when it stops abruptly as it suddenly runs out of resources or is halted by disease or predators. A weakly concave relationship, where θ is between 0 and 1, implies that the net reduction in population growth per individual is greater at low densities than at high densities; this effect becomes especially pronounced when θ is less than zero.

There is an important caveat in using this analytical approach. The time series use estimates rather than exact counts of populations, and they therefore contain measurement errors. Such errors can substantially bias estimates of the strength of density dependence and make density-independent time series appear as if they were generated from a density-dependent model (*4*). From simulations, Sibly *et al*. claim that the effects of measurement error should not bias estimates of θ toward particularly large positive or negative values. A pure error model, in which all meaningful variation in population size is swamped by measurement error, should yield a value of θ = 0. However, it is not yet clear what happens to estimates of θ in the presence of measurement error if density dependence is weak or absent, and how this may be distinguished from true density dependence.

This caveat notwithstanding, the analyses have turned up a major surprise. The values of θ tend to be negative more often than not, which means that plots of population growth rate against population size are concave. This implies that populations experience strong density dependence early in their growth, with a weaker effect as they approach and exceed their carrying capacity. Why might this be the case? One possibility is that the logistic model ignores the age, size, and developmental-stage dependence of population structure. For example, density dependence may act most strongly at just one particular stage such as during the period of juvenile survival. Population growth rate usually includes all individuals in the population, not just those affected most strongly by density dependence. If the whole population exceeds its carrying capacity, there will be an immediate reduction in the recruitment of juveniles due to density dependence. However, as adults are better competitors, their numbers might respond only slowly, or not at all. Therefore, at high densities the population would not reduce rapidly to equilibrium. Conversely, at low densities, juvenile recruitment will be high, and they will grow rapidly into the adult class and swell the population's number. The net effect of this differential behavior above and below equilibrium is to generate a concave density response. However, this is pure speculation and the issue clearly requires a great deal more thought.

The findings of Sibly *et al*. have some general implications. First, their finding that values of θ tend to be much less than 1 violates a key assumption of the classical logistic equation, whereby growth rate should reduce linearly with density. Although this may not be news to most ecologists, the logistic model is still widely used by theoreticians and is a staple of textbooks. Second, the authors comment that as a consequence of concave density responses, many populations appear to live at densities above the carrying capacity of their environments. Another way of putting this is that rates of population decline will be slower than rates of return, perhaps for the reasons suggested above. It might therefore appear that we can reduce populations substantially before impairing their productivity. However, it would be very risky to manage populations on this basis, for example, when attempting to obtain sustainable yields in hunting or fishing. That is because parameters of the population growth curve will change as populations are exploited. This may change the shapes of the density responses. Furthermore, we still have much to learn about how measurement error affects parameter estimates in such models, and hence the shapes of these relationships. Research on these fronts should prove rewarding for further understanding the ways in which populations change with time and for facilitating better wildlife management and conservation.

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NEUROSCIENCE

Similar Is Different in Hippocampal Networks

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When driving your car to work on two alternate but familiar routes, different combinations of neurons in the hippocampal region of the brain assist you in the navigation process. This is because ensembles of hippocampal "place cells" form a map-like representation of the environment (*1*). In addition to spatial cues such as shopping malls and other salient landmarks, hippocampal neurons respond to other features during the drive, including speed changes and local information (such as the type of transmission and the shape and size of the car's interior). So how will the hippocampal map representation be affected if you are driving your spouse's Jaguar instead of your two-seater Lotus on the same routes? According to Leutgeb *et al*. on page 619 of this issue (*2*), local information regarding each car as well as either route you may choose to take will be faithfully encoded in the hippocampus and there will be no interference between the two types of representations.

Instead of cars, routes, and human drivers, Leutgeb *et al*. studied rats under two sets of conditions and monitored the firing patterns, or activity, of their hippocampal neurons. In one condition, the rats were tested in each of two different recording chambers (differing in shape) but the chambers were always in the same part of the same room. In the second condition, recordings were made from rats that were placed in each of two different rooms but in the same recording chamber located in the same part of each room. Collection of data began after the rats had at least 1 week of experience in either scenario. In the second condition, both the spatial positions of activated place cells (representing "place fields" in the chambers) and their discharge rates were statistically independent (a phenomenon known as "remapping"), as expected from previous studies. However, in the first condition, virtually all the activated hippocampal neurons remained anchored to the same Cartesian coordinates, even though the firing rate of the individual neurons varied more than an order of magnitude in the different chambers. This finding led the authors to conclude that local information is coded by rate, independently of the ensemble-coded place.

The most basic functions attributed to neuronal networks are the segregation and integration of patterns of activity. Such function is most pertinent in the hippocampus, often con-

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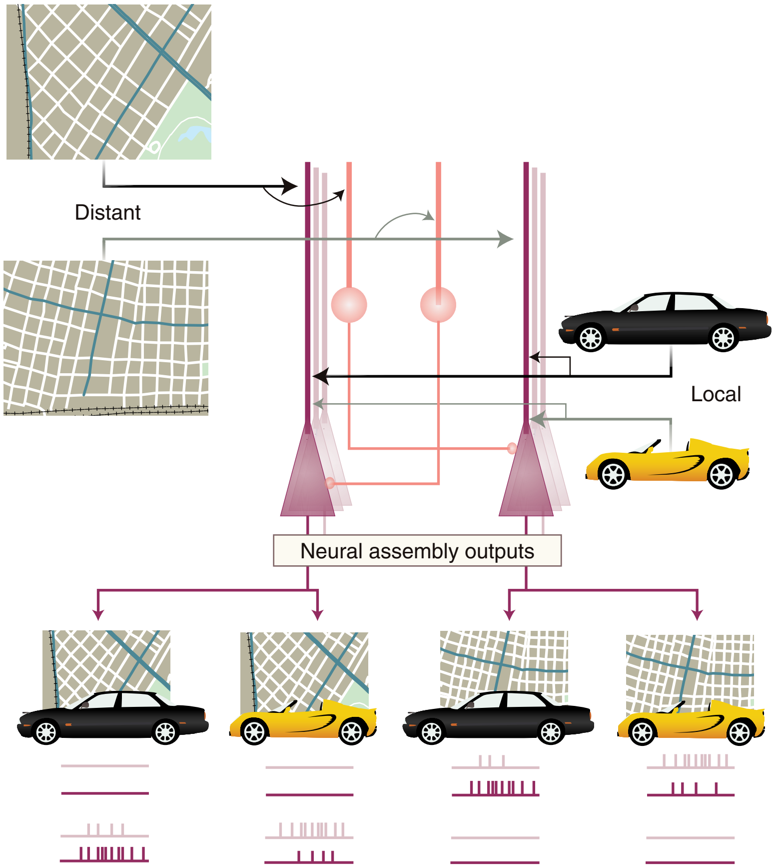

Interneurons allow for pattern separation in cortical networks of the hippocampus. Information from distant cues of one environment (e.g., a city or a given room in the Leutgeb *et al.* study) activates a set of principal neurons (purple). The same input information also activates a single set of interneurons (light red) that prevents the activity of neuronal assemblies that represent other distant environments. Variations in local cues (from a car or the recording chamber in the Leutgeb et al. study) selectively adjust the activity level of the chosen assembly members. This results in distinct patterns of neuronal activity associated with the distant and local cues (shown as line plot patterns).

sidered a single giant cortical module with rich recursive excitatory connections. However, in networks consisting of excitatory neurons only, separation of neuronal assemblies representing different environments is not possible. Inhibitory neuronal connections can provide a high degree of autonomy for individual pyramidal neurons, the principal cell type in the hippocampal cortex ("place cells" are active pyramidal cells). With the help of the inhibitory neurons, excitatory signals can be rerouted within the entire hippocampal network (*3*). Thus, by properly managing the inhibitory networks, minor changes in input excitatory activity can cause instantaneous and large shifts in the assembly behavior of hippocampal neurons. Using the dichotomy of "local" versus "distant" information that is suggested by the authors, a relatively simple circuit can be constructed that can account for their observations (see the figure). The conclusion is that a given environmental context can select the neuronal assembly, whereas gain control (provided by local cues, locomotor speed of the animal, and other factors) can adjust the firing rate of the assembly members.

The observations by Leutgeb *et al.* are backed up by large numbers of neurons and impressive quantitative analysis. However, the hypothesized dual coding scheme of local versus distant inputs is harder to accept. This dichotomy brings to mind our frequent desire to identify the neuronal mechanisms that distinguish numerous qualities: figure and background, context and content, segregated and integrated, separated and completed, aggregated and differentiated, autonomous and dependent, stochastic and deterministic, homogeneous and inhomogeneous, or (in general) the similar and the different. The problem is that nothing in the physical world indicates whether something is near or far. The judgment of local versus distant cues depends solely on the observer, determined largely by the history between those cues and the individual. Past experience may determine which cues will have priority access to the hypothetical assembly-selecting interneurons so that either local or distant cues may cause global remapping in hippocampal representation. In general, one person's judgment of "similar" may be judged as markedly "different" by someone else with more experience, and this may not be so different with rats.

Against this background, it may not be surprising that two recent studies with aims similar to those of the Leutgeb *et al.* study generated different outcomes. In one report, ensembles of place cells abruptly and simultaneously switched as rats experienced either square or cylindrical chambers in the same part of the same room (*4*). In another study, changing the position of objects in the testing apparatus altered most place fields near the objects and caused remapping or cessation of neuronal activity (*5*). Perhaps the most exciting aspect of these and related studies (*6*, *7*) is the consistency of findings within the same laboratories and differences across laboratories. In light of the nonlinear response properties of hippocampal networks, large differences in network behavior are expected even with minor variation of the initial conditions, such as the extent of training and familiarity with the testing conditions.

Leutgeb *et al.* also found remarkable differences between two populations of hippocampal neurons: the CA3 pyramidal cells and CA1 neurons that receive CA3 signals. The firing rate differences observed between chambers in the same room were greater by a factor of 4 in CA3 cells relative to CA1 cells. The differences in the two-room comparison were even greater. This implies a very distinct computation by the CA3 and CA1 neurons. Simultaneous recordings from ensembles of neurons in different stages of information processing, as done by Leutgeb *et al.*, will be required to answer questions regarding the separation and integration of information processing. Such data might explain the inconsistencies between laboratories.

Another important issue is the link between the present findings and episodic memory that is established in the hippocampus. A key feature of episodic memories is their temporal context. In contrast, the representation of a place is assumed to be a temporally independent process (*1*). A fundamental organizational aspect of the hippocampal system is the periodic renewal process of neuron activity by oscillations in their excitation (*8*). Understanding how these oscillations assist in sequential selection of assemblies may pave the way to building a bridge between spatial navigation and episodic memories.

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