Progress in Neurobiology 77 (2005) 215–251

progress in Neurobiology

www.elsevier.com/locate/pneurobio

From brainstem to cortex: Computational models of saccade generation circuitry

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Received 1 October 2004; received in revised form 27 October 2005; accepted 1 November 2005

Abstract

The brain circuitry of saccadic eye movements, from brainstem to cortex, has been extensively studied during the last 30 years. The wealth of data gathered allowed the conception of numerous computational models. These models proposed descriptions of the putative mechanisms generating this data, and, in turn, made predictions and helped to plan new experiments.

In this article, we review the computational models of the five main brain regions involved in saccade generation: reticular formation saccadic burst generators, superior colliculus, cerebellum, basal ganglia and premotor cortical areas. We present the various topics these models are concerned with: location of the feedback loop, multimodal saccades, long-term adaptation, on the fly trajectory correction, strategy and metrics selection, short-term spatial memory, transformations between retinocentric and craniocentric reference frames, sequence learning, to name the principle ones.

Our objective is to provide a global view of the whole system. Indeed, narrowing too much the modelled areas while trying to explain too much data is a recurrent problem that should be avoided. Moreover, beyond the multiple research topics remaining to be solved locally, questions regarding the operation of the whole structure can now be addressed by building on the existing models.

Keywords: Saccade generation circuitry; Computational models; Brainstem; Superior colliculus; Cerebellum; Basal ganglia; Cortex

Contents

Abbreviations: aCG, anterior cingulate cortex; BG, basal ganglia; BN, superior colliculus burst neurons; BUN, superior colliculus build-up neurons; CBLM, cerebellum; CMAC, cerebellar model arithmetic computer; DLPFC, dorsolateral prefrontal cortex; EBN, reticular formation excitatory burst neurons; EP, entopeduncular nucleus; FEF, frontal eye fields; FOR, fastigial oculomotor area; GABA, γ-aminobutyric acid; GCZ, gateable cortical zone; GP, globus pallidus; GPe, external part of globus pallidus; GPi, internal part of globus pallidus; IBN, reticular formation inhibitory burst neurons; IFN, inhibitory feedback neurons; IO, inferior olive; IT, inferotemporal cortex; LIP, lateral intraparietal cortex; LLB, reticular formation long-lead burst neurons; MLB, reticular formation medium-lead burst neurons; MN, ocular motoneurons; NRTP, nucleus reticularis tegmenti pontis; OPN, reticular formation omnipause neurons; PFC, prefrontal cortex; PPC, posterior parietal cortex; pre-SEF, presupplementary eye fields; QV, quasi-visual neurons; RI, resettable integrator; SBG, reticular formation saccadic burst generators; SC, superior colliculus; SEF, supplementary eye fields; SNc, substantia nigra pars compacta; SNr, substantia nigra pars reticulata; SRT, saccade reaction time; STN, subthalamic nucleus; STT, spatio-temporal transform; TLLB, tectal long-lead burst neurons; TN, reticular formation tonic neurons; V4, extrastriate visual cortex area 4; VTA, ventral tegmental area; WTA, winner-takes-all mechanism

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0301-0082/$ – see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.pneurobio.2005.11.001

1. Introduction

There are three main different types of primate eye movements (slow, fast and vergence movements), that are controlled by partially separate brain structures (Henn, 1993). The slow movements include the vestibulo-ocular reflex, the slow-phase of the optokinetic reflex and the smooth pursuit. The fast movements are the fast-phase of the optokinetic reflex and the saccades. Saccades are used by species (like humans and primates) whose retinas have a central high-resolution region (the fovea) to explore visual scenes by redirecting gaze from one important visual stimulus requiring precise analysis to another. Their speed may reach 1000 $^\circ s^{-1}$ in some primate species.