AMAZING PAPERS IN NEUROSCIENCE
Introducing Students to Subcortical Sensory, Motor, and Cognitive Processes Associated with Saccades using a Series of Papers by Goldberg and Wurtz

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The ability to acquire, observe, and analyze neuronal activity in conjunction with behavior in awake, behaving organisms was a great leap forward for the field of neuroscience in the 20th century. While some of the early experiments are relayed in introductory textbooks, rarely are undergraduate students introduced to tractable primary literature that illustrates the genesis of modern techniques, includes raw data that are immediately interpretable based on their basic knowledge of cellular neuroscience and their own experience, and reinforces and/or question basic concepts in neuroscience. This classic paper review introduces four papers published in 1972 by Robert Wurtz and Michael Goldberg focusing on eye movement behavior and superior colliculus physiology that fit these criteria. Taken together these papers introduce students to fundamental concepts (e.g., receptive and movement fields) in the field of behavioral neuroscience by introducing students to visual, motor, and attentional processing using single unit neuronal recordings and lesion studies. I have attempted to provide the basic introductory information for faculty who wish to use these papers for in-class discussions in their introductory or upper level neuroscience courses.

Key words: eye movement, saccade, physiology, single unit, lesion, inactivation, microstimulation, superior colliculus

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Natural (e.g., a pristine forest) and artificial (e.g., a college dining hall) environments are dynamic and filled with information that could be used by an organism to guide behaviors necessary for survival. The extraction of relevant information from the environment is facilitated by an organism's ability to align specialized sensory apparatus with select objects of interest. For example, in order to extract visual information, primates can search their surroundings using rapid eye movements (saccades) meant to align the high-resolution portion of the retina (the fovea) with a relevant object (e.g., a potential food source) for further inspection. If an object of interest is moving at the time at which it is foveated, then a smooth pursuit eye movement (SPEM) can be used to maintain the fovea's alignment with the object until another saccade is initiated. The coordination of saccades and SPEMs provides an opportunity for the efficient search of visual scenes that contain static and moving objects thus facilitating a range of behaviors (both overt and covert) crucial to survival.

Over the course of the last half century, single unit recording, microstimulation, and inactivation experiments using both saccades and SPEMs as a behavioral readout in primates have implicated several brain structures in target selection, decision making, attentional and reward processing, and/or the production of gaze (line of sight) movement commands (for a comprehensive review see Liversedge et al., 2011 or Leigh and Zee, 2015). However, most introductory neuroscience textbooks fail to discuss the behavioral characteristics of eye movements and/or their neural substrate (for an exception see Purves et al., 2012).

The current review is meant to fill this gap by providing background material for faculty who wish to engage undergraduate students in discussions concerning the neural substrates of sensorimotor and cognitive processing using eye movements as a behavioral indicator. This brief review will cover: 1) the basic metrics of primate saccades; 2) superior colliculus anatomy; 3) a summary and critique of four classic papers by Michael Goldberg and Robert Wurtz from the early 1970s (Goldberg and Wurtz, 1972a, 1972b; Wurtz and Goldberg, 1972a, 1972b) that discuss the role of the monkey superior colliculus in visual processing, saccade production, and attentional processing; and 3) a (perhaps ridiculously) brief discussion of the contributions oculomotor physiologists have made to our basic understanding of the superior colliculus processing since the 1970's. It is my hope that the references in the latter section will afford instructors the opportunity to customize and extend their discussion of the theoretical and methodological concepts in the classic papers reviewed here throughout an introductory neuroscience or advanced behavioral neuroscience course.

Assumed Prior Knowledge, Classroom Environment, and Learning Objectives
Prior to reading the aforementioned series of classic papers a student should have knowledge of the cellular mechanism underlying action potential generation in mammalian neurons as well as how electrical potentials are recorded. This will allow students to interpret the raw oscilloscope data that are presented in Goldberg and Wurtz (1972a, b) and Wurtz and Goldberg (1972a) and be able to understand how these data could be quantitatively assessed. Furthermore, students should have had a basic introduction to mammalian brain structures to the point where they would be able to identify the location of the superior colliculus (SC) if provided a picture or cast of a

primate brain. Pertinent SC and oculomotor plant (e.g., eye, extraocular muscles, and connective tissues) anatomy can be introduced during the discussion of the first classic paper and are detailed in subsequent sections of this review for the instructor.

In the author's view, the introduction of primary literature to the classroom is meant to: 1) get students used to the language and format of scientific reports in a given field of inquiry; 2) prompt students to identify what concepts they know and what concepts are foreign. Students should be encouraged to come to class with a list of novel vocabulary words and concepts they needed to look up during their first (or subsequent) reading of the paper so that they are both prepared for discussions and/or identify to the faculty member where there are still misconceptions; 3) illustrate to students the different forms of scientific inquiry (e.g., exploratory versus hypothesis driven); 4) promote students' understanding of qualitative, quantitative, and illustrative techniques that are used in a field of inquiry to form an argument for or against a hypothesis. With this in mind, the learning objectives for this group of classic papers are:

1) Introduce students to the behavioral techniques used to elicit and record visually guided saccadic eye movements in awake, behaving primates.
2) Introduce students to the qualitative and quantitative assessment of saccadic eye movements and neuronal recordings.
3) Introduce students to the potential role(s) the superior colliculus plays in processing visual, motoric, and cognitive signals.
4) Provide an opportunity for students to identify the novel findings and technical limitations of the classic papers as well as how these apply to the modern practice of neuroscience.
5) Provide a platform for further explorations of sensory, motor, and cognitive neuroscience in other animal species.

In the classroom discussion, the instructor should primarily act as a guide rather than a "sage on the stage." S/he should come prepared with a subset of PowerPoint/Prezi slides with figures from the paper(s) for discussion and/or clarifying figures (e.g., anatomical slides), but should not simply talk at the students. It should be the students who walk both the instructor and their peers through the original background, procedure, results, and discussion. In addition, the students should drive the conversation by asking clarification questions to their peers and then their instructor only as a last resort. Students need to learn to engage in a conversation about where science has been and where science could go in the future (i.e., generate new hypotheses). Primary literature discussions are a great way to start this journey.

Saccade Behavior: What are the properties of saccades that make them such a lucrative behavior to study?

There are several characteristics concerning saccadic eye movements that have made them useful as a window into sensory, motor, and cognitive processes. First, movements of each eye are achieved by the coordination of only six extraocular muscles (lateral, medial, superior, and inferior recti, and the superior and inferior obliques) thus restricting the range of movements ("degrees of freedom") relative to those of the vertebrate arm or leg. Furthermore, the extraocular muscles are controlled by three cranial nerves (CN III – Oculomotor; CN IV – Trochlear; CN VI – Abducens) with discrete innervations making the monitoring of nervous system output relatively simple (e.g., Robinson, 1970; Fuchs and Luschei, 1970, 1971). Students interested in pursuing a career in the health professions will appreciate the insight into brainstem function that eye movements afford during a bedside neurological examination (see Leigh and Zee, 2015 for a comprehensive review).

Second, a number of methods have been developed to quantify the metrics and/or kinematics (the evolution of a movement across time) of primate eye movements (Wade and Tatler, 2005). The electrooculogram (EOG) is an inexpensive, non-invasive method that can be used to measure both horizontal and vertical eye movements (Ford et al., 1959) and be implemented in an undergraduate laboratory using BIOPAC (Goleta, CA, USA), iWorx (Dover, NH) or other commercially available hardware platform (e.g., AD Instruments, Colorado Springs, CO). It is also the method that Goldberg and Wurtz used to monitor monkey eye movements in the classic studies described below (Goldberg and Wurtz, 1972a, b; Wurtz and Goldberg, 1972a, b). In brief, the EOG monitors the electrical (potential) difference between surface electrodes placed on the skin near the orbit of the eye of a subject. While this method is beneficial in a clinical context (Leigh and Zee, 2015), it is prone to artifact intrusion (e.g., electrical activity generated by the muscles of the eyelids) and is less accurate and precise than the scleral search coil (Robinson, 1963; Fuchs and Robinson, 1966) and video based eye-tracking methods more commonly used in modern research settings (Kimmel et al., 2012).

Third, saccade metrics are highly stereotyped. Figure 1 illustrates this stereotypy by plotting the peak velocity-amplitude (B) and duration-amplitude (C) relationships for horizontal saccades produced by a human subject during a step saccade task; one of the tasks that Goldberg and Wurtz used in their seminal studies of the superior colliculus (Wurtz and Goldberg, 1972a). In a step saccade task (Figure 1A) subjects are required to acquire an initial fixation target (T0) and maintain fixation of this target for a variable length of time. After this variable length of time has expired T0 is extinguished and a new peripheral target appears (T1). The subject is then required to produce a saccade towards and fixate T1 in order to successfully complete the trial. Typically, human subjects are not informed of their performance on the step task, but monkeys are rewarded after a correct trial with a drop of juice or water (e.g., Goldberg and Wurtz, 1972a). As can be seen in Figure 2B-C, the peak velocity-amplitude relationship is a saturating exponential function and duration-amplitude relationship is linear. These qualitative relationships are typical for both humans and monkeys under these circumstances (Fuchs, 1967; Bahill et al.,

1975; Baloh et al., 1975). Modifications to the peak velocity and duration relationship can be elicited by alterations to the nervous system (e.g., transient lesion of the superior colliculus, Lee et al., 1988) or task parameters (e.g., reward value, Reppert et al., 2015).

Saccade latency (or reaction time) and accuracy are also commonly cataloged metrics in psychophysics and physiology studies. The mean saccade latency for the subject in Figure 1 was 246 ± 33 ms, which is similar to those reported in the literature for human subjects performing a step task (e.g., Fuchs, 1967; Carpenter and Williams, 1995). Differences in latency can be elicited by modifying task conditions (for a review see Gilchrist, 2011). For example, saccade latency can be reduced by introducing a "gap" period between T0 offset and T1 onset in which no visual stimulus is present (Saslow, 1967; Fischer and Boch, 1983).
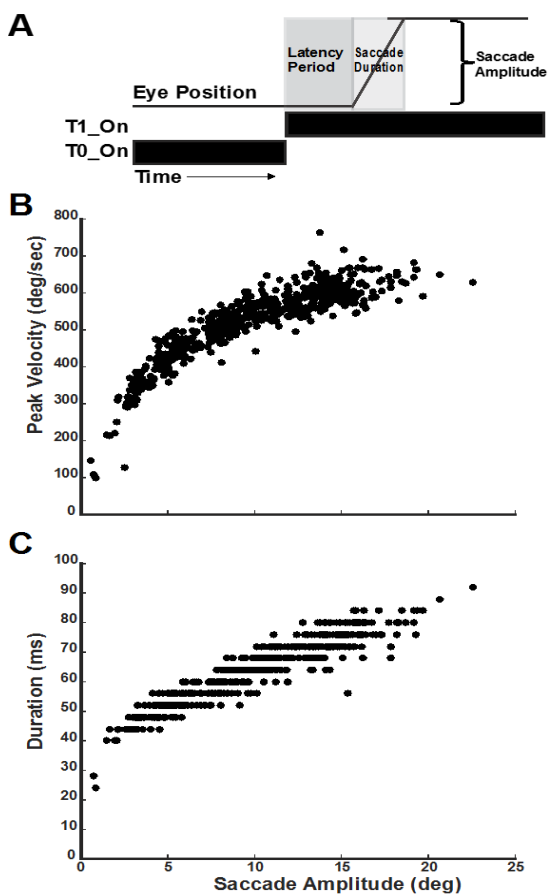
Figure 1. Step Saccade Task and Saccade Metrics. During the step saccade task (A), subjects are initially required to fixate a target (T0) for a variable duration within a computer-defined window. If the subject maintains fixation until the end of the "fixation period", T0 is extinguished and a peripheral target (T1) is presented. The offset of T0 cues the subject to produce a saccade to T1. Saccade peak velocities (B) and durations (C) for saccades with varying amplitudes are plotted for one human subject who performed the step saccade task. Saccades were measured using a video based eye tracking method (EyeLink 1000, SR-Research, Kingston, Ontario). See text for further details.

In contrast, saccade reaction time can increase during more complicated tasks such as the acquisition of a singleton (object of interest) in a visual search task (e.g., Rangelov et al., 2013) or in response to modifications to the nervous system (e.g., lesion to the superior colliculus; Wurtz and Goldberg, 1972b; Hikosaka and Wurtz, 1985). Finally, saccades are accurate to within 5–10% of target displacement (Becker and Fuchs, 1969; Henson 1978, 1979; Prablanc et al., 1978; Kowler and Blaser, 1995) and precise: the standard deviation of saccade endpoints is ~3–6% of target eccentricity (Kowler and Blaser, 1995). Inaccuracy of saccadic eye movements is a sign of impairment to either the oculomotor plant (eye muscles and/or connective tissue) or the neural substrate underlying the saccade production (Leigh and Zee, 2015).

Superior Colliculus Anatomy: A potential hub of sensory, motor, and cognitive processing.

The mammalian superior colliculus [optic tectum in other vertebrate species such as amphibians (Carew, 2000)] is a midbrain structure that receives visual signals either directly from the retina or by way of the visual cortex. Furthermore, a subset of the superior colliculus' efferent projections make contact with the pontomedullary reticular formation which has been shown to be involved in the generation of saccades and SPEMs (Sparks and Hartwich-Young, 1989; Jagadisan and Gandhi, 2014; Krauzlis, 2004). Based on both anatomical and functional characteristics, the superior colliculus (SC) can be divided into the superficial (SCs) visual and deep (SCd) visuomotor layers (Sparks and Hartwich-Young, 1989; Jagadisan and Gandhi, 2014). Across layers, the SC is arranged in a retinotopic map such that neurons with foveal visual receptive fields and/or small amplitude movement fields are represented rostrally and eccentric regions of the visual field and larger saccades are represented caudally (see Figure 2 in Sparks and Hartwich-Young, 1989; functional definitions of receptive and movement fields occur below). Lastly, the SC receives either direct or indirect anatomical input from, and/or projects to, regions of the basal ganglia, cerebellum, and cortex which have implicated the SC in decision making, attention, and the adaptive control of saccadic eye movements (Sparks and Hartwich-Young, 1989; Hopp and Fuchs, 2004; Prsa and Thier, 2011; Jagadisan and Gandhi, 2014; Hikosaka et al., 2014). While it is now accepted that the primate SC plays a role in visual, motor, and cognitive processing, the details of its contribution to these processes were not well established when Michael Goldberg and Robert Wurtz set out on their landmark studies in the early 1970s.

Superior Colliculus Physiology: Visual Processing

A neuron's receptive field, the area of space over which it gathers information, is a foundational concept introduced to students in introductory neuroscience courses and expounded upon throughout their education. The examples used to introduce this concept in textbooks varies, but there is a tendency to use the electrophysiological data David Hubel and Torsten Wiesel collected from anesthetized cats and monkeys (Hubel and

Wiesel, 1962, 1968; see Hubel and Wiesel, 2005 for review and Harrington et al., 2015 for commentary) to generate the aforementioned functional definition. In their Nobel Prize winning classic experiments, Hubel and Wiesel presented visual targets on a tangent screen placed in front of their subjects while simultaneously recording action potentials from neurons in visual cortices. In these studies, individual neurons ("single units") responded to light presented at discrete locations on the screen which correlated with particular locations on a subject's retina. Hubel and Wiesel also noted that the characteristics (shape, size, motion direction) of the visual stimulus influenced the rate of action potential production in the neurons they recorded from. Although a great deal was gained by performing these experiments and they are still relevant today, it was not clear at the time that the response properties of neurons observed in the anesthetized feline or primate would be present in awake, behaving subjects of the same species. Building upon these experiments, Wurtz (1969) used roughly the same techniques (single unit neural recording; visual target presentation) to classify the receptive fields of visual cortex neurons in awake rhesus monkeys trained in a fixation task. In brief, Wurtz concluded that the types and organization of receptive fields of striate cortex neurons in the awake monkey were similar to those in paralyzed, anesthetized cats and monkeys. After confirming the observations made by Hubel and Wiesel, Wurtz's laboratory turned its gaze toward studying the interface between the visual and oculomotor systems in the superior colliculus (SC).

Four papers published in a single issue of the *Journal of Neurophysiology* in 1972 by Goldberg and Wurtz laid the foundation for decades of work on the monkey SC's role in the translation of sensory information to motor output. Using the methodology established by Wurtz (1969), the first article in this series investigated the receptive field properties of single units in the superficial layers of the SC (Goldberg and Wurtz, 1972a). Figure 2 shows the response of a single unit to the presentation of a static (1°x1°) spot of light at various locations on a tangent screen relative to a fixation point. From these neuronal data (and other data not shown) the authors created a drawing of the approximate shape of the neuron's receptive field (top of figure 2) which mirrors the type of qualitative analysis used by Hubel and Wiesel (1962, 1968). From a pedagogical perspective, this very simple figure can be used to introduce the concept of a receptive field as well as introduce a very common form of qualitative neural data analysis, the raster plot. In a raster plot, each dot represents the time at which an action potential occurred relative to an external event (in this case, the onset of the static target). Each line within the plot represents a single "trial" or chunk of time relative to an external stimulus. From this raster plot, one can quickly see under what conditions a particular neuron produced a strong volley of action potentials (e.g., Figure 2D-F) or barely any response (e.g., Figure 2A, G). Raster plots have been used to portray neural responses in data collection software and in thousands of figures in published scientific manuscripts over the last half century. Being able to read these plots will allow students to compare receptive field properties and topographical organization of the SC with what was known about those of the visual cortex at the time (Hubel and Wiesel, 1962; 1968; Wurtz, 1969), interpret two other articles in this series (Goldberg and Wurtz, 1972b; Wurtz and Goldberg, 1972a), and explore a multitude of classic and recently published primary literature in sensory, motor, and cognitive neuroscience.

Superior Colliculus: Motor Control
While technological breakthroughs afforded physiologists of the 1950/60's the opportunity to isolate potentials from single units in animals, little progress regarding how the brain controlled motoric outputs could be gained because few laboratories had developed methods to record in awake behaving subjects under controlled conditions (Cecala, 2012). Those who had attempted such experiments in non-human primates had emphasized manual movements that required activity in several arm muscles to control wrist movements and, potentially, the stabilization of several joints (e.g., Evarts, 1966; 1968). In contrast, the movement of the relatively low mass eyeball by three pairs of muscles presented a markedly easier motor output to use in order to address fundamental principles of motor control. It is useful to point out to students that this is a pragmatic, reductionist approach to designing an experiment and research program. Students often want to answer big questions, and it is useful to illustrate why certain animal models, behaviors, and techniques are chosen early on in a research program before attempting to address complex questions.

The "step saccade" task (Figure 1A) monkeys in Wurtz and Goldberg (1972a) were trained to perform is the basis of almost every saccade task used in modern oculomotor laboratories. In brief, each trial began with the monkey fixating a visual target (the same 1°x1° target described previously). At some point after fixation, this target disappeared and another target was presented to the subject at another location on the tangent screen. This target displacement typically resulted in the subject producing a saccade. As noted above, eye movements were recorded using an EOG.

The astute reader of Wurtz and Goldberg (1972a) will notice there are few details in the methods section regarding the behavioral control of the eye movements and this can be a good teaching moment. For instance, how did the authors calibrate the EOG signal so that they knew the length of the saccade produced by the subject? did they know the subject was fixating a target at a particular location? How long did the subjects need to fixate each target? Was this fixation duration variable or constant? What was the reward criterion? I point out the absence of this information not to belittle the contribution made by the classic manuscript, but rather to note that these details are both necessary if one were to go about repeating this study and commonplace in modern reports so that the data can be interpreted properly. Students need to learn what to look for when critiquing an article in a given field and that

no matter how impactful an article may be, there is always more to be said!
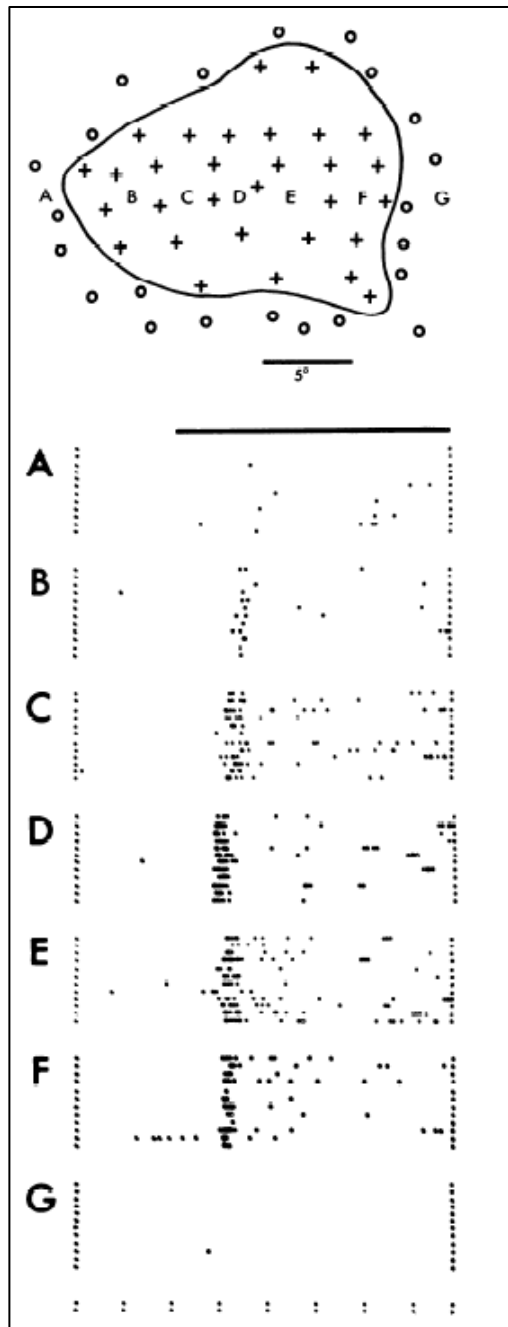
Figure 2. Example visual receptive field of a superior colliculus neuron. Top of figure: Schematic representing the shape of a receptive field (o = no response; + = response). The edge of the "on area" is represented by the solid line. Bottom of figure: Letters A-G show raster plots corresponding to stimulation at the locations shown in the receptive field schematic. Each line represents an individual trial. Each dot in the raster plot represents the occurrence of a single action potential. Solid line at the top of the first series of rasters (A) represents the illumination of 1° x 1° spot of light at one of the aforementioned locations. See original publication (Goldberg and Wurtz, 1972a) for further details. Reproduced with permission from Goldberg and Wurtz (1972a). © 1972 American Physiological Society.

Figure 3 illustrates another fundamental concept in behavioral neuroscience: the movement field. The movement field of a neuron is the motor equivalent of a receptive field. In this case, it is a graphical representation of the activity of a neuron around the time of a series of saccades with different vectors (amplitude and direction). As can be seen on the left hand side of this figure, there is at least a modest amount of activity for saccades with a variety of vectors. On the right hand side of the figure we see that the vigor with which the neuron responds varies as a function of saccade length. Furthermore, if one were to look at other published descriptions of SC movement fields they would see that saccade direction also impacts the firing of these cells and that the activity slightly precedes the onset and offset of the saccade (Gandhi and Katnani, 2011). This movement field activity is considered to be the representation of a motor command to move the eyes a particular amplitude and direction in the orbits of the eyes of a head-restrained subject. The remainder of the paper provides several other examples of movement fields as well as a few examples of cells in the deeper layers of the SC that have both visual receptive and movement fields ("visuomotor cells").
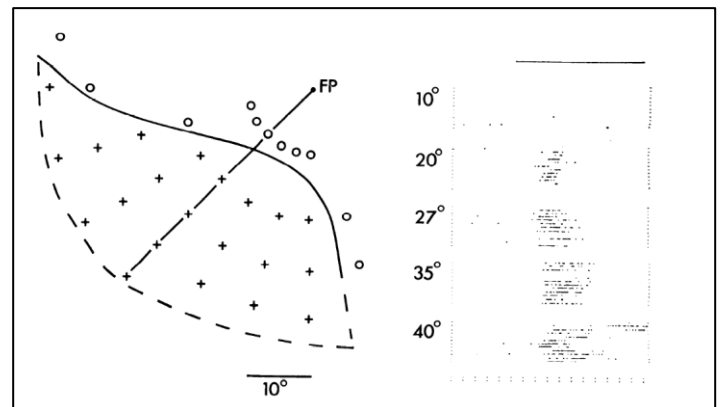
Figure 3. Example movement field of a superior colliculus neuron. Left half of figure: Schematic representing the shape of the movement field of a single collicular neuron (o = no response; + = response). Right half of figure: Raster plots representing the response of the neuron when the subject produced saccades ranging from 10-40° in length. The horizontal line at the top of the right panel represents the illumination of the saccade target. See original publication (Wurtz and Goldberg, 1972a) for further details. Reproduced with permission from Wurtz and Goldberg (1972a). © 1972 American Physiological Society.

The single unit motor physiology study is complemented in this series of articles by a report of the effect of large, electrolytic lesions to the SC on saccades (Wurtz and Goldberg, 1972b). Interestingly, the most robust effect of these permanent lesions was that the latency of saccades contralateral to the lesion was increased for up to 40 days post-lesion. The authors concluded that the monkey superior colliculus is not required for the accurate visual guidance of eye movements. While later studies using small, transient chemical lesions [muscimol (e.g., Hikosaka and Wurtz, 1985) or lidocaine (e.g., Hikosaka and Wurtz,

1986)] have confirmed these initial observations, lesions also seem to have effects on other metrics such as peak velocity. From a pedagogical standpoint, it is worth prompting students to discuss the pros, cons, and interpretive limitations of particular lesion techniques (electrolytic versus chemical) given their common use in modern studies of sensory, motor, and cognitive functions. Lastly, while Wurtz and Goldberg (1972b) was placed last in this series of classic papers, I would suggest that Wurtz and Goldberg (1972b) article be read third in the series before their single unit study on attentional processing (Goldberg and Wurtz, 1972b) because it will prompt to students to ask a question: If the SC is not necessary for the production of saccades, then what is it useful for?

Superior Colliculus Physiology: Attentional Processing

Philosophers have been debating the definition of attention since well before William James discussed the phenomenon in his classic treatise, *The Principles of Psychology*, and it is clear that the modern debate of this term is far from reaching a standard definition (see Wu, 2014 for a recent review of philosophical, psychological, and neuroscientific definitions). At the time that Goldberg and Wurtz (1972b) were engaged in their research, it was generally believed that the neural signature of attention would be manifested as an enhancement of relevant information in the form of an increased neuronal action potential rate. Furthermore, in the subfield of visual attention, a debate was emerging about whether the neural correlates of attention could be dissociated from those related to target detection and motor control (Posner, 1980). It is with this theoretical complexity and overt skepticism that Goldberg and Wurtz set out to design a task where they could dissociate visual, saccadic, and attentional signals.

The task used by Goldberg and Wurtz (1972b), while acknowledged by the authors as an imperfect method for isolating attention (see their discussion on pp. 572-573), began with the monkey pressing a bar that resulted in the onset of a fixation spot. Two trial types were then presented to the animal. In the first, the monkey's primary goal was to release the bar when the initial fixation point's luminance was transiently reduced for 500 ms. According to the authors, "The monkey was sufficiently interested in the fixation point so that if another visual stimulus were flashed elsewhere on the screen during the time the fixation point was on, the monkey did not break fixation to examine the new stimulus" (p. 560). In this case, it was assumed by the authors that the peripheral visual cue was not a potential saccade target and that the monkey would not be attending the target. In the second trial type, the initial fixation target would be turned off and a peripheral target would be simultaneously illuminated; the step task in Figure 1A. In this case, it was assumed that the monkey needed to attend the peripheral target in order for it to make an appropriate saccade to align the fovea with this target. The authors did report an enhancement, relative to the "dimmer/bar release" task, in the visual receptive field response in about half of the cells they recorded when the

subject produced a saccade. This enhancement was specific to the location of the target (i.e., saccade activity only increased if the target was within the cell's receptive field) and the response did not habituate over the course of 30-40 trials. The authors concluded that, "…the enhancement of response to a stimulus results from some central input to the visual system which selects out those stimuli which the animal uses for behavior from those which it does not use" (p. 574) and suggested, "…that this enhancement of response in many neurons is the effect of the mechanism which on the psychological level is the phenomenon of attention" (p. 574). These were bold statements at an early stage in the history of modern neuroscience and given the qualitative nature of the paper's data analyses. Furthermore, a close read of the previous quotations by both students and faculty should note the use of the word "selects" is indicative of the idea of the SC being part of the mechanism that filters out unwanted stimuli, but also perhaps participating in a decision making mechanism that would allow the subject to produce a saccade to one (of perhaps many) targets. The experiment designed by Goldberg and Wurtz was not meant to dissociate the latter two concepts and only recently have physiologists been able to dissociate these possibilities (see Krauzlis et al., 2013 for review).

Information Processing in the Superior Colliculus: What have we learned since 1972?

A search for the keyword "saccade" in the Pubmed.gov database (indexed on 6/10/2016) shows that 11662 manuscripts have been published on this topic since 1972, 984 of which include a description of some aspect of SC function or anatomy. From a functional perspective, a number of neuronal subtypes have been classified in the SC based on their sensorimotor characteristics (see Figure 1 in McPeek and Keller, 2002 for examples) and numerous studies have shown that most neurons in the deeper layers of the SC (SCd) fall along a spectrum in which they exhibit some level of both visual and motor activity. While the bulk of this review has focused on visuomotor processing, several laboratories have shown that the SCd contains multisensory neurons that respond to visual, auditory, and/or somatosensory stimuli in addition to carrying motor signals (Jay and Sparks, 1987a, b; Groh and Sparks, 1996a, b). Furthermore, the activity of some of these cell types may be correlated with reward (Ikeda and Hikosaka, 2003), attention (Kustov and Robinson, 1996; Ignashchenkova et al., 2004), target selection (McPeek and Keller, 2002; Krauzlis et al., 2004), or decision making (Horwitz and Newsome, 2004) in primates. Chemical inactivation of the SC can result in effects on attention, target selection, and decision making that are dissociable from the generation of individual saccades (Krauzlis et al., 2013). Finally, the motoric activity of a number of the cell types in the rostral pole of the SCd has been shown to be crucial for the production and maintenance of microsaccades (see Hafed et al., 2015 for review) and smooth pursuit eye movements (see Krauzlis, 2004 for review) whereas more caudal regions of the SCd are involved in the production of coordinated eye-head gaze

shifts (Freedman et al., 1996; Freedman and Sparks, 1997; Walton et al., 2008) and may even contribute to the generation of reaching movements (Werner et al., 1997; Linzenbold and Himmelbach, 2012; Himmelbach et al, 2013; Philipp and Hoffmann, 2014). While a comprehensive review of all the functional characteristics of the mammalian SC is beyond the scope of this manuscript, it should be clear that the instructor has the opportunity to use the series of reports by Goldberg and Wurtz as a precursor to further discussions of sensory, motor, and/or cognitive processes in the mammalian brain.

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