Functional Organization of the Ocular Motor System

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Various stimuli, other than a moving target, have evoked slow eye movements improperly designated "pursuit." Attempts at explaining these eye movements have provoked convoluted hypotheses. This confusion can be alleviated by conceptualization of the ocular motor control system as a synergistic interaction of the dual-mode version sybsystem with the vergence subsystem which produces only three basic outputs: fast eye movements (FEM), slow eye movements (SEM), and vergence eye movements (VEM).

SLOW EYE movements are evoked by optically stabilized images, optokinetic, vestibular, and tonic-neck inputs, and occur during fixation (microdrifts). A specific type of slow eye movement, smooth pursuit or tracking, was assumed traditionally to require a moving target for generation (7,5). However, reports of "pursuit" movements in the absence of such stimuli are frequent. Westheimer and Conover (19) recorded occasional "pursuit-type" movements in subjects making refixations between two points. Deckert (2) described "pursuit" eye movements under closed lids while tracking an imaginary pendulum. Steinbach (16) described smooth tracking of a moving hand in darkness and postulated a proprioceptive input stimulus. Several investigators have utilized retinal after-images to generate "pursuit" movements (9,10,13,17). Heywood (8) reported a subject who could initiate and voluntarily control "pursuit" eye movements without a moving stimulus. Attempts at explaining these "pursuit" movements have produced hypotheses resulting from, we feel, the improper equating of all slow eye movements with those of true pursuit.

The numerous descriptions of eye movement outputs in response to differing stimuli and experimental conditions permit conceptualization of the version subsystem as consisting of two modes, both responding to a variety of inputs. The *fast* mode mediates all conjugate saccades, and the *slow* mode mediates all conjugate slow eye movements. *The slow mode includes, but is not limited to, the pursuit function.* This dual-mode version subsystem operates synergistically with the *vergence* subsystem to comprise the total ocular motor control system responsible for generating all horizontal eye movements. Fig. 1 represents a simplified schematic flow diagram illustrating the various cortical and brain stem inputs and the three basic eye movement outputs: fast eye movements (FEM) and slow eye movements (SEM) from the version subsystem, and vergence eye movements (VEM) from the vergence subsystem. The actual anatomical areas represented by the arrows between cortex and brain stem are uncertain. Volition and motion are shown as the inputs for the three varieties of voluntary SEM reported in the literature: voluntary motion between two points, voluntary tracking of an imaginary target, and proprioceptive tracking of the subject's moving hand. Target motion is also the input for normal pursuit of a moving target.

Actual eye movements can be distinguished both by their spatio-temporal characteristics and their different neuronal firing patterns within the ocular motor system (6,12). We therefore propose that all the specific types of movement so far identified can be listed under descriptive names commonly found in the literature (Table I) which specify the particular input responsible for generating the sole output for each of the three categories (FEM, SEM, and VEM). Question marks are used in cases where the data seem to us to be insufficient for unequivocal inclusion in specific categories. The placing of microdrifts under VEM, although they were originally attributed to noise in the *version* subsystem, was prompted by the finding of St. Cyr and Fender (15) that significant vergence corrections were accomplished by microdrifts. Discussion of *Gegenrücke* can be found in Jung and Kornhuber (11).

The schema in Fig. 1 and Table I are compatible with current concepts of the functional and anatomical organization of the ocular motor system but refer only to eye movements in the horizontal plane; insufficient information is available concerning vertical or torsional eye movements. The fast and slow modes of the version subsystem are separate and parallel in the cerebral hemispheres and converge at diencephalic and upper brain stem levels, where vestibular and tonic-neck influences operate. The pontine paramedian reticular formation (PPRF), at the segmental level of the abducens nuclei, is the final prenuclear anatomical substrate (pulse generator) for all horizontal versions, whether fast or

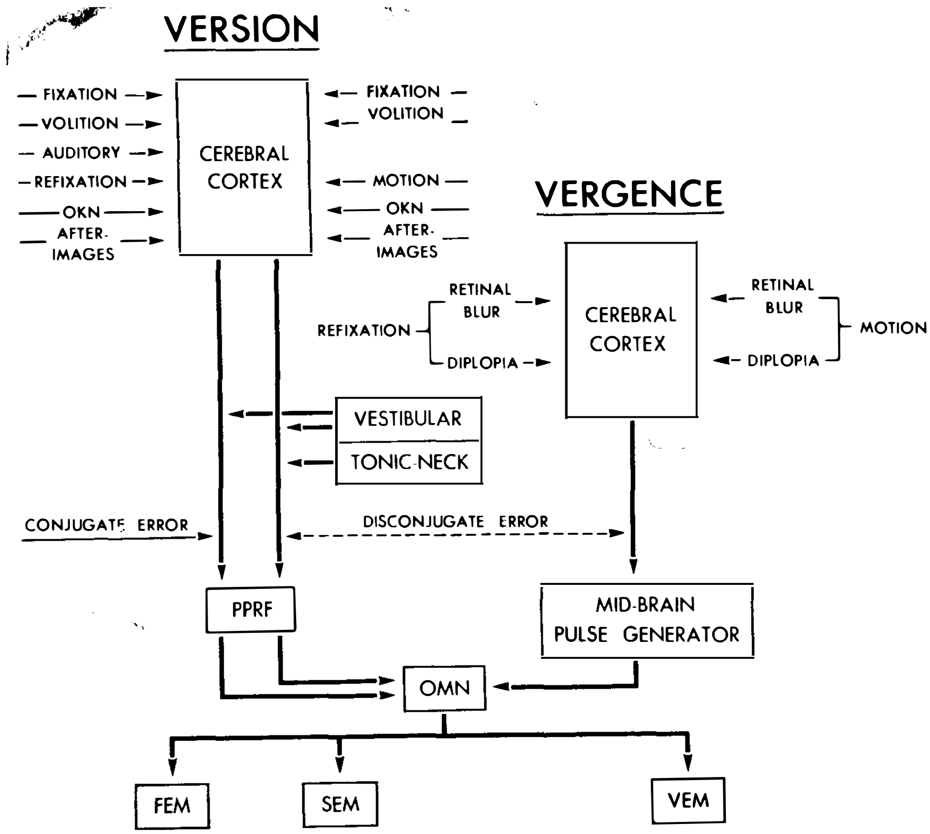

Fig. 1. The ocular motor control system composed of the dual-mode version and the vergence subsystems. The output of the pontine paramedian reticular formation (PPRF) sums with that of the vergence pulse generator at the ocular motor nuclei (OMN) to produce the three basic types of eye movement: fast (FEM), slow (SEM), and vergence (VEM). Refixation saccades which terminate inaccurately but conjugately are followed by saccadic corrective movements; those which terminate disconjugately are corrected by glissades (18). Corrective saccades are generated by either proprioceptive feedback or prenuclear efferent monitoring. Although the pathways for corrective glissades are uncertain, the inherent disconjugacy and shape of the movements suggest mediation by the vergence subsystem in response to internal monitoring of disconjugate efferent commands from the version subsystem. Since this question is presently unresolved, the possibility that they may be versional movements is provided for in the schema.

TABLE I. EYE MOVEMENT CLASSIFICATIONS.

Version		Vergence
FEM	SEM	VEM
Saccade: Refixation Reflex Voluntary	Pursuit (Tracking) Voluntary	Refixation Tracking (Pursuit)
Microsaccade (Flick)	Microdrift	Microdrift
Corrective Saccade	Corrective Glissade (?)	Corrective Glissade (?)
Saccadic Pursuit (Cogwheel)	Compensatory	
Fast Phase of Nystagmus (Jerk)	Slow Phase of Nystagmus	
Square Wave Jerk (Gegenrücke)	Pendular Nystagmus	
After-Image Induced	After-Image Induced	
REM	Slow Sleep Drifts	
	Imaginary Tracking	Imaginary Tracking
	Proprioceptive Tracking	Proprioceptive Tracking

slow (1). Convergence is integrated at a midbrain level (14).

The unitary nature of the substrate subserving the generation of all SEM is also suggested by studies of hereditary congenital nystagmus. Congenital nystagmus has been identified putatively as a high-gain instability in the "pursuit system" (3). More recent investigations (4), however, have established that voluntary *"fixation attempt"* is the adequate stimulus for the nystagmus oscillation. This means that the stimulus for one functional operation (fixation) may cause oscillation in the substrate classically regarded as serving an entirely different function (smooth pursuit) and raises questions of causality analogous to those engendered by the previously mentioned after-image experiments. Moreover, Yarbus has shown that a continuum exists between very slow pursuit and steady fixation movements (20), and the same spatio-temporal characteristics are shared by all SEM.

In summary, we are suggesting that the term, "pursuit eye movement," be restricted to slow movements evoked by efforts to maintain fixation on a visible moving target and that other SEM be so designated as to specify the responsible input (i.e., proprioceptive tracking, imaginary tracking, etc.).

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