ESSAYS ON APS CLASSIC PAPERS

Studying the visual system in awake monkeys: two classic papers by Robert H. Wurtz

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This essay looks at the historical significance of two APS classic papers that are freely available online:


IN 1969 ROBERT WURTZ (Fig. 1) published three papers in the Journal of Neurophysiology on the physiology of the visual system in the awake monkey, of which two are reviewed here. The first paper described the technique of recording the activity of single neurons in the visual system of the awake monkey, and this study replicated Hubel and Wiesel’s finding in the anesthetized monkey of cells with motion selectivity and orientation selectivity. The second paper showed that this system could be used to answer a cognitive question: could neurons in the striate cortex distinguish, as do normal humans, between the motion across the retina of stimulus moving in the world and the motion across the retina induced by the eye’s moving across a stimulus stable in the world. All of the work today studying the physiology of visual cognition, looking at phenomena like attention, motion perception, and motivation, must trace its genesis back to these two papers.

Until the 1960s the great discoveries in neurophysiology were made in anesthetized animals. As a result, neurophysiology was predominantly the study of inputs and outputs. This was especially true in the visual system. Kuffler (1953) had discovered the center and surround organization of retinal ganglion cells in the cat, Barlow and Levick (1965) had discovered motion selectivity in the rabbit retina, and Hubel and Wiesel had discovered that neurons in the striate cortex of the anesthetized, paralyzed cat (1959) and monkey (1968) were selective for the orientation and motion of stimuli (Wurtz 1969c). In this paper, Wurtz used the monkey’s own oculomotor system to turn its owner transiently into a paralyzed preparation. In the discussion, Wurtz pointed out that although he had purposely dissociated factors like attention and reward from the stimulus, such factors might be expected to affect the activity of neurons in the awake animal.

Wurtz then asked a classic psychological question: “An image moves with respect to the retina both when our eyes move and when the object moves, but in one case we perceive a stationary object, in the other case a moving object. How can we tell the difference?” (Wurtz 1969a) Wurtz first asked the monkey to hold its eyes still, found the receptive field and optimal direction of a motion sensitive neuron, and measured the neuron’s response to a stimulus swept rapidly across its receptive field in its optimal direction. He then asked the monkey to make a saccade in the opposite direction across the same stimulus held stationary on the screen. The retinal event was the same, but in one case the retinal motion arose from the motion of the stimulus in the world; in the other case the retinal motion arose from the motion of the eye. Humans and monkey could tell the difference—could neurons in striate cortex?

The answer was no. Every neuron that responded to a spatially stable stimulus swept across the retina by a saccade (1966) of techniques by which the activity of single units could be studied in animals operantly trained to perform a task. Soon thereafter David Robinson and Albert Fuchs (Robinson and Fuchs, 1966; Fuchs, 1967) showed that monkeys could be trained to make eye movements. Robert Wurtz then realized that if a monkey could be trained to hold its eyes still for a few seconds, then for that evanescent epoch a stimulus flashed on a tangent screen in front of the monkey would occupy a predictable area of the retina, and the receptive field properties of neurons in the awake monkey could be studied in great detail. In 1969 Wurtz replicated Hubel and Wiesel’s discovery in the striate cortex of awake monkeys: he found cells with selectivity for the orientation and motion of stimuli (Wurtz 1969c). In this paper, Wurtz used the monkey’s own oculomotor system to turn its owner transiently into a paralyzed preparation. In the discussion, Wurtz pointed out that although he had purposely dissociated factors like attention and reward from the stimulus, such factors might be expected to affect the activity of neurons in the awake animal.
responded to the same stimulus swept across the receptive field while the monkey held its eyes still. Not all neurons responded during a saccade, but not all neurons responded to stimuli moving at saccadic speeds. This demonstration that striate cortex could not distinguish between self-generated and externally generated motion indicated that the problem must be solved elsewhere in the brain. More importantly, it was now possible to use a microelectrode to ask cognitive questions. The many studies correlating neural activity with cognitive processes like attention (Goldberg and Wurtz 1972), perception (Newcombe et al. 1989), and motivation (Schultz et al. 1992) all stem from Wurtz's original insight that he could use the monkey as a partner in the project, enlisted the rest of the monkey's brain to help him study one area. And Wurtz soon showed that the superior colliculus did make the distinction between self-generated and world-generated retinal motion that striate cortex failed to do (Robinson and Wurtz 1976).

GRANTS
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REFERENCES


