# On the nature of visual-oculomotor connections

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Recent results are reviewed describing the behavior of extraocular muscle motoneurons in the alert, behaving monkey during a variety of eye movements, namely, saccades, fixation, pursuit and vergence movements, and vestibular stabilizing movements. Combining this with recent results on the behavior of vestibular neurons, it is possible to present a fairly complete picture of the neuronal arrangement of the vestibulo-ocular reflex. It is proposed that this phylogenetically old motor apparatus used for stabilizing the visual axes is utilized by the visual system in stabilizing retinal image slip and making smooth pursuit and saccadic eye movements. Consideration is given to the types of neural networks needed to transform visual information into oculomotor commands.

Key words: oculomotor system, eye movements, motoneurons, extraocular muscles, vestibulo-ocular reflex, saccades, smooth pursuit movements

The following is a brief review, for visual neurophysiologists, of recent developments in oculomotor neurophysiology. It also tries to extrapolate a bit into the future by speculating on the nature of the neural transformations that are required between cortical and tectal visual inputs and the commands which are subsequently sent out along the final common path. These transformations will be considered for both pursuit and saccadic movements after first reviewing the vestibulo-ocular reflex, a basic brainstem system thought to underlie both of these visuomotor systems.

## The final common path

Fig. 1 shows the behavior of an abducens motoneuron in the alert, intact rhesus

monkey during saccades and fixation. During steady fixation, the discharge rate is very constant, varying by only six per cent (standard deviation) of the mean rate. This rate constancy and reproducibility upon subsequent refixations gives a remarkable machine-like quality to the motor nuclei. As the eye assumes positions from the off- to the on-direction (the direction of action of that motoneuron's muscle), the discharge rate of a motoneuron increases linearly from the angle $\theta_T$, at which it is first recruited into activity (threshold), until the maximum on-position is reached (about 40 degrees) at which time the unit's fixation rate is generally between 200 and 300 spikes per second. These high discharge rates and the great use of rate modulation in eye movements is a distinguishing feature of extraocular neuromuscular control.

Thresholds range from the extreme off-position to 25 degrees in the on-direction (0 degrees being the primary position), and their constancy for any one unit reflects an invariant rank order of recruit-
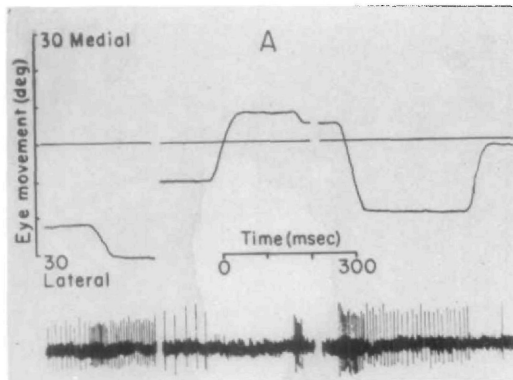
Fig. 1. The discharge rate behavior (*lower trace*) of an abducens motoneuron during saccades and fixation at different eye positions. Note steadiness of rate for steady fixation, increase in fixation discharge rate for increasing eye position laterally, and the intense burst of rate (or total inhibition) for lateral (or medial) saccades.

ment within the nucleus. The spectrum of thresholds is thought to reflect the spectrum of muscle fiber types found in extraocular muscles.[1] These results have been reported in detail in 1970 by a number of authors.[2-4]

Our laboratory[3] had extended this description by noting that discharge rate depends on eye velocity as well as position. Thus, discharge rate is a function of both position and velocity according to Equation 1, where R is discharge rate, $\theta$ is eye

$$R = k\,(\theta - \theta_T) + r\,\frac{d\theta}{dt} \qquad (1)$$

position, $\dfrac{d\theta}{dt}$ is eye velocity, and k and r are the slopes of the rate-position and rate-velocity relationships, respectively. This equation confirms former mechanical studies of the eyeball, muscles and suspensory tissues which indicate that the mechanical system is predominately viscoelastic.[5] Thus, the coefficients k and r are simply the central reflection of the orbital viscoelasticities. Their ratio r/k, the time constant of the equation, is, on the average, the time constant of the globe-muscle system which is about 160 msec. for the monkey.

A major effort has been to demonstrate that motoneurons fire according to Equa-

tion 1 regardless of the type of eye movement being executed. We have trained monkeys to make vergence movements[6] and rotated them, in darkness, to obtain vestibularly induced movements[7] and can show that Equation 1 does predict the behavior of motoneurons during all of these eye movement types. For example, the velocity term in Equation 1 would predict a high discharge rate during the high-velocity period of saccades which is clearly seen in Fig. 1. It appears that motoneurons obey Equation 1 for all types of eye movements, which is to suggest that the final common path is shared equally by all the eye movement subsystems.

It has also been possible to demonstrate unequivocally that there is no stretch reflex in the extraocular muscles of the rhesus monkey by rotating the animal's eye, by an opaque suction contact lens, and failing completely to detect any related change in the discharge rates of the motoneurons of that eye.[8] Thus, stretch afferents bypass the motoneurons and pass centrally, possibly to the cerebellar vermis.[9] When one adds the lack of a stretch reflex to the fact that each oculomotor subsystem is only capable of performing a single stereotyped movement pattern and deals with a single unchanging mechanical load, free from external disturbances, it's clear that the oculomotor system is considerably simpler than other neuromuscular systems.

### The vestibulo-ocular reflex

As soon as animals developed a rudimentary visual system, it became advantageous to prevent image movement on the retina to simplify the process of pattern recognition. A major source of image movement is head rotation. This reflex prevents this by changing the position of the eye in the head by an amount equal and opposite to the change in position of the head in space. To do this, the oculomotor system needs to know the change in head *position*. Unfortunately the semicircular canals are stimulated by head *acceleration*. Thus, from a dynamic stand-
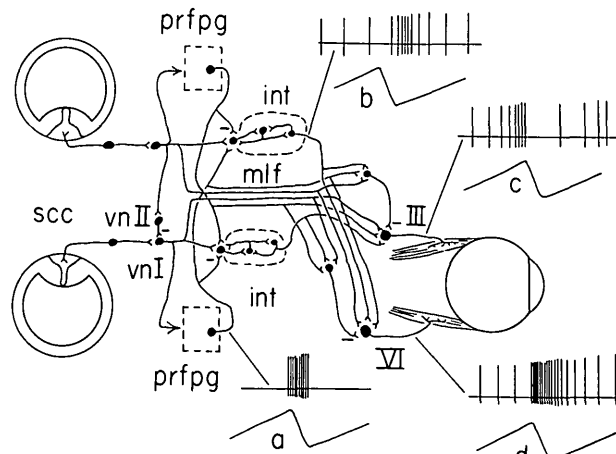
Fig. 2. The neural elements necessary and sufficient for the complete dynamic operation of the vestibulo-ocular reflex, both slow and fast components. *scc*, Semicircular canals; *vnI* and *II*, vestibular nuclei neurons, types I and II[16]; *mlf*, medial longitudinal fasciculus feeding velocity information directly to the motoneurons; *int*, a brainstem neural network which integrates velocity signals into position signals; *III,VI*, oculomotor and abducens nuclei; *prfpg*, pulse generator neural network in the pontine reticular formation[13]; *a*, unit activity of pulse generators; *b*, ouput of integrator circuits; *c*, *d*, activity seen in agonist and antagonist motoneurons shown in upper traces during slow and fast phases of nystagmus (*lower traces*).

point, the function of this reflex is to convert the acceleration signal back into a position signal by integrating it twice.

Fortunately, it has been known for some time that one integration occurs mechanically in the cupula of the semicircular canals,[10] because a constant angular force (head acceleration) produces a constant endolymph flow (cupula velocity) in the fine bore tubing of the canal. Thus, cupula deflection is proportional to head *velocity* (in the frequency range above 0.016 Hz.). This fact has been observed in the firing rates of vestibular primary afferents in the monkey[11] and of second-order units in the vestibular nuclei of the cat.[12]

Thus, one more integration is needed between the discharge rate modulation in the vestibular nuclei and the final eye movement, and one is forced to acknowledge a brainstem neural network (probably in the reticular formation[13]) to perform this integration (Fig. 2). Moreover, Equation 1 predicts that the eye will lag behind the motoneuron activity at high frequencies, e.g., by about 45 degrees at 1 Hz. for a sinusoidal stimulus. This has

been tested by rotating monkeys sinusoidally (without vision) and verifying that Equation 1 correctly predicts the phase shift between R and $\theta$.[7] Since no such phase shift occurs in the total reflex, the phase lag created by the extraocular muscles must be compensated by a phase lead in the central signal processing. This lead comes from the medial longitudinal fasciculus (MLF), a monosynaptic pathway from the vestibular nuclei to the motoneurons which passes a velocity signal directly to the final common path in parallel with the neural integrator. Such a pathway has the correct properties (velocity feed-forward) for supplying just the right amount of lead action to overcome the mechanical lag of the orbital contents. Most of the simple connections shown in Fig. 2 are well established.[14-16] The principal new element is the integrator. It should be stressed that the existence of this network is not in doubt, only its anatomic location and manner of working.

If the smooth vestibular stabilizing movements become too large, quick phases, indistinguishable from saccades,[17] are gen-
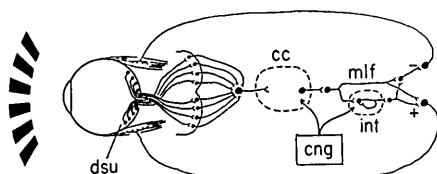
Fig. 3. The retinal image-stabilizing system of the rabbit adapted from a description by Collewijn.[19] *dsu,* Directionally selective ganglion cells sensing retinal image slip velocity; *cc,* central controller network whose function is to maintain a high gain at low frequencies for accuracy and a low gain at high frequencies for stability; *cng,* central noise generator which creates eye drift in the absence of vision; *int,* interior network which converts a central command to an eye velocity; *mlf,* medial longitudinal fasciculus.

erated. As pointed out above, saccades are created by a pulse step of motoneuron firing rate—a pulse of discharges to drive the eye at high velocities and a step to hold the eye in its new position. This process is thought to originate in a neural circuit which generates pulses lying in the paramedian pontine reticular formation.[13] Many units have been seen in the brainstem[18] whose bursts (Fig. 2, *a*) exactly coincide with the pulsatile part of the motoneuron activity (Fig. 2, *d*). The pulse must be distributed to the motoneurons to execute the saccade itself, but, equally important, it must reset the integrators so that they may generate a new slow phase from a new initial position (Fig. 2, *b*). This is equivalent to creating the step part of the pulse-step. The simplest way to do this is to simultaneously pass the pulse through the integrators. This resets the integrators and creates the needed step in firing rate automatically. Admittedly, this arrangement is speculative but is the least complex compared to alternate schemes of nervous organization to accomplish the given task. It is also compatible with the behavior of prenuclear single units observed in the brainstem (e.g., Fig. 2, *a* and *b*) in the vicinity of the oculomotor, abducens, and vestibular nuclei.[18] Fig. 2 thus represents the simplest working hypothesis to describe the entire dynamic processing of signals required for the vestibulo-ocular reflex.

## The smooth pursuit system

Although the vestibular system is a great aid in stabilizing retinal images, it is fundamentally limited because it does not have access to that which is to be stabilized—the retinal image motion itself. Consequently, even the most primitive visual systems have developed a feedback control method of stopping retinal image motion. An excellent model of this system in the rabbit has recently been published by Collewijn[19] (Fig. 3). As Collewijn has shown,[20] a rabbit's eye in the dark (when the loop is open) wanders about. These movements reflect random signals or imbalances generated in the central motor networks (central noise generator, Fig. 3). Consequently the function of the system is to stop the eye from being moved by these central disturbances.

There are three major parts to the system. The central controller establishes the open loop gain (G) of the system which should be large because the amount by which the eye drift is attenuated is 1/G. Collewijn[21] has shown that at low frequencies in the rabbit, G is 100 so that eye drift with vision is 100 times less than without. The directionally selective units sense the error signal, retinal slip velocity. Maximum slip velocity (with vision) is about 0.01 degree per second (36 degrees per hour). Since it had not been previously appreciated to what low velocities these units must respond, they were recently reinvestigated.[22] It was found that on and on-off directionally selective units had different ranges of best velocity transduction and could nicely explain the observed over-all behavior of this reflex including important nonlinearities.[19]

Finally, since the neural signal from the retina is a command to produce a certain eye velocity, the final step in the reflex must be an integration. There is no reason to suppose that this integrator is not the same as that used in the vestibulo-ocular reflex. Proof that the two systems share the final integrator may soon come from future single-unit studies.

The system just described should more

properly be called the image-stabilizing system because its primary function is to stop the eyes from moving, not to track moving targets. When a large part (over 50 per cent) of the rabbit's visual field moves (e.g., a striped drum; a thoroughly unnatural situation for the rabbit), its eyes will follow in optokinetic nystagmus. As a result, the past emphasis has been on the ability of the rabbit to *track* or make movements, hence the name opto-*kinetic* system which has obscured the fact that the primary purpose of the reflex is to hold the eyes still, not to make them move.

The appearance of foveal vision adds new complications to this scheme. In the afoveate eye, only movement of most of the visual field induces following. In the foveate eye, a small image on the fovea elicits tracking even though the background may be moving in a different direction. Has a different system been developed for foveal tracking or is the new system an extension of the old? The latter hypothesis is the simplest. One can imagine adding to Fig. 3 a dense foveal concentration of directionally selective units which far outnumber those in the periphery. Such a system would preferentially reduce retinal slip velocity in the fovea at the expense of peripheral slip. This behavior is compatible with human ocular tracking when central and peripheral stimuli are pitted against each other. However, it remains unsettled whether the human smooth pursuit system is, or is not, a refinement of the image stabilizing system of the rabbit.

## The saccadic system

The element which is important here is what might be called a spatial-temporal translator. Its output information is in the discharge rate of its neurons which is the temporal signal needed by the motoneurons to execute a saccade. As previously mentioned, the time course of discharge rate needed is a pulse-step. The timing of the pulse is critical because saccade size (which determines which visual object will be brought onto the fovea) is determined by saccade duration which, in turn, is deter-

mined entirely by the neural pulse duration.

The input to the spatial-temporal translator arrives from regions of the visual system such as the superior colliculus in which exists a retinotopic map. The appearance of a visual target in a certain direction and distance from the fovea will excite units in a certain anatomically localized region of the colliculus. Thus, activity in the colliculus may be said to be spatially coded. If one now stimulates (electrically) that region of the tectum, a saccade will be evoked which will carry the eye in just that direction and by just that distance needed to bring the image of the target onto the fovea.[23] This visual-orienting response, called foveation by Schiller,[24] is now well established from the sensory map of the colliculus described by Cynader and Berman[25] and the motor map of the colliculus described by Robinson.[23]

Of course the events leading to a saccade are much more complex than this. In a natural environment many new visual stimuli come and go and some form of target selection must precede the release of neural excitation from any region of the colliculus to the motor apparatus. Also, saccades are possible in the absence of the superior colliculi so that it represents only one of several paths to the motor apparatus. The essential feature here is that the information on saccade size and direction is contained not in the time course of any activity but only in the spatial location of the origin of the activity.

There is some evidence that the pulse generator circuits lie in the paramedian pontine reticular formation.[13] It must be remembered that in the generation of nystagmus quick phases the inputs to the pulse generators from the vestibular system are *not* spatially coded. If, as seems the case,[17] saccades and quick phases are produced by the same pulse generators, it is clear that new circuitry is needed to interface the spatially coded visual signals to the pulse generators. Thus, it may well be that the interface itself, a phylogenetic latecomer, may not be in the brainstem at all.

Stimulation of the vermis lobes V, VI and VII produces saccades[26] which form a motor map similar to that which one finds in the colliculus, visual cortex, and frontal eye fields[27] with, however, one important difference: The amplitude of the saccades *are* a function of stimulus strength so that the vermis is *not* spatially coded. This suggests that the vermis may well lie *between* the interface and the pulse generators, that is, within the spatial-temporal translator itself.

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## Discussion

DAW: What is the high-frequency cutoff for the vestibular system and how does this compare with the cutoff of the whole system?

ROBINSON: The high-frequency cutoff of the vestibulo-ocular reflex is not known but lies above 5 Hz. From a functional standpoint it should be above the highest expected frequency of natural head movements and this appears to be the case.

The high-frequency cutoff of the semicircular canals is unknown but probably also lies above 5 Hz. The high-frequency cutoff of the extra-ocular muscles is 1 Hz. so that central mechanisms (that introduce phase lead) must compensate from 1 to 5 Hz. The pursuit system begins to cut off between 0.5 to 1 Hz. so that it can compensate for slow head movements while the vestibular system compensates for rapid head movements.

RATLIFF: In some cases your integrator seemed to be ideal and in other cases leaky.

ROBINSON: The integrator is not likely to be ideal. Its time constant (of the leak) need only be larger than a typical slow phase duration of nystagmus, say 2 to 5 sec. Its time constant may be revealed by the fact that, on eccentric fixation in the dark, the eyes tend to drift back toward the primary position at a velocity which suggests a leak time constant of 10 sec.

RODIECK: Isn't it curious that in an animal with a fovea one finds less directional selectivity in colliculus and lower visual centers than one finds in afoveate animals?

ROBINSON: Yes. In lower animals it may be that directionally selective units form a special subset of ganglion cells that are used to stabilize the eye with respect to the visual world but do not participate in form discrimination. Lack of such cells in foveate animals would suggest that this system has been abandoned in favor of an equivalent system which utilizes the more complex processing of the visual cortex. This observation is a serious problem in trying to draw an analogy between Collewijn's model for the rabbit's ocular stabilizing system and the smooth pursuit system of man.

LEVICK: The output of these directional selective units is a signal which corresponds to the velocity of the retinal image. So that if you really want the system to stay put you can't use these units because they don't go down to dc. Couldn't you consider the concentric units which do give you absolute position?

ROBINSON: The directionally selective on-units in the rabbit detect velocities of 0.01 degrees per second and stabilize the eye drift to comparable values. If the drift disturbance were unidirectional (it usually isn't) the eye would travel six minutes of arc in ten seconds or about 0.5 degree in a minute. Since the drift disturbance is not unidirectional, the long-term drift of mean eye position is so slow that it would be difficult to distinguish it from a true dc mechanism. All one can say from Collewijn's experiments is that the directionally selective units appear to be capable of explaining the observed behavior. This, of course, does not exclude the possibility of an absolute position system based on concentric units.

# Light and dark adaptation

## W. A. H. Rushton

The nature of visual adaptation is an extremely complex question and our understanding of it received a mighty setback when Hecht and Wald used their outstanding force and eloquence to insist that everything depended simply upon the level of rhodopsin in the rods and the photopic pigments in the cones. Thus all desensitization by light was called 'bleaching' and all recovery 'regeneration.' I am

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sorry to note that American psychologists and others still use this misleading terminology and there has been widespread belief that it rested upon experimental proof, though in fact it was a lively speculation which not only was unsupported by any measurements of pigment kinetics, but which resolutely ignored the work of Dartnall, Goodeve, and Lythgoe (1938) who had made those kinetic measurements in the '30s and proved the photochemical theory of visual performance to be untenable.

In fact the vision of everyday life is