management. For example, just 35% of MPAs were appropriately funded, only 13% were informed by scientific monitoring, and 9% reported adequate staffing. Staffing and funding gaps were the strongest predictors of conservation outcomes, quantified as increases in fish biomass in an MPA relative to that in unprotected areas nearby. Despite their shortcomings, 71% of MPAs still secured substantial positive outcomes. But the degree to which they succeeded was mainly a function of human and financial resources.

To some extent, these results might not surprise. To use an analogy, we cannot just build hospitals and hope that they will somehow ensure public health — the number of staff, the quality of their training and the level of funding clearly are crucial. The same goes for ocean conservation efforts, but it takes careful analysis to quantify capacity gaps and to show empirically where new investment is most likely to pay off. For example, Gill and colleagues' analysis suggests that raising staff capacity to adequate levels might increase fish biomass almost threefold. This investment would translate into downstream benefits for both tourism operators inside the MPA and fishermen outside it, who would benefit from fish spilling over reserve boundaries[8].

Gill and colleagues' work raises a broader point about the value of integrating social sciences into the study of human-dominated ecosystems. Another study[9] reported that the effectiveness of management schemes for small-scale fisheries depended mainly on factors such as leadership and social cohesion in the fishing community, and less strongly on biophysical aspects of the system under study. Other work has shown that enforcement of fishing rules is one of five key features that predict conservation outcomes on reefs worldwide[6]. Clearly, meaningful conservation measures need to be embedded in a social fabric that enables appropriate measures both inside and outside protected zones.

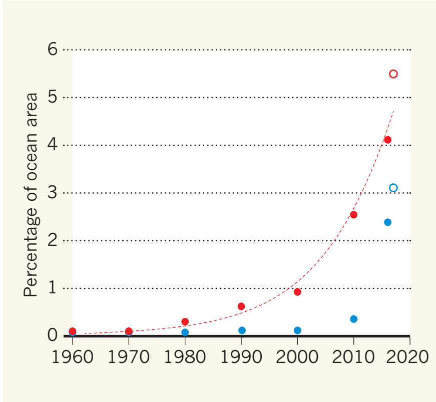

Figure 2 | Rapid growth of marine protected areas (MPAs). The percentage of the global ocean that has been designated and implemented as MPAs has grown exponentially since the 1960s (red symbols and line). Blue symbols indicate the subset of MPAs that are strongly protected — where commercial extraction of natural resources such as fish, minerals or oil is banned, and recreational or subsistence fishing is light. Open circles indicate coverage if current MPA proposals or announcements were implemented in 2017. (Adapted from ref. 2; data from J. Lubchenco, K. Grorud-Colvert and MPAtlas.org)

Later this year, policymakers will gather at the United Nations to discuss global development goals related to the conservation and sustainable use of the ocean. They should take note of Gill and colleagues' study, because it provides a timely warning that rapid expansion of protected areas by itself will not provide desired outcomes if there are large shortfalls in our capacity to manage, monitor and finance those areas. If the billions of dollars of subsidies that are currently spent on unsustainable fisheries were channelled into marine conservation, then the cited capacity gaps could be erased in one broad stroke[10].

Of course, money is only part of the solution. Public engagement, staff training and the capacity for scientific assessment should all be enhanced to build a truly robust, global MPA network. There is certainly no easy recipe for success, but global meta-analyses such as that of Gill *et al.* and others[6,9] will help us to further constrain what is needed to heal the ocean, and to provide long-term benefits to people. ■

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NEUROSCIENCE

Auditory landscape on the cognitive map

Subpopulations of neurons fire at specific geographical locations, providing a mental map of an animal's position in space. The finding that the circuitry can also support auditory maps sheds light on the neuronal structure of cognition. SEE LETTER P.719

JON W. RUECKEMANN & ELIZABETH A. BUFFALO

All animals face the challenge of navigating their environment, and are aided by an internal, mental map of where they have been and where they are going. Neurons in a brain region called the hippocampal formation are thought to form the substrate of such maps in mammals. But whether mental maps can also be used to organize other types of information is not known. On page 719, Aronov *et al.*[1] provide evidence that the same neuronal circuitry can be used for both spatial and non-spatial mental maps in rats.

Neurons in the hippocampal formation, which includes the hippocampus and the adjacent entorhinal cortex[2], provide an intricate representation of an animal's location in space. Hippocampal place cells and entorhinal grid cells fire at specific physical locations as a rat traverses an environment[3,4]. Some researchers think that these neurons function primarily as the brain's navigational system. However, others[5,6] suggest that these neuronal ensembles might instead contribute in a more general way to the organization of information. This hypothesis accordingly raises the question of whether such neurons might represent non-spatial aspects of experience in a map-like way, similarly to their representation of space.

To address this question, Aronov *et al.* investigated whether neurons in the hippocampal formation can represent a 'map' of a non-spatial environment, choosing for their example an auditory landscape. They trained rats to use a joystick to manipulate a tone that got higher the longer the joystick was pressed. The rats were rewarded with a drop of water for releasing the joystick when the sound reached a particular frequency range. In this way, the authors could analyse the pattern of neuronal activity that occurred as the frequency changed, and compare this with the neuronal responses that represent a rat's changes in position as it navigates during a foraging task.

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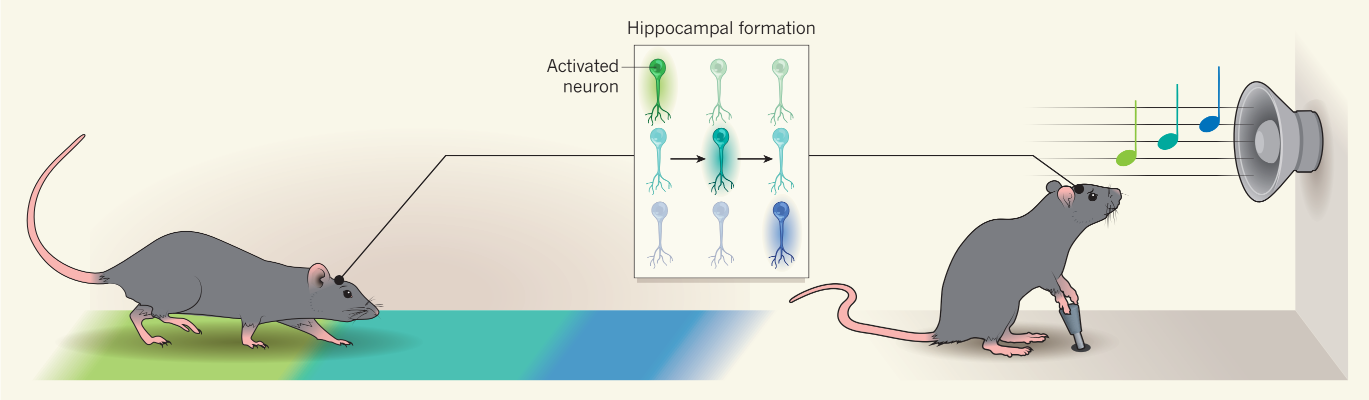

Figure 1 | Shared maps of space and sound. When a rat runs along a linear track, neurons in a brain region called the hippocampal formation fire at different points in space. For instance, neurons labelled in green represent the green section of track, and fire when the rat is in this area, followed by activation of 'light blue' neurons when the rat enters the light blue area, then dark blue. Aronov *et al.*[1] tested the response of these neurons to changes in sound. Rats used a joystick to manipulate a tone that got higher the longer the joystick was pressed. This demonstrated that the neurons respond to changes in sound frequency in a similar way to changes in location.

To ensure that the rats were responding to a particular frequency and not simply to a set period of elapsed time, the researchers varied the speed at which the frequency increased across trials.

Just as neurons in the hippocampal formation respond when a rat is in a particular physical space, neurons fired in response to a particular tone in the auditory task (Fig. 1). Some of the tone-specific neurons in the auditory task were also place-specific neurons in the foraging task, suggesting that a common neuronal network supports both types of information map.

Next, Aronov and colleagues asked whether the neurons were merely responding to a particular frequency (as one might expect for simpler sensory areas of the brain), or whether the neuronal responses depended on a rat being engaged in a behavioural task. To test this, the authors presented rats that were not performing the joystick task with the same sound sweeps. Very few hippocampal cells were active during passive playback. Interestingly, when the investigators gave rats a water reward at the end of passive playback, hippocampal neurons did show frequency-modulated activity, albeit in fewer cells and with less precision than during the behavioural task. Thus, the predictability of reward might have directed the animals' attention to the stimuli. This attention might be a general prerequisite for forming a neuronal map.

The authors propose that a crucial feature of the mapping observed in their task is that frequencies are organized along a continuum. Just as the hippocampal map adopts the structure of the tonal scale, it might be expected that this network could map any stimulus dimension that has some graded, ordinal structure — such as light to dark, or hot to cold. However, the hypothesis that a continuum is important also places heavy constraints on the type of organization that the hippocampal formation can map. In particular, this hypothesis supposes that the hippocampus maps particular features of a given stimulus, rather than a temporally ordered series of discrete events. An alternative interpretation would be that the map tracks progress towards the reward, using the tones as milestones.

Future work could address this issue by changing the way in which tones progress as the rat presses the joystick — for instance, following an arcing pattern instead of merely increasing. If neuronal activity does truly represent a map of frequency space, each tone-specific neuron would fire twice because the same frequency would be played on either side of the arc. Alternatively, neuronal activity might track progression through the tonal series from the beginning of the trial to the reward. This distinction would shed light on whether hippocampal processes are constrained by the intrinsic features of their inputs (representing changes in frequency or space, for example), or whether this brain region can form relational maps that link arbitrary stimuli together.

Further questions are also inspired by the authors' data. To what extent can content-specific neuronal subpopulations, such as those that fire at certain times or frequencies, truly be considered to form a 'map'? What would be the purpose of such maps? Aronov *et al.* suggest that frequency representations have a key property that makes them map-like: the combined activity of the neuronal population completely reflects the progressing events of the task. Thus, at any point in time, a downstream brain region could decode the precise task phase by reading out which neurons are active within the population. This would imply that sequential neuronal activity represents the progressive flow of experience during the behavioural task, linking events into a singular memory — which may offer a more fundamental description of hippocampal activity than the activity patterns of individual neurons.

The current study provides strong evidence at the single-neuron level that activity in the hippocampal formation can reflect organization of non-spatial content. These findings add to a growing body of literature that indicates that the hippocampus can provide a structured organization for experience beyond navigation. Along with place cells that represent space, studies[7,8] have identified hippocampal cells that are active at distinct time intervals during memory tasks. More recently, the hippocampal formation has been shown to be involved in humans' structured organization of social[9] and conceptual relationships[10].

Taken together, Aronov and colleagues' work expands our understanding of the function of the hippocampal formation. Future studies that extend this work to other species and identify the conditions that promote sequential firing within neuronal ensembles will help to clarify how these hippocampal representations organize information and support memory formation. ■

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