

clear whether participants have perfect knowledge of their own uncertainty. Finally, Jazayeri and Shadlen<sup>1</sup> found that participants' behavior was consistent with a quadratic loss function so that the optimal estimate is the mean of the posterior distribution. However, other combinations of assumed priors, temporal uncertainty and loss functions might have been consistent with their results (Fig. 1).

For the Bayesian modeler, there are three unknown functions: the likelihood, prior and loss function. This multiplicity of unknowns is particularly vexing, as the data only tell us the participant's average response to any given stimulus. This stimulus-response function might result from more than one Bayesian model. For example, larger bias for long durations results from a likelihood implementing scalar variability combined with a quadratic loss function, but similar results are obtained if the participant assumes variability is constant and uses an asymmetrical loss function with high cost for overestimation (Fig. 1). Previous studies have used a variety of approaches to reduce the number of unknowns. For sensory experiments, the likelihood function can be measured by determining the observer's ability to discriminate similar stimuli (for example, ref. 10). The prior distribution can be imposed, as it is in Jazayeri and Shadlen's study<sup>1</sup>, with training sessions so that participants have an opportunity to learn the prior. It can be measured from the environment and one can ask

whether perceptual biases are consistent with the participant computing a Bayesian estimate using this natural prior (for example, ref. 11). Alternatively, experiments can be designed to estimate the shape of the prior used by the observer<sup>12</sup>. The loss function can be imposed by the experimenter<sup>13</sup>. Finally, sensory information can be removed so that performance can only be based on the prior and loss function.

How can the experimenter be assured the participant is truly carrying out the Bayesian computation, rather than a simpler heuristic that has the same net effect? In Jazayeri and Shadlen's experiment<sup>1</sup>, participants received feedback for responses that were sufficiently close to the correct duration. Thus, it is reasonable to ask whether the resulting biases were learned by effectively computing a linear regression of produced intervals that led to positive feedback as a function of the corresponding measured intervals. A true Bayesian computation would imply that the participant has knowledge of the likelihood, prior and loss function, and can use those elements when one of them, such as the context (prior), is changed<sup>14</sup>. One strength of the Jazayeri and Shadlen study<sup>1</sup> is that observers were naturally exposed, in different sessions, to three different temporal contexts (ranges of displayed durations) and these priors were learned effortlessly. Other priors can be updated given sufficiently convincing feedback, such as the default prior knowledge that light comes

from above our head<sup>15</sup>. It is also surprisingly easy for participants to form nearly optimal strategies in pointing tasks to a visual target with arbitrary, experiment-imposed payoffs and penalties<sup>13</sup>. The ability of human participants to readily adapt to changes in context or loss function constitutes strong evidence for Bayesian decision theories of perceptual-motor performance<sup>14</sup>.

#### COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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## An abundance of grid cells

Several different classes of neurons are involved in the mapping of allocentric space. Two such classes, place cells and head-direction cells, have been found throughout the medial temporal lobe memory areas, including the presubiculum, parasubiculum and entorhinal cortex. Place cells represent spatial locations and features of the environment and head-direction cells are sensitive to the orientation of a rat's head with respect to the environment. A third major class of cells, known as grid cells, was recently identified in the medial entorhinal cortex (MEC). Grid cells, which encode abstract spatial structure, are of great interest because, unlike place cells, their response properties are independent of any particular environment, suggesting that they are involved in path integration mechanisms. On page 987, Boccara and colleagues report that grid cells are not unique to the MEC, where they were first found, but are also abundant in the pre- and parasubiculum.

Boccara and colleagues recorded from neurons throughout the presubiculum, parasubiculum and MEC of rats during food-motivated running in an open environment. They found grid cells in all three of these areas, interspersed with head-direction cells and border cells (another recently reported cell class that encodes the boundaries of a local environment). The relative proportions of each of these cell classes were comparable across presubiculum, parasubiculum and the deep layers of MEC. However, the rotational symmetry of the grid pattern and the theta modulation of presubiculum neurons were significantly weaker than those in MEC.

The pre- and parasubiculum project strongly to MEC, raising the possibility that they may be the sources of grid-cell properties in MEC neurons. However, it is also possible that grid properties are generated locally in each of these regions. Although the existence of grid cells in multiple areas does not definitively identify the mechanism for generating these unique response properties, it further specifies the neural network that supports the mapping of allocentric space.

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