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What the Future Holds for the Study of Saccades

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Here we review the state of the art using saccadic eye movements as windows to the function of the normal brain and of the abnormal brain plagued by disease or trauma. By combining sophisticated behavioral paradigms with rigorous mathematical analysis and the latest imaging techniques one can use saccades as biomarkers of the highest level decision making to the lowest level basic machinery that generates premotor saccade commands. As technology advances saccades will become even more useful as immediate monitors of the state of the brain in disease and trauma and as a way to evaluate therapies.

K e y w o r d s: saccades, eye movements, superior colliculus, frontal eye fields

1. Introduction

Saccades are a fundamental motor behavior vital for survival for any animal that sees. We are above all visual creatures and saccades are widely represented in every part of the brain [1]. Early in evolution saccades served the needs of lateral-eyed afoveate animals with panoramic vision so they could be ready to respond to what might be coming into view as they moved through the environment. As animals became frontal-eyed and foveate, and especially in primates, saccades have become a more complex motor behavior that both reflects and serves the needs of higher cognitive processes including memory, attention and neglect, reward, choice, prediction and learning and adaptation. We understand well the functions of saccades and know much of their physiological and anatomical underpinnings [2, 3]. Functional and anatomical imaging studies and measurements of the electrical activity of the brain have revealed the widespread but interconnected nature of the neural networks that participate in

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the generation of saccades [4–6]. Saccades are easy to elicit, easy to measure and easy to quantify. Technology has made it possible to record eye movements at the “bedside”, even in ill patients in intensive care units, and so learn both the immediate effects of disease and trauma as well as the early compensatory mechanisms and strategies that the brain invokes in its attempt to assure survival.

As we develop new treatments we need easy to obtain and easy to quantify biomarkers that provide objective means of assaying brain function. Saccades are ideal for this task, and provide the necessary correlations among the anatomical, physiological and biochemical changes that occur with disease and its response to treatment. Saccades are also amenable to the rigor of mathematical and computational approaches, which has made them a model paradigm, for example, to understand how the brain learns to optimize its motor performance in the face of disease and trauma as well as with natural development and aging [7–13]. Saccades can also be used to probe higher level cognitive contributions to adaptation, for example, using saccades as an index to adaptation of the vestibulo-ocular reflex. The vestibulo-ocular reflex can be adapted in paradigms when, during sustained head rotation, a subject simply imagines a target in a new location or just pays attention to a target in a new location without actually looking at it [14]!

2. A Physiological and Control Systems Approach

The two pillars upon which much recent research about saccades has been based emerged about four decades ago. First there was the physiological and control systems approach. A key advance was the ability to record eye movements simultaneously with activity from single neurons within the brainstem of alert behaving monkeys. This activity could be related to the kinematic and dynamic characteristics of eye movements around all three axes of rotation: horizontal, vertical and torsion. These physiological findings were interpreted using control systems models of the flow of information within the neural circuits that produce the premotor commands for saccades. It followed naturally that one could interpret disorders of eye movements using the mathematical models of the bioengineer. On a personal note, I reached my epiphany for a career in eye movement research when David A. Robinson give a lecture to my class of neurology residents in which he used a control systems approach to dissect the abnormalities in internuclear ophthalmoplegia (a supranuclear deficit of adduction of one eye due to a lesion in the medial longitudinal fasciculus (MLF) that contains the axons of abducens interneurons that project to the oculomotor neurons that innervate the medial rectus muscle) [15]. He was able to pinpoint the lesion using a control systems diagram in which the flow of information from the premotor neurons generating eye position and eye velocity commands to the eye muscles was interrupted by the lesion in the MLF. Conversely, quantification of abnormal eye movements in patients, who unfortunately become experiments of nature caused by