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Physiology of Eye Movements

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- Abstract -

Eye movements serve vision by placing the image of an object on the fovea of each retina, and by preventing slippage of images on the retina. The brain employs two modes of ocular motor control, fast eye movements (saccades) and smooth eye movements. Saccades bring the fovea to a target, and smooth eye movements prevent retinal image slip. Smooth eye movements comprise smooth pursuit, the optokinetic reflex, the vestibulo-ocular reflex (VOR), vergence, and fixation. Saccades achieve rapid refixation of targets that fall on the extrafoveal retina by moving the eyes at peak velocities that can exceed 700°/s. Various brain lesions can affect saccadic latency, velocity, or accuracy. Smooth pursuit maintains fixation of a slowly moving target. The pursuit system responds to slippage of an image near the fovea in order to accelerate the eyes to a velocity that matches that of the target. When smooth eye movements velocity fails to match target velocity, catch-up saccades are used to compensate for limited smooth pursuit velocities. The VOR subserves vision by generating conjugate eye movements that are equal and opposite to head movements. If the VOR gain (the ratio of eye velocity to head velocity) is too high or too low, the target image is off the fovea, and head motion causes oscillopsia, an illusory to-and-fro movement of the environment.

Key Words : Physiology, Eye movement, Saccades, Smooth pursuit, Vestibulo-ocular reflex

(fovea) 가 가 (retinal slip)가 2-3,
, /s 1.
saccade
0.5.
(fovea) (smooth eye movement)
(smooth pursuit), (vestibulo-ocular
(, gaze reflex), (optokinetic reflex), (ver-
shift), (fixation) (Table 1).
(, gaze holding).

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Table 1. Ocular motor subsystem

<i>Fast eye movement : Gaze shift</i>
Saccades
Fast phase of physiologic or pathologic nystagmus
Saccadic intrusion / oscillation
<i>Smooth eye movement : Gaze stabilization</i>
Smooth pursuit
Vestibulo-ocular reflex
Optokinetic response
Vergence : convergence, divergence
Fixation

SACCADES

Saccade
, 가
(conjugate)
(volitional, voluntary) saccade
saccades가
(visually-guided)
(memory-guided) (reflexive)
saccade
가
(spontaneous)
saccade . antisaccade
가
(quick phase) saccadic
intrusion / oscillation saccade .

Saccades

Saccade (triggering signal)
error signal) . saccade
(posterior
parietal cortex)
saccade
(frontal eye field), (supplementary eye
field) (parietal eye fields) .
sac-
cade , saccades
(extraretinal
signal) saccades, (sequential) sac-
cades saccade (motor programming)
(prefrontal cortex),
,

saccade ³.
Saccade
(premotor area)
(caudate nucleus) (sub-
stantia nigra pars reticulata) (superior
colliculus) . saccade

saccades .
saccade ,
saccade .
saccade,
(disengagement), saccade ⁴.
Saccade pulse-step
(phasic-tonic) ^{5,6}.
Pulse (viscous force)
,
(velocity command).
pulse 가 , 가
() (, viscoelastic
force)
step .
saccade pulse
(paramedian pontine reticular formation,
PPRF) burst ^{7,13},
saccade burst
(rostral interstitial nucleus of medial longi-
tudinal fasciculus, riMLF) ⁸ (Table
2). Saccade가
, burst 가
가
Burst
saccade () 가
800 spikes/s ⁹. Burst
saccade
가 , burst
burst 가 saccade
Saccade 가
pause 가 ¹⁰. Pause burst
가 burst 가
Saccade가 burst 가
pause 가 ,
saccade (trigger signal)가
. Pause nucleus

Table 2. Anatomic substrate of saccadic generation

	Pulse		Step
	Burst	Pause	Neural integrator
Horizontal	PPRF	Nucleus raphe interpositus	Medial vestibular nucleus Nucleus prepositus hypoglossi Flocculus
Vertical	riMLF	Nucleus raphe interpositus	Interstitial nucleus of Cajal Medial vestibular nucleus Nucleus prepositus hypoglossi Flocculus

raphe interpositus . pause
saccadic intrusion / oscillation ,
saccade ¹¹ .
Step (central neural
network) (neural integrator)
pulse (step)
saccade
(nucleus prepositus hypoglossi)
(medial vestibular nucleus) ,
saccade Cajal
(interstitial nucleus of Cajal),
¹² .
(gaze-evoked nystag-
mus) .
saccade
(hypermetria)가 , saccade
가 . saccade가
(centripetal) 가
macrosaccadic oscillation .
pulse-step , saccade
가
(postsaccadic drift, glissade). (dysme-
tria) (dorsal vermis) 가
(fastigial nucleus) , postsaccadic drift
(flocculus) (paraflocculus)
(deep) ¹⁶ ,
(hypometria) saccade가
saccade가 ,
saccade가 (contrapulsion)¹³ .
Saccades 가
saccade 1. , 2. , 3.
, 4. 가 .

Table 3. Low peak saccadic velocity

Damage to burst or pause neuron	(ocular excursion) : 50 가 45 (, 43 ; , 47), ¹⁵ . 가 (, 가 . Saccade , saccade 가 , 가 , 가 (Table 3). Saccade 700°/s saccade . Saccades (peak velocity) 가 saccade saccade가 200ms 가 가 , (processing time) 가 (Table 4). saccade 가 (, gap effect).
Internuclear ophthalmoplegia	
Ocular motor nerve palsies	
Ocular myopathies or neuromuscular junctional disorder	
MG	
dysthyroid myopathy	
CPEO	
Others	
Cerebral hemispheric lesion	
Drugs	
Mental fatigue	

Table 4. Prolonged saccadic latency

Congenital ocular motor apraxia
Ataxia telangiectasia
Hemispheric lesion
frontal lobe
posterior parietal lobe
dorsolateral prefrontal cortex
Superior colliculus lesion
Basal ganglia disorders
HD
parkinsonism

(rostral pole) (fixa-
tion cell) . (fixa-
tion cell) . saccade , saccade
가 . saccade가

(fixating cell) sac-
cade 가 . sac-
cade : 15.
saccade (.
) , 200ms . saccade가 . saccade
가 . saccade
(dorsal cerebellum, VI, VII)
가 . Saccade 가
. Saccades가 3
saccade가
sac-
cade . sac-
cade

Saccade
(Memory-guided Saccade)
(spatial working memory) 가
¹⁷ . saccade
(spatial memory) ,
가 .

Antisaccades
saccade ,
saccade , 가
(%) 가 (MST

(response suppression errors)². Antisaccade
saccade
saccade sac-
cade가 .

(Smooth Pursuit)
가 . (visual input)
가 .
slip,) . 가 (retinal
100-125 ms 가 ¹⁸ .
가 (pursuit initiation)
가 100-
300 ms 가
가
(pursuit maintenance) 가
efference copy (extraretinal
signal) .
(magnocellular layer)
, - - (MT/MST
)
(dorsolat-
eral pontine nucleus, DLPN)
(mossy fiber)
pulvinar
(fastigial
nucleus), (flocculus),
VI VII
가 (MST

가
VI, VII
Purkinje
가
가
가
catch-up saccade
(saccadic cogwheel pursuit)가
20-40, 0.25 - 0.5Hz
(asymmetry) 가
(trajectory)
100/s, 가
100/s, 가¹⁹
가²⁰
가
가
(unidirectional),
(retinotopic),
(craniotopic)
(omnidirectional) (Table 5)
paresis) : (Unidirectional pursuit paresis) :
가²¹, 1-2 가
(contralateral hemi-
anopia), (lateral geniculate body)
가

Table 5. Impairment of pursuit

<i>Directional</i>
Unidirectional
Bidirectional
<i>Retinotopic</i>
<i>Craniotopic</i>
<i>Omnidirectional</i>

Table 6. Unidirectional impairment of smooth pursuit

<i>Ipsilateral</i>
Parieto-temporo-occipital lobe (MT/MST)
Frontal eye field
Internal capsule
Midbrain tegmentum
Basis pontis
Cerebellar flocculus
<i>Contralateral</i>
Caudal pontine tegmentum
Lateral medullary syndrome
Fastigial nucleus

(nondominant hemisphere)
(angular gyrus) - (temporo-occipito-parietal junction)²¹
가 (middle temporal, MT)
가 (middle superior temporal, MST)
(motion perception)²³
MT/MST
가
²⁴
가
(pretectum)²⁵
가²⁶
(Retinotopic pursuit paresis) :
가
saccade²⁷
(Craniotopic pursuit paresis) :
(inattention)
가

Table 7. Omnidirectional impairment of smooth pursuit

		(Vestibulo-ocular reflex, VOR)
<i>Degenerative</i>		
AIDS		
AD		
PD		
PSP		
SCA		가
Schizophrenia		
<i>Drugs</i>		
Ethanol		
Barbiturates		
Benzodiazepines		
Carbamazepines		
Chloral hydrates		
Lithium		
Methadone		
Phenytoin		
<i>Others</i>		
Senescence		가 1Hz
Inattention		(visual system)
	가 100%/s	
		가
가		
suit paresis) :	(Omnidirectional pur- 가	가 ²⁸ 16ms , 350°/s
	(Table 7).	(rotation) (lin-
value)	가 (localizing	(semicircular canal) (otolithic
		organ)
		(angular VOR, aVOR)
(optokinetic nystagmus, OKN)		가
		(torsion)
(optokinetic system)		yaw, pitch, roll
		0.9
	(visual association	(roll)
area, Brodman's area18,19)		0.5
		(linear VOR, IVOR)
		가
	OKN	
		(tilt)
OKN 가		(translation)
	(functional)	(utricle)
		(sacculus)
		(Canal-Otolith interaction)
cade		. sac-
		(eccentric rotation), (off-verti-

cal axis rotation, OVAR)

Ewald's second law :

(ampulla) (resting activ-
ity) 70-100 Hz
500 Hz
0 Hz

(VOR pathway)
pathway) (indirect pathway) (direct
3 trisy-
naptic pathway (3 neuron arc)
MLF
, PPRF,
(polysynaptic path-
way)

29,30

(Canal-VOR pathway) :

(prime mover)
(Ewald's first law).
가

(Horizontal VOR) :

Deiter (ascending tract of Deiter)
31. Deiter

(interneuron)

가
가 Deiter

(Vertical VOR) :

(anterior semicircular canal)
(superior rectus) (infe-
rior oblique) (elevation)
(torsion) 32.
가
(medial vestibular nucleus)
(subnucleus) 가
(superior vestibular
nucleus) , brachium
conjunctivum

가
(superior
oblique) (inferior rectus)

(Otolithic-VOR pathway) :

(utricle nerve)
가 가

(VOR adaptation)

가

, saccade (quick phase)

가 , (oscillopsia), (visual blurring)

(Velocity Storage Mechanism)

1Hz

(time constant, TC) 15-20

cupula

3-5

(postrotational nystagmus)

cupula

(optokinetic afternystagmus, OKAN)

가

(velocity storage integrator)

(nodulus)

(uvula)

가

가

(tilt suppression),

(periodic alternating nystagmus)

가

(gain)

1

180

(phase difference) 0

lead),

(phase lag)

(phase

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