

# Cognitive Set and Oculomotor Control

## Minireview

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One of the goals of a cognitive neuroscientific approach to studying the nervous system is to elucidate how individual neurons code higher cognitive processes. Because the execution of voluntary actions often involves processes such as memory, planning, and expectation, motor systems are well suited to serve as model systems for investigations of cognitive processes. The work of Evars and colleagues (Evars et al., 1984), which demonstrated that activity of neurons in motor cortex reflects what movement a monkey is getting ready to make long before the movement actually begins, is a good example of using this approach to study the neurophysiology underlying cognitive processes. These investigators conceptualized many issues related to planning or preparing to make a particular movement, defining this cognitive process or processes as “motor set.” Issues relating to motor set will be the focus of this minireview, and will be illustrated by recent experiments in the saccadic eye movement system.

### *The Saccadic System*

Saccades are rapid movements of the eyes which change the line of sight, typically toward objects of interest. Saccades are relatively simple movements requiring coordination of only six extraocular muscles, and the neural network in the brainstem required for the production of saccades is well understood (for review see Hepp et al., 1989; Moschovakis et al., 1996). Located on the roof of the midbrain, the superior colliculi (SC) are important centers for the control of saccades (reviewed by Sparks and Hartwich-Young, 1989) and project directly to the paramedian pontine reticular formation, which contains neurons responsible for driving extraocular motor neurons. Each SC receives inputs from the retina and virtually the entire cerebral cortex, including all of the cortical areas containing neurons with activity related to saccades. Our relatively thorough understanding of the organization of the saccadic system makes it well suited for examining the cognitive mechanisms involved in higher aspects of motor control, such as motor set.

### *Motor Set Is a Measurable Cognitive State*

Investigations of motor set began with behavioral studies. In 1888, Ludwig Lange asked subjects performing a reaction time task to focus either on the stimulus that would be presented or on the response that would be made (for history and conceptual review, see Woodworth and Schlosberg, 1938). When subjects concentrated on the response, reaction times were faster than when they focused on the stimulus. Thus, the instruction given to the subjects created a condition that influenced the rapidity with which the motor act was initiated. The

condition, subsequently called *einstellung* or *set*, describes a state of motor readiness, a cognitive process that influences behavior. Around the turn of the century, Edward L. Thorndike proposed *The Law of Readiness*, describing the motivational state of an organism quite independent of the investigations of set. Thorndike appreciated that the readiness of an organism for a particular event influenced the associations between stimuli and responses and thus the resulting behavior. He proposed that internal states could produce more efficacious behavior.

Thorndike's predictions have been confirmed numerous times by behavioral experiments in nonhuman primates. In the saccadic system, for example, Paré and Munoz (1996) trained monkeys to make the same saccade repeatedly to one target location for many days. On a subsequent day of testing, monkeys made saccades to many different target locations, including the previously trained location. They found very short saccade latencies to the trained target location, whereas saccade latencies to other target locations remained normal. This kind of explicit training is not always required to produce a change in an internal state. Using a slightly more natural task, Sommer (1997) had monkeys freely scanning an array of visual stimuli arranged in a three by three grid. As is typical in scanning behavior, monkeys made stereotyped sequences of saccades interspersed with brief periods of fixation. On some trials, a visual stimulus was briefly illuminated during moments when the monkeys were fixating and preparing to make the next saccade. The monkeys were required to make a saccade to the flashed target. This second target either occurred near the location of the next planned saccade in the scanning sequence or at a distant location. Commonly, saccades made to locations near the planned scanning saccade occurred with a shorter latency than saccades made to other locations, evidence that behavioral efficiency can be influenced by cognitive state.

### *Motor Set Can Be Measured Physiologically*

What could the physiological correlate of this increased efficiency of behavior be? Thorndike, although probably not referring to actual physiological constructs, suggested that conduction units with lower activation thresholds resulted in the state of readiness. Experimental situations in which the activity of single neurons is recorded, while monkeys associate particular stimuli with particular responses, provide a means to examine how this state may be represented in the brain. For example, are neuronal thresholds for discharging action potentials reduced when organisms are in a state of readiness? Recent experiments in primate superior colliculus provide evidence for the physiological basis of motor readiness. Recordings from neurons in the SC, while monkeys perform saccades to flashed spots of light, reveal some neurons with activity tightly linked to the presentation of the visual stimulus and some neurons with activity tightly linked to the saccade. Other neurons contain activity tightly linked to both the stimulus presentation and the movement generation. Having monkeys perform tasks in which a delay is imposed

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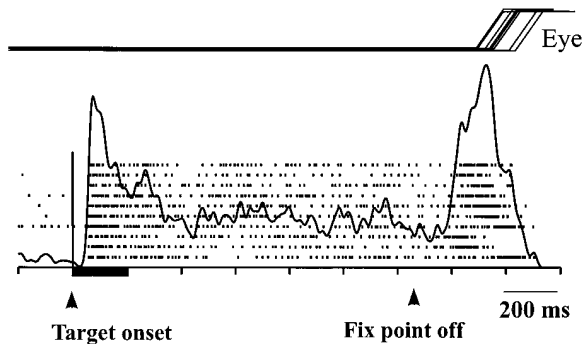


Figure 1. An Example of a Saccade-Related Neuron in the SC of the Monkey during a Delayed Saccade Task

The top traces (Eye) are schematics of the eye position on ten individual trials. Rightward is up. Each tick mark identifies an individual action potential, and each row of marks is an individual trial. An average spike density function of the ten trials is superimposed on the trials. During neuronal recording, the monkey fixated a centrally located spot and a peripheral spot of light was illuminated briefly. After a delay of several hundred milliseconds, the fixation spot was removed and the monkey made a saccade to the location of the previously flashed target spot. The activity of these neurons typically consists of three phases: visual, delay, and presaccadic or motor.

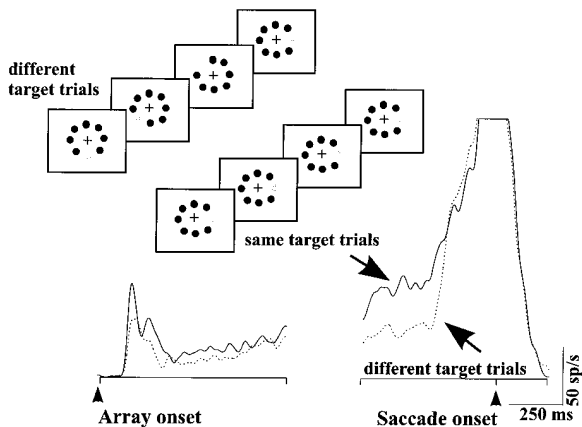
between the stimulus presentation and the cue to initiate a movement (delayed response task) reveals SC neuronal activity during the delay period (Figure 1). It is important to note that this activity occurs independent of the visual stimulus, linking the activity to an internal process, perhaps one of saccade preparation (Munoz and Wurtz, 1995; Dorris et al., 1997), an aspect of motor set (Evarts et al., 1984; Wise, 1985).

Experiments with monkeys can be designed that are similar to Lange's instructing his subjects to attend to a stimulus or a response. With monkeys, instructions about motor set can be presented in the form of visual cues. For example, Glimcher and Sparks (1992) changed the color of a centrally located fixation spot to indicate which of two other peripherally located spots was the saccade target, while they recorded from SC neurons. Monkeys performed the task correctly by making saccades to the indicated peripheral target. Because SC neurons discharge only for saccades made to restricted locations in the visual field, one target was placed in the neuron's preferred field and one target was placed outside of the preferred field. When the monkey was cued to make a saccade to the location in the neuron's preferred field, the neurons began to discharge and maintained their discharge until the saccade occurred, in some cases for up to 7 s. Thus, the neural activity occurred while the monkey prepared to saccade, indicating a change in motor set. In addition, Glimcher and Sparks examined the trials in which the target in the nonpreferred location was cued, but the monkey made an error, choosing instead to saccade to the target in the preferred location. In this case, the neuron also remained active until the preferred, but incorrect, saccade was made. The comparison between these two conditions showed that the activity of these neurons is not predictive of the instruction stimulus, but rather of the saccade choice, and is evident long before the saccade is actually made.

If the activity of some SC neurons reflects motor set, changes in the activity of neurons should correlate with changes in motor set. Applying Thorndike's conceptual idea to the nervous system, in situations of high readiness neurons should have lower thresholds for activation and should discharge at high rates. Similarly, in situations of low readiness, thresholds for activation should be high and neurons should exhibit little activity. To test this, Basso and Wurtz (1997) manipulated motor set by changing the probability of making a particular saccade. On any given trial, one, two, four, or eight possible saccade targets appeared simultaneously. Only later, one of the stimuli changed luminance, indicating it was the saccade target. In the period of uncertainty before indicating the saccade target, the number of items in the visual display served as a cue for the likelihood of making a particular saccade, thus influencing motor set. For example, in trials presenting a single stimulus in the preferred location of neurons, monkeys could be 100% certain that the stimulus would later become the target of the saccade. Because the probability of making a particular saccade was high in the single target condition, this condition would produce a high level of saccade readiness. In contrast, with eight possible saccades, monkeys could be only 12.5% certain that the stimulus in the preferred location would later become the target of the saccade. Because the probability of making a particular saccade was low, this condition would produce a low level of saccade readiness.

During the period of uncertainty, when the saccade target was not yet known, the changes in neural activity correlated with changes in motor set. In the single target condition and at a high level of saccade readiness, the activity of neurons was high; with the decrease in saccade readiness with multiple targets, the activity of SC neurons was lower. These changes occurred in both the initial response, tightly linked to the onset of the stimulus presentation, and in the later, delay period activity. This result suggests that despite the temporal association between the initial response of these neurons and the stimulus presentation, the responses do not represent the visual stimulus per se but reflect motor set, at least in part.

A more compelling demonstration of this phenomenon would use a constant visual display to demonstrate that changes in neuronal activity reflect changes in motor set. To address this, Basso and Wurtz (1997) presented monkeys with a visual display containing eight possible saccade targets, and manipulated motor set by varying the probability of correct saccade targets over a series of trials. For example, by cueing the same saccade target on every trial, monkeys could anticipate the upcoming saccade, a condition of high saccade readiness. In contrast, by randomly cueing any one of the eight possible saccades on each trial, the monkeys' ability to anticipate the correct saccade was reduced, a condition of low saccade readiness. Despite the unchanging visual stimulus, both the initial visual response and the later activity of neurons reflected the changes in motor set: neuronal activity was high when saccade readiness was high and low when saccade readiness



**Figure 2. Changes in Motor Set Alter the Activity of SC Neurons**  
An example of a neuron in the intermediate SC recorded while a monkey performed the same saccade in two conditions: one in which the saccade was made to the same target repeatedly, and one in which a saccade was made to a different target on each trial. A schematic of the visual display is indicated by the black circles within the boxes representing the screen on which the display was presented. The cross in the center indicates the fixation point and the gray circle indicates the target. The spike density functions from the average of 35 trials in each condition are superimposed. The solid line is from same target trials; the dashed line is from different target trials.

was low (Figure 2). Consistent with the change in saccade readiness, the reaction time of the saccades was shorter in the high readiness condition than in the low readiness condition. Thus, the experimental situation produced a change in a cognitive process that resulted in a more or less efficient behavioral response, which was associated with a change in the activity of single neurons.

An interesting observation in the experiment described above was that the motor set developed over time. For example, comparing the saccade reaction time revealed that the latency of the last few saccades was shorter than the latency of the first few saccades. Correspondingly, the neuronal activity was greater in the last few trials than in the first few. Depending on the probability of *where* the target of a saccade would be, monkeys learned to change their motor set to maximize performance.

Similarly, monkeys can learn to change their motor set depending on *when* a response is likely to occur. Experiments conducted in the dorsomedial frontal cortex (DMFC) have manipulated the timing of appropriate motor responses. DMFC contains neurons with activity related to eye movements and the visual stimuli that evoke them; it is anatomically connected with other eye movement-related cortical areas, and it has direct projections to the SC. Heinen and Liu (1997) recorded from neurons in DMFC while monkeys moved their eyes slowly to track a small spot of light that moved at a constant speed away from the fovea. The same neurons were recorded from in two different conditions. In one, the time between turning on the spot and moving the spot was constant and therefore predictable. In the other, the time until the target began moving was varied

and therefore unpredictable. Neurons in DMFC had a much higher rate of discharge when the timing of spot movement was predictable. The higher activity of these neurons indicated that the monkeys learned that the target motion would occur at a particular time after onset, allowing them to prepare their response in advance.

#### **Future Inquiries and Conclusions**

In its original formalization, the concept of readiness is an internal state influencing the expression of behavior. Motor set as formalized by Evarts and colleagues (1984) included the idea of readiness but also the notions of target expectancy and movement preparation (see also Wise, 1985). Indeed, in the experiments described here, the separation of a readiness signal from one reflecting the expectation of a target or preparation of a particular motor action has not been done. For example, in the behavioral experiments in which monkeys are trained to make a saccade to the same location repeatedly, we do not yet know whether the shorter latency saccade results from advanced preparation or from the expectation that a target will appear at that location. If we simply flashed a target repeatedly at the same location, never asking the monkey to make a saccade, would we then in subsequent testing immediately observe shorter latency saccades? Additionally, in the scanning experiments, would preparation of a particular saccade also facilitate a pointing response of the arm to the target? In other words, is the facilitation motor system-specific or is it a general readiness signal?

The physiological experiments described raise similar questions. For example, the experiments in DMFC demonstrate a signal correlating with the facilitation of smooth eye tracking. Would this same signal be evident during predictive saccades? Because smooth pursuit and saccadic eye movements are generally considered separate control systems (Robinson, 1968), signals such as these may be overseers of multiple motor modalities and serve to provide a common, facilitating influence on motor actions. Moreover, do the results obtained in the SC reflect the expectation of a particular target or the preparation of a particular saccade? Other recent experiments in SC demonstrate that certain neuronal elements are active before eye movements other than saccades (Krauzlis et al., 1997) and before other motor actions such as combined movements of the head and eyes (Freedman and Sparks, 1997). It is thus tempting to speculate that this activity of SC neurons reflects a more general signal of readiness or perhaps even target expectation.

Combining behavioral, cognitive, and physiological investigations in the saccadic system provides important clues into how cognitive processes are represented in the brain and how they influence motor behavior. These types of experiments reveal that neural representations of even simple movements are extremely flexible and are strongly influenced by the cognitive processing demands in behavioral tasks.

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