mines the information is the *a priori* uncertainty in the stimulus set. To quantify this uncertainty, Shannon defined a measure H(S) called entropy, which is in many regards analogous to the entropy (disorder) defined in thermodynamics. Once we analyze the response to the stimulus we will typically still be somewhat uncertain about which stimulus was presented; this residual uncertainty, called equivocation, can be quantified by H(S|R), i.e., the entropy about the stimulus given the response. Two factors contribute to equivocation: first, because of noise, two presentations of the same stimulus may evoke different responses. Second, the difference between the responses to different stimuli might be small. H(S|R) is thus a function of the overlap between the responses to one stimulus and the responses to the other stimuli. The difference between H(S) and H(S|R) is the average reduction in uncertainty about the stimulus given the response, called the mutual information.

One advantage of the mutual information is that it is independent of any mechanism or model of how the stimulus and response are related. This can be particularly useful when the firing pattern of the neuron (e.g., a complex spike in a PC) is known, but when the cause of this response is not known (i.e., what generates climbing fiber activation?). Calculating information content requires only that the stimuli and the responses be represented by a code. Information theory does not specify which code to use, but simply says, for a given code, how much information is present. The key to applying this method in neurophysiology is to define an appropriate stimulus set code and a response set code[13]. Kitazawa *et al.* used information theory in their study to relate features of the pointing movement of a monkey's finger (stimulus set code) with the probability of occurrence of a complex spike in a time window (response set code). Unlike firing rate modulation, which is fairly meaningless at the low frequency observed for complex spikes, probability of occurrence is both easy to calculate and intuitively meaningful at all rates. Probability is easy to calculate from repeated trials, even if the number of spikes is low. Probability of occurrence is meaningful at low rates because it encompasses when a spike may occur relative to some epoch, as well as how often it can be expected to occur. At low rates, however, firing rate modulation just becomes binary, the cell fires during the trial at either 0 or 1 spike per epoch. Furthermore, probability measures are easily applied to a population of PCs; probability values between

0 and 1 can be thought of as the fraction of a population that fired a spike.

In the task used by Kitazawa *et al.*, monkeys made rapid reaching movements toward a target that was transiently displayed on a screen. Applying information theory, the authors used a measure of the uncertainty about where a monkey touched a screen to show that complex spikes at the beginning of a movement encode its destination, whereas complex spikes at the end of a movement encode its mistakes. This is an important breakthrough; not only does it show a direct encoding of movement features in complex spikes, but it also shows that the encoding is dynamic, representing the amplitude and direction of motor error accurately at both the beginning and end of the movement. Thus, the complex spikes can be said to encode a vector error, i.e., the difference between where you are and where you want to be.

The new results of Kitazawa and colleagues have profound implications for theories of the cerebellar control of movement because they tell us what signals are encoded by the climbing fibers. Whether and how this information is used, however, is still open to debate. Investigating these questions will likely be a top priority for experimentalists and theoreticians interested in understanding cerebellar function in movement control. Certainly models that depend on the inferior olive simply to provide a clock or perturbation signal for movements[14] would not explain the encoding of error vectors in complex spikes. In contrast, models of the cerebellum as a learning machine[15], or as a feedback control system[10], could both benefit from a robust vectorial error signal from the climbing fibers.

Application of information theory to results of experiments on other parts of the cerebellum would allow a uniform measure of the relationship between movement features and neuronal activity for all cells, irrespective of high or low firing rates. Thus, information theory is an excellent way to compare the information encoded by the mossy and climbing fiber inputs, the intracortical neurons, and the outputs of Purkinje and deep nuclear cells. Indeed, information theory may ultimately provide us with a clearer understanding of the role each part of the cerebellum plays in controlling movements.

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Neglecting the cat

Patients with damage to certain parts of the right parietal cortex show a condition called neglect, in which they are systematically unaware of stimuli in the left side of space. The deficit is much more profound than a simple 'blind spot'; neglect patients may fail to notice objects, hear sounds, or feel touch on their left, and

they are often unaware of the left half of individual objects, as revealed in the copied drawing below. They typically fail to acknowledge their disabilities, and think no more of their lack of awareness on the left than does a normal person about seeing nothing behind their head. On page 17 of this issue, Driver & Mattingley review the literature on visual neglect; they discuss how the human clinical data may be related to physiological findings in the monkey parietal cortex, and they argue that the parietal cortex plays a key role in mediating visual awareness.

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