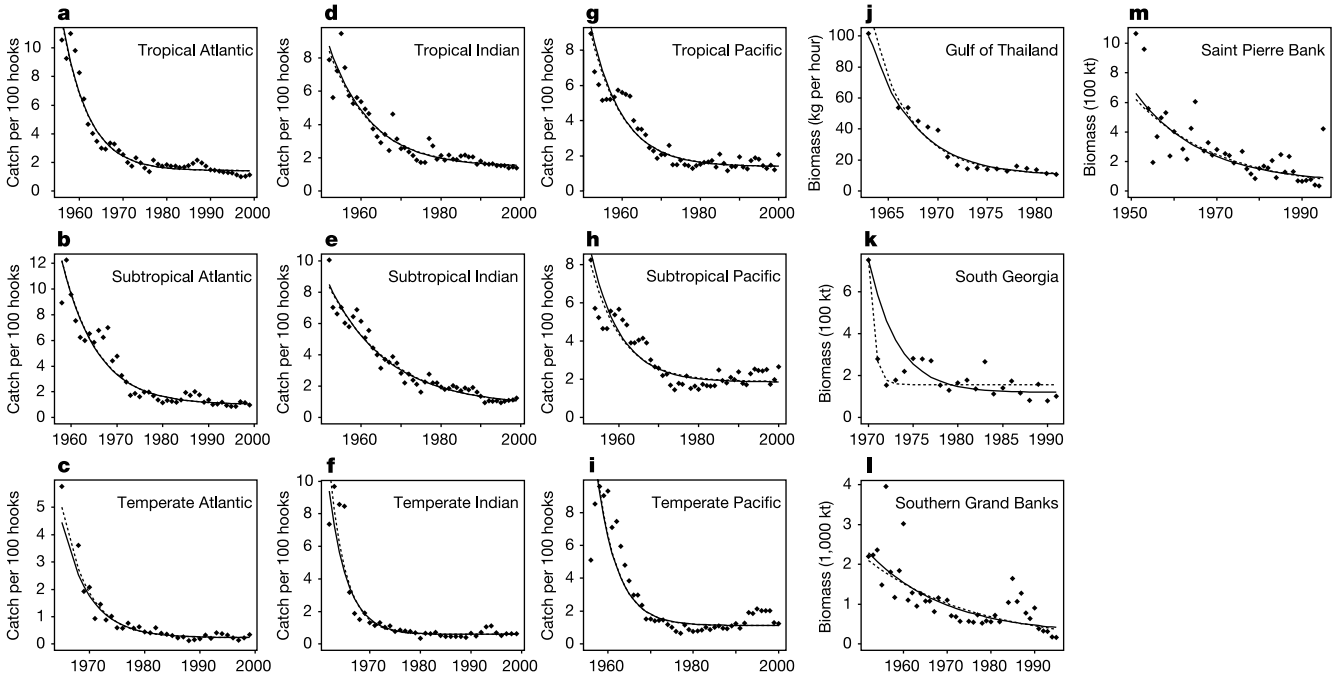

Figure 1 Time trends of community biomass in oceanic (**a**–**i**) and shelf (**j**–**m**) ecosystems. Relative biomass estimates from the beginning of industrialized fishing (solid points) are shown with superimposed fitted curves from individual maximum-likelihood fits (solid lines) and empirical Bayes predictions from a mixed-model fit (dashed lines).

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Table 1 **Meta-analysis of time trends in predatory fish biomass**

Region	r_i (× 100)			δ_i (× 100)		
	Individual fit	CL	Mixed model	Individual fit	CL	Mixed model
Tropical Atlantic	16.6	13.5–19.7	16.7	12.1	10.0–14.5	11.9
Subtropical Atlantic	12.9	10.1–15.7	13.0	8.1	6.4–10.2	8.3
Temperate Atlantic	21.4	15.8–26.9	20.3	4.7	3.2–6.9	5.3
Tropical Indian	9.2	7.1–11.4	9.5	17.6	14.9–20.6	16.8
Subtropical Indian	6.5	5.1–7.8	6.8	8.2	5.5–12.3	9.2
Temperature Indian	30.7	23.7–37.8	27.7	5.5	3.9–7.7	6.3
Tropical Pacific	12.1	9.4–14.8	12.4	15.5	13.0–18.6	14.9
Subtropical Pacific	12.8	8.5–17.1	13.5	23.5	18.9–29.3	21.5
Temperate Pacific	20.8	14.3–27.3	20.4	8.2	5.6–12.1	8.5
Gulf of Thailand	25.6	18.2–33.0	22.2	9.3	6.8–12.6	9.8
South Georgia	166.6	2.2–331.1	30.8	20.9	17.5–25.0	16.0
Southern Grand Banks	4.0	2.9–5.1	5.7	0.0	–	10.0
Saint Pierre Banks	5.1	0.1–10.1	6.3	2.7	0.0–36600	7.9
Mixed model mean			16.0			10.3
Mixed model CL			10.7–21.3			7.7–13.9
Distribution			4.5–31.6			4.6–23.6

Two parameters were estimated: r_i is the initial rate of decline (in per cent per year), and δ_i the residual biomass proportion at equilibrium (in per cent). Point estimates and 95% confidence limits (CL) are presented for the individual maximum likelihood fits, and for the mixed-effects model that combined all data (see Methods for details). The random-effects distribution (95% limits) provides a measure of the estimated parameter variability across communities.

before industrialized exploitation, and r_i is the initial rate of decline to δ_i, the fraction of the community that remains at equilibrium. The initial rate of decline in total biomass—that is, the fraction lost in the first year—is $(1-\delta_i)(1-e^{-r_i})$. Then we combined all data using nonlinear mixed-effects models[13], where $r_i \sim N(\mu_r, \sigma_r^2)$ and $\log \delta_i \sim N(\mu_\delta, \sigma_\delta^2)$, to estimate a global mean and variance of r_i and δ_i.

In the open ocean communities, we observed surprisingly consistent and rapid declines, with catch rates falling from 6–12 down to 0.5–2 individuals per 100 hooks during the first 10 years of exploitation (Fig. 1a–i). Rates of decline were similar in tropical and subtropical regions, but consistently highest in temperate regions in all three oceans (Fig. 1c, f, i and Table 1). Temperate regions also showed the lowest equilibrium catch rates (Table 1). Spatial pattern of expansion and decline of pelagic fisheries are shown in Fig. 2. During the global expansion of longline fisheries in the 1950s to 1960s, high abundances of tuna and billfish were always found at the periphery of the fished area (Fig. 2a–c). Most newly fished areas showed very high catch rates, but declined to low levels after a few years. As a result, all areas now sustain low catch rates, and some formerly productive areas have been abandoned (Fig. 2d). In shelf communities, we observed declines of similar magnitude as in the open ocean. The Gulf of Thailand, for example, lost 60% of large finfish, sharks and skates during the first 5 years of industrialized trawl fishing (Fig. 1j). The highest initial rate of decline was seen in South Georgia (Fig. 1k), which has a narrow shelf area that was effectively fished down during the first 2 years of exploitation[14]. Less-than-average declines were seen on the Southern Grand Banks

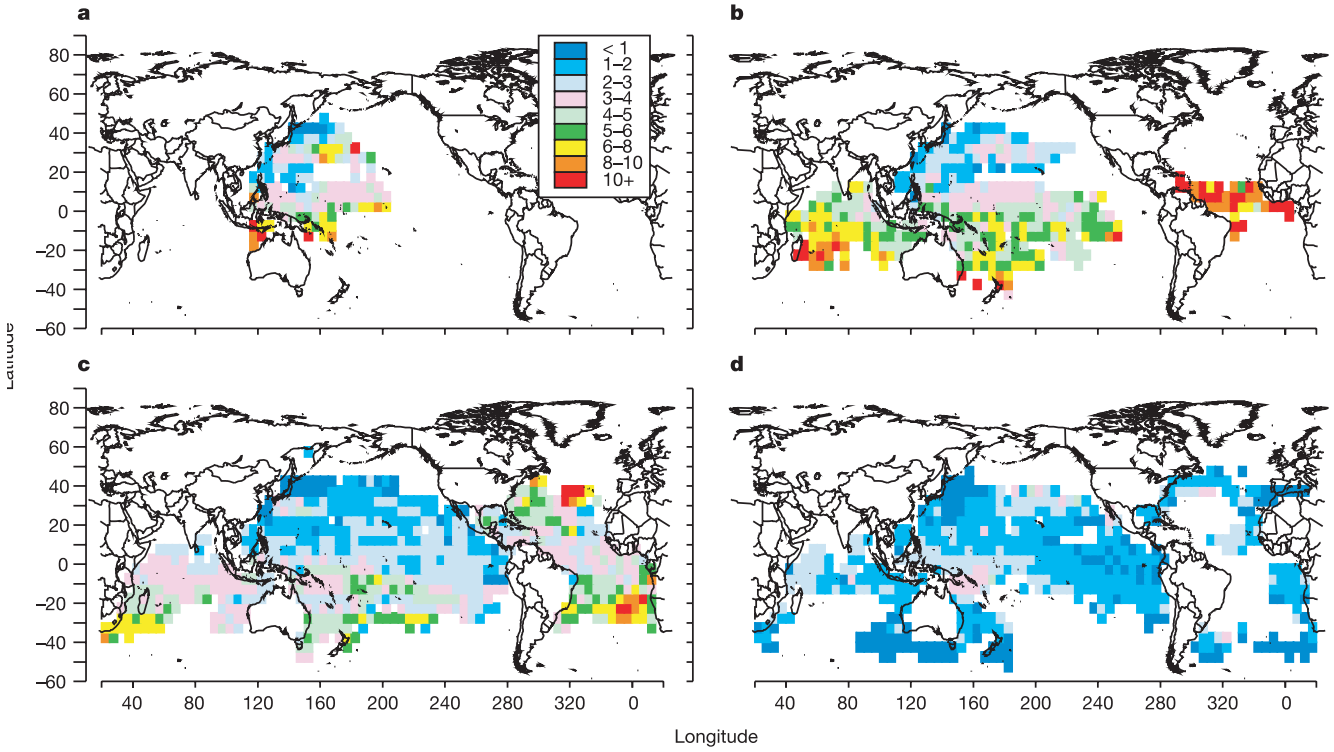

Figure 2 Spatial patterns of relative predator biomass in 1952 (**a**), 1958 (**b**), 1964 (**c**) and 1980 (**d**). Colour codes depict the number of fish caught per 100 hooks on pelagic longlines set by the Japanese fleet. Data are binned in a global 5° × 5° grid. For complete year-by-year maps, refer to the Supplementary Information.

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(Fig. 1l) and Saint Pierre Bank (Fig. 1m); these communities may already have been affected by intense pre-industrial fisheries[15].

By combining all data using a mixed-effects model, we estimated that the mean initial rate of decline, r_i, is 16% per year, and the mean residual equilibrium biomass, δ_i, is 10% of pre-exploitation levels (Table 1). So, an 80% decline typically occurred within 15 years of industrialized exploitation, which is usually before scientific monitoring has taken place. The proportion of residual biomass, δ_i, showed remarkably little variation between communities (Table 1): the mixed-effects model estimates imply that 95% of communities would have a residual biomass proportion between 5% and 24%. We believe that these still represent conservative estimates of total predator declines for the following reasons: (1) pre-industrial removals from some of the shelf communities[15]; (2) gear saturation at high catch rates in the early longlining data, as well as higher initial levels of shark damage leading to an underestimation of initial biomass[16] (see Supplementary Information); (3) increasing fishing power of longline vessels over time owing to improved navigation and targeting of oceanographic features[17]; and (4) targeting of some migratory species, such as southern bluefin tuna (*Thunnus maccoyii*), at their tropical spawning grounds before widespread exploitation in temperate areas occurred[18]. Furthermore, declines in other large predators such as sharks are not fully captured by our data, but may be of similar or greater magnitude than those of bony fishes[19,20].

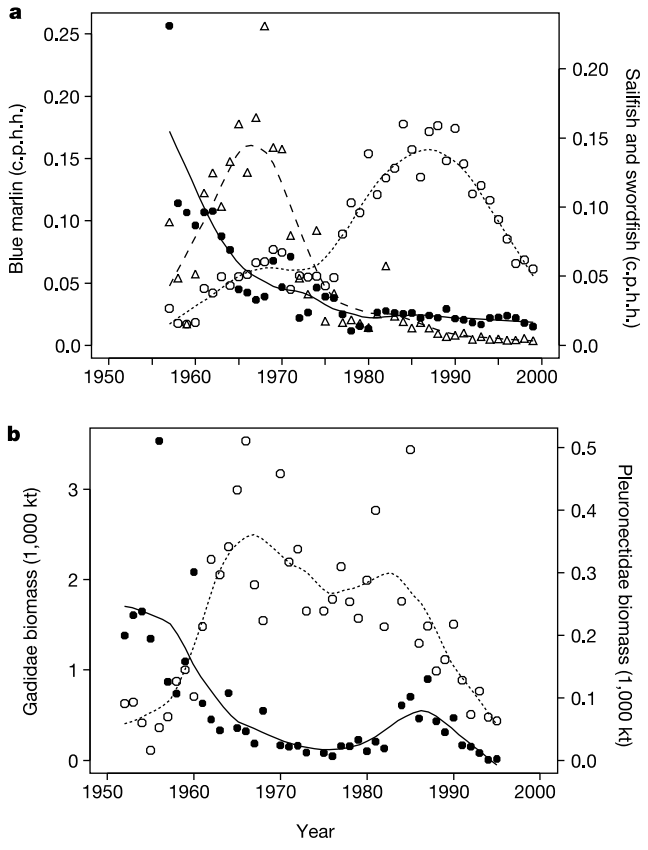

Figure 3 Compensation in exploited fish communities. **a**, Oceanic billfish community in the tropical Atlantic, showing the catch per 100 hooks (c.p.h.h.) of blue marlin (*Makaira nigricans*; solid circles, solid line), sailfish (*Istiophorus platypterus*; open triangles, dashed line) and swordfish (*Xiphias gladius*; open circles, dotted line). **b**, Demersal fish community on the Southern Grand Banks, showing the biomass of codfishes (Gadidae; solid circles, solid line) and flatfishes (Pleuronectidae; open circles, dotted line). Lines represent best fits using a local regression smoother.

One mechanism that could compensate for the effects of overfishing is the increase in non-target species due to release from predation or competition[21]. In our analyses, we see evidence for species compensation in both oceanic billfish and shelf groundfish communities (Fig. 3). According to the longlining data and to early surveys[11,12], blue marlin was initially the dominant billfish species, but declined rapidly in the 1950s (Fig. 3a). Simultaneous increases in faster-growing species such as sailfish were observed, followed by a decrease, possibly due to increased 'bycatch' mortality (Fig. 3a; neither species was targeted by the Japanese fleet). Coincidentally, swordfish catch rates increased until these fish became prime targets of other fleets in the late 1980s. Surprisingly consistent patterns of compensatory increase and decline were seen in most pelagic communities (see Supplementary Information). Similarly, in the North Atlantic demersal communities, we observed rapid initial declines, particularly in large codfishes, but also in skates and rockfish. Although the dominant codfishes declined sixfold between 1952 and 1970, sixfold increases were seen in the flatfishes, which were not initially targeted by the trawl fishery (Fig. 3b). Some increase in the gadoids occurred when implementation of the 200-mile limit in 1977 curtailed foreign overfishing in Canadian waters. However, as in the billfish data, we observed an ultimate decline in all species groups (Fig. 3b) as fishing pressure from Canadian and other fleets intensified in the late 1980s, leading to the collapse of all major groundfish stocks[10]. We conclude that some species compensation was evident, but often reversed within a decade or less, probably because of changes in targeting or bycatch.

Our analysis suggests that the global ocean has lost more than 90% of large predatory fishes. Although it is now widely accepted that single populations can be fished to low levels, this is the first analysis to show general, pronounced declines of entire communities across widely varying ecosystems. Although the overall magnitude of change is evident, there remains uncertainty about trajectories of individual tuna and billfish species. Assessments of these species are continually improved by the international management agencies. However, most scientists and managers may not be aware of the true magnitude of change in marine ecosystems, because the majority of declines occurred during the first years of exploitation, typically before surveys were undertaken. Management schemes are usually implemented well after industrialized fishing has begun, and only serve to stabilize fish biomass at low levels. Supporting evidence for these conclusions comes from the United Nations Food and Agriculture Organization (FAO) data set, which indicates declining global catches[22] and a consistent decline in the mean trophic level of the catch[23], which is a result of removing predatory fishes. Furthermore, on seamounts and on continental slopes, where virgin communities are fished, similar dynamics of extremely high catch rates are observed, which decline rapidly over the first 3–5 years of exploitation[24]. We suggest that this pattern is not unique to these communities, but simply a universal feature of the early exploitation of ecosystems.

Our results have several important management implications. First, we need to consider potential ecosystem effects of removing 90% of large predators. Fishery-induced top–down effects are evident in coastal[5] and shelf[25] ecosystems, but little empirical information is available from the open oceans. This is worrisome, as any ecosystem-wide effect is bound to be widespread, and possibly difficult to reverse, because of the global scale of the declines (Fig. 2). Another serious problem in heavily depleted communities is the extinction of populations, particularly those with high ages of maturity[26]. Local extinctions can go unnoticed even in closely monitored systems such as the northwest Atlantic[27], let alone in the open ocean. Finally, the reduction of fish biomass to low levels may compromise the sustainability of fishing, and support only relatively low economic yields[3]. Such concerns have motivated a recent UN resolution to restore fish stocks to healthy

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levels[4]. Our analysis shows that it is appropriate and necessary to attempt restoration on a global scale, and provides a benchmark against which community recovery could be assessed. □

Methods

Data selection

For shelf communities, we compiled data from research trawl surveys from the Southern Grand Banks (43–46° N, 49–53° W) and Saint Pierre Banks (45–47° N, 55–58° W) (ref. 28), the Gulf of Thailand (9–14° N, 100–105° W) (ref. 29) and South Georgia (53–56° S, 35–40° W) (ref. 14). All other trawl data sets that we considered (for example, North Sea, Georges Bank and Alaska) did not capture the beginning of industrialized exploitation. We included only demersal predators; pelagic species, which were not well sampled by the trawl gear, were excluded. Longlining data obtained from the Japanese Fishery Agency were divided into temperate (Atlantic, 40–45° S; Indian, 35–45° S; Pacific, 30–45° S), subtropical (Atlantic, 10–40° S; Indian, 10–35° S; Pacific, 15–30° S) and tropical communities (Atlantic, 20° N–10° S; Indian, 15° N–15° S; Pacific, 10–15° S). These divisions were based on their dominant species: yellowfin (*T. albacares*), albacore (*T. alalunga*) or southern bluefin tuna (*T. maccoyii*), respectively, and excluded areas previously fished by the Japanese, Spanish and US fleets. Running the models with alternative divisions (±5°) did not change the results significantly. The catch rates in each community were determined as the sum of the catches divided by the sum of the effort in each region in each year. Years with very low effort (<20,000 hooks for the entire region) were excluded. Alternative treatment of the data, including removing seasonal effects and taking the average catch rates over 5° × 5° squares, had little effect on the results. For longlines, we assume that the catch rate is an approximate measure of relative biomass, which is probably conservative because the average individual weights of fish in exploited populations tend to decline over time. Our data capture the abundance of larger fishes that are vulnerable to baited hooks and bottom trawls, respectively. Many smaller species have low catchabilities and are not recorded reliably by these methods. Changes in the longline fishery occurred around 1980 when the fishery began to expand into deeper regions; however, this was only after the declines in biomass were observed. For more details on species composition, data treatment and interpretation of trends, refer to the Supplementary Information.

Data analysis

Our model (equation (1)) assumes that for each community, i, the rate of decline to equilibrium is exponential with rate r_i from a pre-exploitation biomass $N_i(0)$, where $t = 0$ is the first year of industrialized fishing. Exploitation continues until equilibrium is approached, where a residual proportion, δ_i, of the biomass remains. We fit this model separately to each community under the assumption of a lognormal error distribution using nonlinear regression (Procedure NLIN in SAS, version 8). We also used nonlinear mixed-effects models[13] to determine whether the patterns were similar across communities. Mixed-effect models were fitted by maximizing the likelihood integrated over the random effects using adaptive gaussian quadrature (Procedure NLMIXED in SAS). To account for the fact that biomass was recorded in different units (kilotonnes (kt), catch rates), the initial biomass, $N_i(0)$, was assumed to be a fixed effect for each community with appropriate units. For South Georgia, $N_i(0)$ was fixed at the first biomass estimate to capture the high initial rate of decline. This first estimate (750 kt; ref. 14) was considered to be realistic because it was very close to the sum of total removals (514 kt; ref. 30) plus the residual biomass estimate (160 kt; ref. 14) after the first 2 years of fishing. Autocorrelation in the residuals of some time series may cause the standard errors to be underestimated. The results were robust to alternative error assumptions (separate error variances for the time series and alternative error distributions); for example, under the assumption of normal errors, the rate of decline was 13.9% and residual biomass was 10.9%, respectively.

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Attractor dynamics of network UP states in the neocortex

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The cerebral cortex receives input from lower brain regions, and its function is traditionally considered to be processing that input through successive stages to reach an appropriate output[1,2]. However, the cortical circuit contains many interconnections, including those feeding back from higher centres[3–6], and is continuously active even in the absence of sensory inputs[7–9]. Such spontaneous firing has a structure that reflects the coordinated activity of specific groups of neurons[10–12]. Moreover, the membrane potential of cortical neurons fluctuates spontaneously between a resting (DOWN) and a depolarized (UP) state[11,13–16], which may also be coordinated. The elevated firing rate in the UP state follows sensory stimulation[16] and provides a substrate for

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