

# Decisions arising from opposing views

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**A new study suggests that the brain makes decisions about the direction of movement of a stimulus by a subtraction operation between neurons tuned to opposite directions. The winner of this computational battle determines the final perceived direction.**

Imagine sitting next to a window in a restaurant atop a high building. You see people moving in the plaza below, and you instinctively direct your gaze in the direction that most people are moving. This effortless action—identifying the net direction of motion of a more-or-less randomly moving group of objects—involves cortical neurons from the middle temporal area (MT) of the brain. These neurons activate in response to visual objects moving in a particular direction and inform the brain that an object is in motion<sup>1</sup>, but understanding how this neuronal representation is used to decide which direction a stimulus is moving has remained elusive. The answer may be that the brain combines sensory information from neurons tuned to opposite directions, suggest Ditterich *et al.*<sup>2</sup> in this issue.

To examine this question, the authors trained monkeys to make an eye movement (saccade) toward one of two targets to indicate their decision about the net direction of a group of moving dots (Fig. 1). By varying the percentage of dots moving in the same direction, the authors could alter the difficulty of the task. A key feature was that the monkeys were able to decide freely when to perform the response—that is, they could view the display for short or long periods before reaching and communicating a decision about the movement direction. Thus, the estimation of not only the probability of choosing any response target, but also the time that monkeys took to reach that decision, allowed Ditterich *et al.* to gain insight into the possible operations involved in the decision mechanism and test current models of decision making<sup>3</sup>.

Next, the researchers used microstimulation (activation of neurons by weak electrical currents) to manipulate sensory representations of motion in the monkeys' visual cortex. The technique has proven successful for biasing<sup>4</sup> and even creating artificial sensory percepts<sup>5</sup> in monkeys, revealing

causal relationships between neuronal firing patterns and perception. Because MT neurons are very selective about the physical attributes of the stimuli that activate them, the researchers first determined the appropriate combination of size, location, velocity and direction of the moving dots that optimally activated the neurons in the vicinity of the recording electrode. Once the best activating stimulus was found, the monkeys' task was designed such that the dots moved in the direction preferred by the neurons near the recording electrode in half of the trials, and in the opposite direction in the other half. For example, if the recording electrode was near a group of neurons with upward direction preference, the stimulus set was designed such that monkeys had to decide whether the net motion of the dots was upward or downward. Thanks to this design, the authors could artificially activate neurons while monkeys performed the direction discrimination task and add motion information that was either congruent or opposite to the direction of the moving dots. They could then evaluate how the addition of either type of information affected the monkeys' choice behavior.

How this artificial addition of information affected the monkeys' behavior depended on the direction of the dots being presented with respect to the microstimulated neuron populations. If the dots were moving in the direction preferred by the microstimulated neurons, the authors found that the monkeys were substantially more likely to choose to make an eye movement in that direction. Additionally, the stimulus-viewing intervals (reaction times) were faster. This suggested that microstimulation was adding information to the stimulus, biasing the monkeys' behavioral responses in the direction preferred by the stimulated neurons and causing the monkeys to reach faster decisions, presumably due to a quicker accumulation of sensory evidence. These results elegantly confirmed the causal relationship between the activity of MT neurons and the perception of motion direction<sup>4</sup>.

However, the more exciting insight into the nature of the decision mechanism came

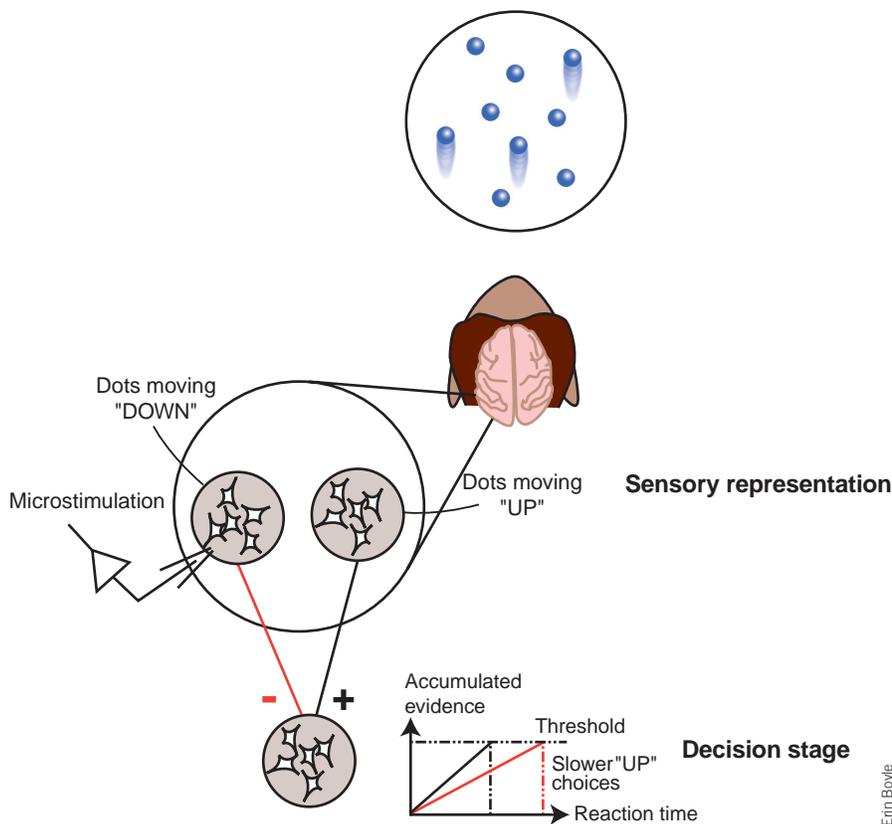
from trials in which the direction of the moving dots was opposite to the direction preferred by the stimulated neurons. In some cases, mostly those in which motion information about direction was weak (dots had low coherence), microstimulation was strong enough to make the monkeys choose the direction preferred by the stimulated neurons. However, in some cases, the information added by microstimulation was not enough, and the monkeys made a saccade in the direction of dot motion. The key finding from these trials was that when microstimulation added sensory information opposite to the direction of the moving dots, monkeys took longer to choose a direction than they did without microstimulation (Fig. 1). Thus, the monkey behaved as if the stimulus had weaker motion information than it actually did. This behavior suggested that adding information from neurons that respond to the reverse direction of a stimulus slows the process of accumulation of motion information.

This delay in decision making due to artificial addition of opposing motion information is consistent with a mechanism in which the determination of the direction of motion arises from the accumulation of motion information favoring one direction minus the motion information of the opposite direction<sup>3</sup>. Thus, neurons with opposite direction preferences contribute in an opponent manner to the final decision. In this way, the decision to perform a saccade, say, upward, is not based only on the activity of upward-preferring neurons; it is based on the difference in the activities of populations signaling upward versus downward motion.

The idea that perceptual decisions arise from a subtraction operation between the activities of neurons with opposite sensory preferences is exciting because experiments using a different perceptual task reached similar conclusions<sup>6</sup>. In the somatosensory system, in making the decision about which of two vibratory stimuli has a higher vibration frequency, the optimal strategy is to subtract the responses of two populations of sensory neurons, one preferring low frequencies and the other preferring high frequencies<sup>6</sup>. As in the

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**Figure 1** The visual motion discrimination task. Monkeys decide in which of two directions the dots are moving (in this case up or down), and report their choice by making an eye movement (a saccade) in the chosen direction. By artificially activating a neuronal population with direction preference opposite to the displayed stimulus, Ditterich *et al.*<sup>2</sup> found that reaction times increased, consistent with the idea that a decision mechanism accumulates sensory evidence from a subtraction operation between the activities of two neuronal populations with opposite sensory preferences.

mechanism that contrasts information from sensory neurons with opposite stimulus preferences develops in animals performing distinct perceptual tasks is promising. Could this be a general decision mechanism implemented by the brain?

With the results obtained by Ditterich *et al.*<sup>2</sup> at hand, we can now return to that window of our imaginary top-floor restaurant. When we observe the group of people moving in the plaza, decision areas in the brain are comparing and accumulating motion information arising from direction-selective neurons in MT. Once the resulting computation favors one of the competing alternatives, our brain guides the eyes in the direction that we think the majority of people are moving. Answers to questions about how we manipulate our sensory representations of the outside world will greatly influence how we think about the neural mechanisms that link sensory information processing and cognition.

experiment of Ditterich *et al.*<sup>2</sup>, the subtraction operation between the activities of two oppositely tuned sensory neurons is a simple way to determine which of the two is more strongly activated, and thus which of two sensory events is more likely to have occurred.

It seems that a subtraction operation between two opposite sensory representations may be a general processing strategy used by the brain to reach decisions and ultimately trigger behavior<sup>3,7</sup>. These results raise important questions about where in the brain the subtracting operation is performed, and which cellular circuits are involved. A given population of MT neurons is only weakly affected by activity of other MT populations<sup>8</sup>. Thus, the cellular and network mechanisms responsible for combining the information of opposite populations are not likely to be present in MT. Instead, all higher areas receiving direct or indirect inputs from MT<sup>7,9</sup>, including the motor areas<sup>10</sup>, are candidates for elaborating the subtraction operation and, therefore, the decision. We must also

consider that decisions might not arise in a single location but may be the consequence of many areas working synergistically<sup>11</sup>.

An unexplored part of the picture discussed above, however, is the history of intensive training that preceded the recording and microstimulation experiments. What we see in a laboratory animal might be a brain circuit optimized—or possibly even created by training—to perform a particular task in a highly constrained sensory context. This fact leads to two interesting questions: how are the decision-making cortical circuits developed through training, and do these circuits exist in non-trained animals that nevertheless are constantly choosing behaviors based on sensory information? In contrast to laboratory tasks, the relationship between contextual sensory information and potential behaviors in more natural circumstances is not predefined. For this reason, the examination of cortical circuits transforming sensory information into action in freely behaving animals is a crucial object for future research. However, the fact that a decision

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