

Probing consciousness with an electrode

Okihide Hikosaka*

Department of Physiology, Juntendo University, School of Medicine, Tokyo, Japan

[Received 17 May 1999; Accepted 17 May 1999]

Voluntary behavior is unpredictable, unlike a reflex. Can we understand voluntary behavior in terms of neural processes, as we understand a reflex? The question was nothing but an intractable fantasy until Robert Wurtz and Michael Goldberg published a series of four papers in *Journal of Neurophysiology* in 1972 [3–6]. While studying single cell activities in the monkey superior colliculus in relation to visual and oculomotor functions, the authors discovered that cells' visual responses changed depending on the monkey's subsequent behavior even though an identical stimulus was presented.

Goldberg and Wurtz started off the second paper [4] by writing,

“In all previous studies on visual receptive fields of single neurons . . . , the properties of the cells were studied without regard to the behavioral significance of the visual stimuli. . . . The awake animal does not treat objects in the visual world uniformly: it responds to some and ignores others. At some point in the brain neurons must reflect not only the external parameters relating to the physical properties relating to whether or not the animal will respond to the stimulus.”

Goldberg and Wurtz trained monkeys on two tasks, a fixation task and a saccade task (Fig. 1), which are now commonly used by behavioral neuroscientists. Neurons in the superficial layer of the superior colliculus respond to visual stimuli at a particular location (receptive field) as they receive direct connections from the retina. Goldberg and Wurtz found that the visual response was enhanced when the monkey was going to make a saccadic eye movement to the receptive field stimulus (in the saccade task) compared with when the monkey kept fixating (in the fixation task). However, the enhancement of the visual response could simply be due to the heightened level of arousal in the saccade task. This possibility was excluded because, when the monkey made a saccade to another stimulus outside the receptive field, there was no enhancement. Goldberg and Wurtz concluded the paper by writing,

“We suggest that this enhancement of response . . . is the effect of the mechanism which on the psychological level is the phenomenon of attention”. [4]

The Goldberg and Wurtz study opened up the era of cognitive neuroscience. Previously there were only two variables—stimulus and neuronal activity—and the question was to determine the transfer function between these variables. Goldberg and Wurtz successfully introduced another variable—the internal state (which may represent “mind” or “consciousness”). More importantly, they developed the method to characterize the third variable. They did so by keeping the stimulus constant

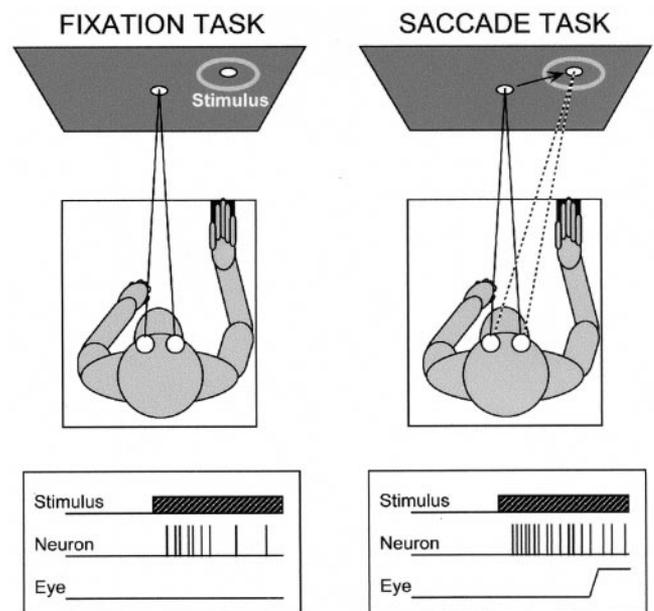


FIG. 1. The spike activity of a single neuron was recorded from the superior colliculus while the monkey was performing the fixation task and the saccade task. The monkey sat on a chair facing a screen. In either of the tasks, when the monkey pressed a lever on a chair, a spot of light (fixation point) appeared at the center of the screen and, after some time, another spot of light (stimulus) appeared at a peripheral location. In the fixation task, the monkey had to keep fixating on the fixation point to detect its dimming and release the lever. In the saccade task, the monkey had to make a saccade to the stimulus if it was located in the neuron's receptive field (indicated by a circle). Goldberg and Wurtz found that the visual response was stronger in the saccade task than in the fixation task, although the stimulus was physically the same.

while changing the behavioral context, thus focusing on the relationship between the internal state and the neuronal activity. This new strategy changed the attitude of neuroscientists so profoundly and gave them confidence to study the internal state of the brain. The currently flourishing studies on attention, action, working memory, and mental imagery are all originated from this idea. The same strategy has also been applied to human imaging studies.

* Address for correspondence: Prof. Okihide Hikosaka, Department of Physiology, Juntendo University, School of Medicine, 2-1-1 Hongo, Bunkyo-ku, Tokyo 113-8421, Japan. Fax: +81-3-3813-4954; E-mail: hikosaka@med.juntendo.ac.jp

Critical in this approach was how the experimenters could manipulate the internal state of the brain. One cannot simply ask the animal subject to "think" in this way or that; one has to set up the behavioral context in which the animal subject supposedly possesses a certain state of mind, such as attending to object A while ignoring B. In the case of the Goldberg and Wurtz study, the monkey would attend to the receptive field stimulus when it was going to make a saccade to the stimulus. Their suggestion then was that the enhancement of the visual response was due to attention. However, the subsequent studies from the same laboratory [1] argued against this idea. Here the same visual stimulus was presented and the monkey responded to it in three different ways: saccade, hand reaching, and dim detection. It was considered that the subject had to attend to the stimulus in any of these conditions. Yet, the enhancement compared with the fixation condition occurred only in the saccade condition. However, this failure was never a disappointment; it was another start of the continual search for the cognitive functions. Thus, neurons in different parts of the brain behaved in different ways in these behavioral contexts [7]. Unlike the superior colliculus, neurons in the parietal cortex showed the enhancement in all of the three conditions [1]; neurons in the frontal eye field behaved similarly to those in the superior colliculus [2]; neurons in the visual cortex showed the enhancement even when the subject reacted to the nonreceptive field stimulus [8]. These results suggested the sequential steps of neural processing in which information is selected in the brain until it acquires behavioral significance.

Since the Goldberg and Wurtz study, we, neuroscientists, started to understand that voluntary behavior and consciousness

emerge from the interactions of many neural processes. The endeavor has just begun, disentangling the unpredictable mind and behavior.

REFERENCES

1. Bushnell, M. C.; Goldberg, M. E.; Robinson, D. L. Behavioral responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. *J. Neurophysiol.* 46:755–772; 1981.
2. Goldberg, M. E.; Bushnell, M. C. Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades. *J. Neurophysiol.* 46:773–787; 1981.
3. Goldberg, M. E.; Wurtz, R. H. Activity of superior colliculus in behaving monkey. I. Visual receptive field of single neurons. *J. Neurophysiol.* 35:542–559; 1972.
4. Goldberg, M. E.; Wurtz, R. H. Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. *J. Neurophysiol.* 35:560–574; 1972.
5. Wurtz, R. H.; Goldberg, M. E. Activity of superior colliculus in behaving monkey. III. Cells discharging before eye movements. *J. Neurophysiol.* 35:575–586; 1972.
6. Wurtz, R. H.; Goldberg, M. E. Activity of superior colliculus in behaving monkey. IV. Effects of lesions on eye movements. *J. Neurophysiol.* 35:587–596; 1972.
7. Wurtz, R. H.; Goldberg, M. E.; Robinson, D. A. Brain mechanisms of visual attention. *Sci. Amer.* 246:124–135; 1982.
8. Wurtz, R. H.; Mohler, C. W. Enhancement of visual responses in monkey striate cortex and frontal eye fields. *J. Neurophysiol.* 39:766–772; 1976.