Decision making: **From sensory evidence to a motor command**
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New insight into how the brain makes a decision has come from a study of the effects of the decision-making process on an eye movement evoked by electrical stimulation of the frontal cortex. The accumulation of sensory evidence was found to cause a gradual commitment toward a choice.

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"*I must have a prodigious quantity of mind; it takes me as much as a week sometimes to make it up*"

In his famous remark, Mark Twain articulates the basic fact that making decisions takes time. What happens in the brain that takes so much time? In an illuminating recent study, Gold and Shadlen [1] used electrical stimulation of the brain to probe the evolution of a perceptual choice. They found that preparation of the movement that will signal the choice proceeds in proportion to the quality and duration of the sensory evidence on which the choice is based. Furthermore, a quantitative model links a formal representation of the sensory stimulus with the decision and motor planning process.

The use of electrical stimulation to probe brain function dates back to a technological and conceptual breakthrough made in 1870 when Fritsch and Hitzig [2] discovered that electrical stimulation of particular parts of the cerebral cortex of a dog could elicit movements of particular parts of the body. This landmark study was a compelling demonstration of the localization of function, at a time when Flourens' view of 'distributed equivalence' was dominant and it was believed that the cerebral cortex was not responsible for producing body movements. Experimental electrical stimulation of the brain was used fruitfully by other investigators, notably Ferrier. Among many other observations, Ferrier [3] described a representation of eye movements in the frontal lobe that he called the 'frontal eye field'.

Gold and Shadlen [1] have now shown that the direction of an eye movement evoked from the frontal eye field is influenced by the direction of another eye movement the monkeys will make to signal the direction of motion in a random dot display. The magnitude of the deviation was proportional to the strength of the motion signal and the duration of the display. This phenomenon resembles an observation made by Kustov and Robinson [4] when stimulating the superior colliculus in an attention-cueing task. The basic phenomenon seems to be that creating conditions — through cueing or motion discrimination — that call for a eye movement in one direction can cause a deviation in the direction of an eye movement elicited by other means (electrical stimulation) in the orthogonal direction.
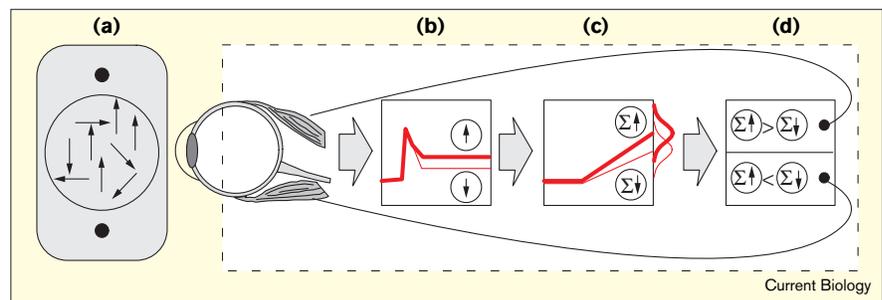
Gold and Shadlen [1] trained monkeys to judge the net direction of motion in a collection of dots moving in an aperture. The monkeys reported their choice by shifting gaze to one of two spots positioned outside the aperture (Figure 1). The strength of the motion signal was manipulated by adjusting the fraction of dots moving in the same direction relative to the fraction of dots moving randomly. The viewing duration was varied from short — 100 milliseconds — to long — 1000 milliseconds — across trials. Critically, the monkeys could not predict when they would be called on to report their choice, because the viewing times were distributed as unpredictably as radioactive decay. At different times in random trials, electrical stimulation of the frontal eye field was applied to probe the state of the oculomotor system.

Gold and Shadlen [1] observed that the saccade evoked by stimulation of the frontal eye field showed a systematic deviation in the direction of one or the other of the choices, providing evidence that the decision process, and not just its outcome, seems to occur in brain circuitry that governs the movement response. It would be misleading to believe that this evidence localizes the decision process specifically in the frontal eye field. The same result would probably obtain if the stimulating electrode were located in the superior colliculus. The outcome of stimulating the posterior parietal cortex is not as certain, but that is the promise of this technique for probing how different cortical areas and subcortical structures participate in decisions and motor planning. This new work should be clearly distinguished from an earlier study by Salzman and Newsome [5], in which a monkey's motion discrimination was influenced by electrical stimulation of the motion-processing cortical area MT. Whereas stimulation of area MT influenced the choice the monkeys made, stimulation of frontal eye field probed the extent to which monkeys had formed the choice.

Gold and Shadlen [1] have taken an important step beyond their empirical finding, by furnishing an explanation based on a quantitative model of the sensory encoding process.

Figure 1

Sequence of visual processing and choosing in the recent work of Gold and Shadlen [1]. **(a)** Monkeys viewed a display with a field of dots moving in random directions with a variable fraction moving in one of two directions, in this case upward. Monkeys reported which net direction of motion was present by shifting gaze to one of two spots that appeared on either side after the field of dots was removed. **(b)** The visual representation of the alternative directions of motion for a unit that responds preferentially to upward motion. After an initial transient response, the maintained activity remains at a constant level corresponding to more (thick) or less (thin) motion in the preferred direction. **(c)** The accumulating sum of motion in the alternative directions. Due to variability in neuronal responses in the visual representation, the magnitudes of accumulated evidence form distributions of high (thick) and low (thin) values. **(d)** When required, the choice of which eye movement to produce is dictated by the larger of the alternative accumulated values. Because of the random variability in the accumulated values, it can happen that a monkey will report downward motion even though net upward motion is present. The model portrayed by this figure accounts for the correct and incorrect performance of the monkeys.

The model, which is derived from earlier work by Shadlen, Newsome and co-workers [6], posits that the deviation is the result of an accumulating signal that corresponds to the extent of discrimination of the direction of motion (Figure 1). The sensory evidence grows over time, with a rate proportional to the strength of the motion display. Note that the accumulation does not happen in the sensory system, where the level of maintained neural activity reflects the amount of motion in the preferred direction. Instead, neural recordings from the frontal eye field [7] and the superior colliculus [8] in the same task have demonstrated a neural representation of the decision that grows over time.

The general notion that perceptual decisions arise through accumulation of information over time is at the heart of models of reaction time [9,10]. Gold and Shadlen [1] develop an explicit and straightforward relationship between the accumulator and the very well characterized neural representation of motion displays in area MT. As illustrated in Figure 1, one accumulator, representing the motion in the direction of the correct choice, grows with some baseline rate compounded in proportion to the strength of the signal over time. Another accumulator, representing the motion in the direction of the incorrect choice, grows as simply the baseline rate compounded over time. Notably, Gold and Shadlen's evidence is that, at least under the conditions used in their investigation, the accumulation was linear over time. Furthermore, Gold and Shadlen showed that the deviation of the eye movement elicited by frontal eye field stimulation was proportional to the difference between the accumulated-correct and accumulated-incorrect values, whichever value being greater dictating which alternative was chosen. Thus, accumulation of the sensory evidence, and activation that is preliminary to but does not obligate the eye movement, happen together.

But sensory coding and movement preparation cannot be the same thing, for we can produce different movements in response to the same stimulus, or responses to locations that were not occupied by a stimulus. To explain the variability and flexibility of visually guided behavior afforded by the arbitrary linkage of sensory coding and motor actions, it is necessary to posit the existence of separate stages of processing. How arbitrary the mapping of response onto stimulus can be is illustrated dramatically by eye movements called 'antisaccades', which are gaze shifts to a location opposite that of a flashed visual stimulus. For example, recent neurophysiological studies have reported the pattern of neural activation in the frontal eye field in monkeys producing antisaccades [11].

The framework that there are more-or-less distinct stages of processing entails the additional issue of how signals flow between the stages. Do signals flow between stages in a continuous or discrete manner? The finding of Gold and Shadlen [1] may be interpreted as showing that the motor system is influenced by accumulating sensory evidence, which can be seen as evidence for continuous flow [12,13]. But this is a knotty issue that should not be decided conclusively based on a single experiment, because whether signal flow appears continuous or discrete can vary with conditions [14]. The conditions used by Gold and Shadlen [1] favor continuous flow, because of an over-learned mapping of response onto stimulus. In general, the motor system may be activated in proportion to, and as a function of, the resolution afforded by sensory processing in the context of some learned association.

Some views of visual processing suppose, or imply, that a complete representation of the image is constructed before any movements are planned. An important implication of the work of Gold and Shadlen [1] is that an

intermediate discrete decision stage may not be necessary. In fact, how would such a separate decision stage work? If the decision stage is distinct from the sensory and motor representations, then it would have to plug in to them somehow. A discrete decision stage would need some kind of sensory representation, but why duplicate what has already been encoded? A discrete decision stage would need to represent the response to activate the motor system, but what properties would such a preliminary to a motor plan have — for example, in what coordinate frame would it be? Research such as that of Gold and Shadlen [1] should prevent us from endowing decision processes in the brain with the properties of a homunculus.

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