Decision Making: Neural Correlates of Response Time
Dispatch

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Recent studies have measured the time taken by neural processes to decide between alternative stimuli. Overt responses are produced only as soon as neural processes are completed. The brain throttles the mind.

The study of human behavior rests on two cornerstones laid down over a century ago. First, Fechner showed how the mental could be grounded in the physical through precise measurement, and thus was born psychophysics. Second, Helmholtz's measurement of the modest speed of conduction of nerve impulses gave birth to the analysis of response time. The importance of this observation was noted by William James [1]:

"*One of the lines of experimental investigation ... is that of the ascertainment of the time occupied by nervous events. Helmholtz led off by discovering the rapidity of the current in the sciatic nerve of the frog. But the methods he used were soon applied to the sensory nerves and the centres, and the results caused much popular scientific admiration when described as measurements of the 'velocity of thought'.... the way in which Science laid her doomful hand upon this mystery reminded people of the day when Franklin first [took the lightning from the sky], foreshadowing the reign of a newer and colder race of gods.*"

A new paper by Roitman and Shadlen [2] builds on both cornerstones. Their work extends a well-known line of research on the neural basis of visual discrimination. Macaque monkeys are trained through operant conditioning with positive reinforcement to report the net direction of motion of a field of moving dots by making an eye movement to one of two targets on either side. When most dots move in the same direction with the remainder moving randomly, few errors are produced. When few dots move in the same direction, with most moving randomly, more errors are produced. Evidence from neural recordings, microstimulation and ablation have demonstrated that performance on this task is based on the representation of the motion stimulus in cortical area MT [3,4]. But the signals in area MT are not sufficient to produce the saccade by which the discrimination is reported, because neurons in area MT do not innervate the necessary ocular motor structures.

To investigate how the stimulus representation in area MT may be read out, activity has been monitored in sensorimotor parts of the brain that MT innervates, such as superior colliculus [5], area LIP in posterior parietal cortex [6] and dorsolateral prefrontal cortex,

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including the frontal eye field (FEF) [7]. Unlike the studies of area MT, where the motion stimulus was located in the receptive field, in these studies the motion stimulus was placed at the gaze focus, with one of the saccade targets in the neuron's response field and the other in the opposite hemifield. The results showed that neurons in sensorimotor areas are different from those in area MT and more directly related to the overt choice of the monkeys.

None of these studies, however, investigated the time needed to accomplish the discrimination. Indeed, until recently, most studies with behaving monkeys have treated response time as an experimental confound to be avoided by imposing arbitrary delays in tasks with the aim of separating in time the sensory-evoked from the movement-related modulation of discharge rate. So in spite of its importance in theories of cognition, neurophysiological studies aimed at explaining the duration and variability of response times have only recently appeared. A pioneer in this was Jean Requin [8]. More recently, it has been shown that the activity of saccade-related neurons in the FEF [9] and superior colliculus [10] is closely related to the timing of saccade initiation. Saccades are initiated when the level of activity in this population of neurons reaches a threshold, and the variability in response time can be accounted for by the time taken by the neurons to reach the threshold. This pattern corresponds to certain models of response time [11,12].

Roitman and Shadlen [2] modified the motion discrimination task to permit monkeys to report the direction of motion as quickly as they could. When most dots moved in the same direction, monkeys produced a high fraction of correct responses with short response times. When a small fraction of dots moved coherently, then monkeys required much more time to produce correct responses. Roitman and Shadlen [2] analyzed the relationship between the evolution of LIP neural activity, the quality of the stimulus and the time of the saccade. They report that, if the motion signaled a saccade to the target in the receptive field, the activation of LIP neurons increased gradually after appearance of the motion stimulus. The increase was more rapid in trials with stronger motion and shorter response times.

To distinguish the contributions of exogenous stimulus factors and endogenous response factors, Roitman and Shadlen [2] also examined the growth of activity on trials with different response times in response to a given stimulus. In response to a given stimulus, variability in response time was predicted by variability in the rate of growth of an average of activity of LIP neurons. A potential weakness of this approach is the averaging across cells. Roitman and Shadlen [2] performed an additional analysis at the level of single trials by fitting lines to the function of firing rate over time in each trial. The slope of the best-fit line was an estimate of the rate of change of firing rate. Roitman

and Shadlen [2] found a weak but significant relationship between the rate of increase of LIP neural activity and response time measured trial-by-trial.

Roitman and Shadlen [2] emphasize the incremental growth of the activity, especially evident on the trials with the longest response times. They interpret the results as indicating that the signal conveyed by LIP neurons corresponds to an accumulation of the evidence for and against the alternative outcomes through integration of the signals arriving from area MT [13]. When the accumulated quantity reaches a threshold, they suggest, the movement is committed. The authors are not, however, clear about just how a measure of evidence reaching a threshold is translated into a motor command.

Other research indicates that a post-perceptual stage of processing produces overt responses. For example, in our recent study, my colleagues and I [14] found an equally clear relationship between response time and the evolution of neural activity in the FEFs. This experiment presented arrays of eight apertures of random dot motion and required monkeys to shift gaze to the one moving in the unique direction (for example, rightward among many leftward). We found that the time taken for the neurons to represent the location of the array was fixed if the discrimination of the direction of motion in each array was easy, but the time to locate the target was longer and more variable, accounting for more of the variability of response time if the discrimination of the direction of motion in each array was difficult. But this difference was not seen when response time was longer because of response conflict. This can be explained in terms of a response preparation stage that follows the perceptual processing stage. In fact, the neurons originally reported to show a variable growth to a fixed threshold [9] have other attributes of a response preparation process [15].

The key insight into decision making from this line of research is that alternatives that are more difficult to distinguish result in a longer period of less differentiated activity representing the alternatives. The longer the response time, the later and less the difference in neural activity — response time is only as quick as neural activity allows. This interpretation is attractive because the form of neural activity observed in these sensorimotor association areas corresponds to the general form of sequential sampling models known as random walk or diffusion, in which a single accumulator represents the relative evidence for two alternative stimuli [11]. According to such models, errors arise from noise in the representation of the stimuli. The representation of the motion stimulus in area MT, however, is actually too good to account for monkey performance; additional noise, attributed to the decision process, must be added [16].

The alternative to a diffusion of the difference between alternatives is a race among accumulators representing each alternative, with the first to reach a threshold dictating the response [17]. The formula describing the outcome of this model is at the heart of biased choice theory, which is the historical and conceptual counterpart to signal detection theory. Both signal detection and choice theories provide quantitative descriptors of discriminability and response criterion, and they are mathematically equivalent under reasonable assumptions. But choice theory attributes the unpredictability of the response to the decision process instead of the stimulus representation. Race models can explain stimulus discrimination and categorization as well as diffusion models can [18]. In fact, race and diffusion models can account for common sets of data [19], and hybrid models have been formulated [20]. In agreement with these computational developments, Roitman and Shadlen [2] suggest that the variability in response time can be explained ultimately by momentary variability in the stimulus representation and also in the accumulation process. As in the beginning with Helmholtz, so today, time provides leverage on understanding how cognitive processes are instantiated by the brain.

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