EPPENDORF

When Attention Wanders

Examining the neural process of visual attention helps decipher how the brain extracts important sensory information.

Marlene R. Cohen

Everyone, from a child in a classroom to a driver on the road, has had the experience of having their thoughts meander far from the task at hand. Our minds wander when we rest (*1*–*3*) and about half the time we are engaged in an activity (*4*). A goal of my postdoctoral work with John Maunsell at Harvard Medical School was to understand how these internal fluctuations affect behavior. This knowledge is useful for determining the neural basis of internal mental states.

We measured the effect of fluctuations in one internal factor, visual attention, on perception. Attention allows observers to focus on the important locations (spatial attention) or features (feature attention) in a complex visual scene without looking at the attended object. For example, a baseball pitcher might focus his eyes on the catcher at home plate but also allocate part of his attention to the location around a runner at first base (spatial attention) or attend to the color of the opposing team's uniforms to keep track of runners at any location (feature attention).

Although attention has long been known to affect perception, a detailed study of attentional fluctuations had been essentially unapproachable. Measuring fluctuations requires estimating a subject's attentional state at each moment. Attention improves a subject's average performance on perceptual tasks, but it is hard to know whether any particular mistake was caused by a lapse in attention or because the task was simply difficult.

Attention also affects parts of the brain that control vision: Attending to a particular location or feature causes the neurons in visual cortex that encode that location or feature to become more active (*5*–*8*). However, the responses of individual neurons cannot be used to estimate attention instantaneously because neural responses are noisy. It is impossible to separate out variability caused by changes in attention from variability that is inherent to the neuron.

The brain is thought to combat this noise by combining the responses of many neurons (*9*–*12*), so we used the same approach. We reasoned that if we recorded from many neurons simultaneously, we could tease apart the noise from responses that signaled changes in attention. After teaching monkeys a task that measured their ability to detect subtle changes in a visual stimulus, we simultaneously recorded the responses of about 80 neurons in cortical area V4, which encodes visual information and is affected by attention. The monkeys looked at a computer screen and a pair of striped stimuli flashed on and off [see the figure (A)]. At a random time, the orientation of one stimulus changed slightly. If the monkey correctly indicated that he noticed the change by looking at the changed stimulus, he was rewarded with a drop of juice.

To control their attention, we cued the animals as to which stimulus was most likely to change. When the monkeys knew to expect a change on the left, they shifted their attention to the left. We measured responses to the stimulus before the change [black outline in (A)] when the only difference from one trial to the next was the monkey's attention.

Single-neuron studies typically compare the neuron's average response across many trials in each attention condition (e.g., when the monkey expected a change in the left or the right stimulus). We modified this idea to estimate the monkey's attentional state

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Eppendorf and *Science* are pleased to present the prize-winning essay by Marlene Cohen, the 2012 winner of the Eppendorf and *Science* Prize for Neurobiology.

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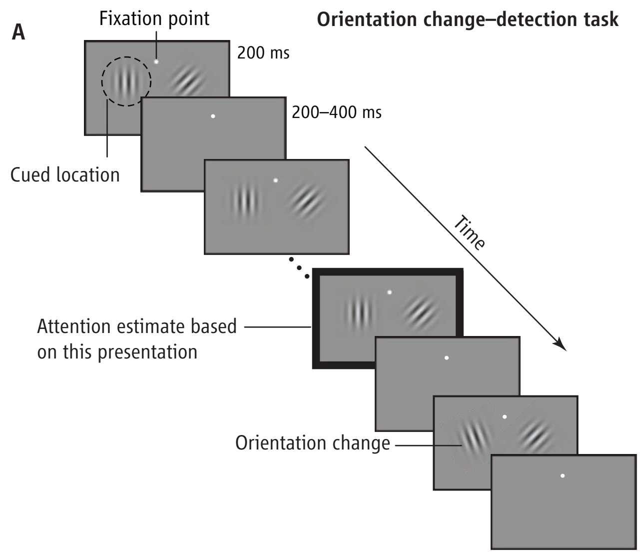

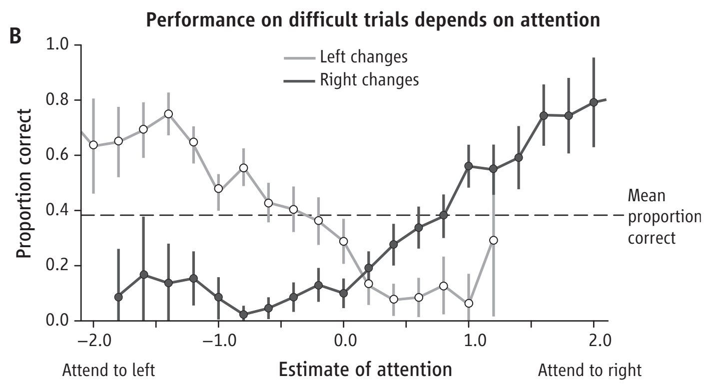

Change-detection task. (**A**) Rhesus monkeys were trained to perform a task that measured their ability to detect subtle visual changes. Two stimuli flashed on and off, and at a random time, the orientation of one of them changed. The monkeys were rewarded for looking at the stimulus that changed. Before each set of trials, the monkeys were cued to expect that one stimulus (the left one in this example) would be more likely to change, which gave them incentive to pay attention to that stimulus. (**B**) The monkeys' proportion correct on the change-detection task is plotted as a function of the estimated location to which they allocated attention (which was calculated based on the responses of the neurons that were recorded while the monkey performed the task). [Modified from Cohen and Maunsell (2010) (*22*)] at a single moment by comparing the combined response of the 80 neurons at a given moment to the average in each attention condition. We defined a measure of attention in which positive numbers signaled rightward attention and negative numbers indicated leftward attention [see the figure (B)].

Like humans (*4*), the monkeys' attention wandered, and our neuronal measure of attention varied greatly. Moreover, these attentional fluctuations profoundly affected how well they could do the task. When the measure showed strong attention to the left, the monkey was able to detect a subtle orientation change on that side about 70% of the time. However, when the measure showed that attention had drifted toward the right, he almost never detected that same change on the left [see the figure (B)]. This estimate of attention, based on just a few dozen of the ~100 billion neurons in the monkey's brain, allowed us to predict whether he was about to get the trial correct with about 80% accuracy.

Having a near-instantaneous measure of attention provided a new and powerful approach to investigate how attention affects performance and is controlled in the brain. To our surprise, whereas attention improved the monkeys' ability to detect subtle orientation changes, it worsened their performance when the change was very obvious (*13*), which suggests that strongly attending to one feature (e.g., vertical stripes) makes it more difficult to see a very different feature (e.g., horizontal stripes) (*8*, *14–21*). Also, although the monkeys allocated attention to the two locations independently [they could attend to the left, right, both, or neither stimulus (*22*)], they nevertheless attended to a single feature in all locations (*21*). This suggests that spatial attention involves local groups of neurons whereas feature attention is coordinated throughout the brain.

Together, our results suggest that the baseball pitcher's spatial attention can wander from the catcher's mitt to first base or to both or neither location. When he attends to the color of the opposing team's uniform, however, he is sensitive to that color at all locations. But this improved sensitivity comes at a cost: When attending strongly, he might be completely unaware of his own manager running onto the field wearing a different color.

Our results show that when the mind wanders, so too do our perceptual abilities. Grasping the implications of variability in attention and other cognitive states on our basic abilities may be an important step toward understanding how our internal state affects our ability to interact with the outside world.

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2012 Grand Prize Winner

The author of the prize-winning essay, **Marlene Cohen**, is an assistant professor in the Department of Neuroscience and the Center for the Neural Basis of Cognition at the University of Pittsburgh. Dr. Cohen received her Ph.D. from Stanford University studying how interactions between neurons depend on how an animal is planning to use the sensory information they encode. Her postdoctoral research at Harvard Medical School used visual attention as a tool to understand which aspects of a cortical population code are most important. Her group at the University of Pittsburgh uses physiological, behavioral, and computational methods to study what information groups of neurons in visual cortex transmit to downstream areas and how variability in sensory neurons affects perception.

Finalists

Aryn Gittis, for her essay "Striatal interneurons: Causes or cures for movement disorders?" Dr. Gittis is an assistant professor in the Department of Biological Sciences and the Center for the Neural Basis of Cognition at Carnegie Mellon University. She received her Ph.D. from the University of California, San Diego, where she studied intrinsic firing mechanisms of vestibular nucleus neurons. In 2008, she became a postdoctoral fellow at the Gladstone Institute of Neurological Disease, where she studied inhibitory circuits involved in movement disorders such as Parkinson's disease and dystonia. Her laboratory uses electrophysiology, optogenetics, and anatomy to study how neural circuits in the basal ganglia control movement in health and disease. http://scim.ag/Gittis

Bertrand Coste, for his essay "The cellular feeling of pressure." Dr. Coste is a CNRS Research Scientist at the Research Center of Neurobiology-Neurophysiology of Marseilles, France. He received his Ph.D. in Neurosciences from the University of the Mediterranean Aix-Marseille II. In his doctoral work, he worked on pain sensitivity and investigated the modulation of nociceptive neuron excitability during inflammation. After receiving his Ph.D., he moved to The Scripps Research Institute in La Jolla, California, USA, where he was a postdoctoral fellow from 2007 to 2012. His work focused on the identification of molecular components involved in the transduction of mechanical forces into biological signals and led to the identification of a new family of ion channels. http://scim.ag/Coste

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