TRANSLATIONAL MECHANISMS BETWEEN VISUAL INPUT AND SACCADIC MOTOR OUTPUT[†]

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Abstract

The location of a new visual target, represented by a single locus of activity in the deep layers of the superior colliculus, is eventually decoded into the appropriate activation of the various motorneuronal pools, so as to direct the eyes to the new target. This paper investigates both the spatial and temporal aspects of the decoding process, with particular reference to the problem of mapping from the retinocentric representation of the visual input to the headcentered representation of the motorneuron output to the extraocular muscles.

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1. Introduction

The oculomotor system for saccadic eye movement has long fascinated both engineers and psychologists by its apparent simplicity. A stimulus, at some location in the visual field, causes a rapid, precise eye movement directing the gaze to that location. Variability in trajectory is small (Bizzi et al., 1971; Bizzi et al., 1972). The load, at the eyeball, does not alter and hence the system need not adjust to changing environmental conditions.

Yet it has proved a difficult system to study, because of the difficulty in probing the successive stages in the translation of a visual input stimulus to a motor command. The most direct, and one of the most important pathways, for the control of saccadic eye movement, is the retino-collicular pathway. However, a portion of the pathway, from the superior colliculus to the oculomotor neurons, lies in the neuropil of the brainstem, and it has been difficult, both neuroanatomically and neurophysiologically, to trace the location of this pathway, and the stages of translation or remapping that occur.

In this paper, we consider, as a black box, the neural pathway from the deep layers of the superior colliculus to the oculomotor neurons in the brainstem nuclei III, IV, and VI, innervating the extraocular muscles, which turn the eye. We use available neuroanatomical and neurophysiological data to probe and predict the structure of the pathways within the black box. Finally, we develop a qualitative spatio-temporal model of the translation mechanism that converts activity in the deep layers of the superior colliculus into motor neuronal output.

2. Definition of the System

The input and output of the system under consideration can be reasonably well defined, both anatomically and electrophysiologically. The input to this system is the outflow from the deep layers of the superior colliculus. This is a spatio-temporal pattern of neural firing, and is described in greater detail in the next section. The output is the firing of the motor neurons in nuclei III, IV, and VI.

The following sections also discuss the anatomy and physiology of structures within the black box, though relevant data is scarce.

2.1. Electrophysiology

In the deep layers of the superior colliculus, a choice is apparently made about the particular stimulus to which the eyes will move next (Wurtz and Goldberg, 1972). The representation in the deep layers is retinocentric, that is, a topographic, though distorted, map of the retina. The firing of a neuron in these layers correlates with eye movement towards the direction specified by the location of the neuron in the layer. It can be inferred (Didday, 1970), though it has not been directly tested, that a selection process occurs at or before these deep layers which permits only a single peak of activity to occur in these deeper layers. The location of this peak in the layer determines where the eye will move to next.

Moving to the output end of the pathway, the neural activity in the nuclei of the extraocular muscles demonstrates a clear-cut relation to the position of the eyes in the head, that is, the representation is a head-centered rather than a retinocentric one relative to the current direction of fixation.

In each nucleus (III, IV, or VI), the motorneurons show a burst of high activity prior to and during those saccades which would require contraction of the muscle innervated by that nucleus. For example, the abducens nucleus innervates the lateral rectus muscle, which causes a sideways deviation of the eye. Motor neurons in the abducens show a burst of spikes correlated with the occurrence of saccades to the side. Further, the tonic firing rate of the motorneuron, during fixation, is linearly related to the amount of eye deviation to the side - the greater the deviation, the greater the tonic firing rate. Different neurons have different thresholds (that is, deviation beyond which tonic firing rate can be observed) and the increase in firing per unit increase in deviation is generally greater for neurons with higher thresholds. Thus, for an increased deviation, there is an increase both in the number of neurons firing and in the firing rate of active neurons. This correlates with the fact that greater force is needed to deviate the eye further when the eye is already deviated. (Fuchs and Luschei, 1970; Fuchs and Luschei, 1971; Robinson, 1970; Schiller, 1970).

2.2. Neuroanatomy

The motor nuclei innervating the extraocular muscles lie in the brainstem. There are three pairs of nuclei -- nucleus III, or oculomotor nucleus; nucleus IV, or trochlear nucleus; and nucleus VI, or abducens nucleus. Motor neurons in these nuclei form distinct pools, each pool innervating a separate muscle (Warwick, 1964).

Input to these nuclei has not yet been well defined. Being embedded in the brainstem reticular formation, they are believed to interact strongly with the neurons of the surrounding reticular formation. They also receive input directly or indirectly from the cerebral cortex, the cerebellum, the superior colliculus, and the vestibular nuclei. The nuclei of the extraocular muscles also interact with each other, presumably to coordinate the movements of the two eyes, and to regulate the differential activity of the muscles of each eye.

The neural pathways from the superior colliculus to the nuclei of the extraocular muscles are not known. No direct projection appears to exist (Altman and Carpenter, 1961; Szentágothai, 1950a). Degeneration data from lesions of the deep layers of the superior colliculus suggest that the pathway is an indirect one, via the brainstem reticular formation surrounding these nuclei, that is, via the pontine paramedian reticular formation. It has been shown (Scheibel and Scheibel, 1958) that neurons of the reticular formation project collaterals to at least some cranial nerve nuclei, including the nuclei of the extraocular muscles.

The most important projections from the brainstem to these nuclei are from the vestibular nuclei. Functionally, a clear correlation can be shown to exist between the stimulation of particular semicircular canals and the generation of eye movements in specific directions (Szentágothai, 1950b; Cohen, 1971). Moreover, the pathway from the vestibular nuclei to the nuclei of the extraocular muscles forms a direct, monosynaptic link (Szentágothai, 1950b) via the medial longitudinal fasciculus. Functionally, this pathway probably plays a major role in maintaining fixation under a variety of head movements (Bizzi et al., 1971; Bizzi et al., 1972).

Cerebellar output to the extraocular motor nuclei originates from lobules VI and VII of the vermis (Llinas, 1972). The exact pathway is not known but, electrophysiologically, a direct correlation can be observed between the amount of Purkinje-cell firing and the amplitude of saccades (Llinas, 1972). Stimulation experiments show a rough map in the cerebellum relating location of stimulation with direction of saccade (Robinson, 1972).

3. Translation Mechanisms

3.1. Definition of the Problems

Translation from the saccade command at the colliculus to the motor command at the brainstem nuclei involves, at least, the following problems:

a) What transformation converts from a retinocentric representation at the superior colliculus to a head-centered representation at the motor nuclei III, IV, and VI?

b) How is information from a retinocentric spatial array such as in the superior colliculus distributed to the six muscles of each eye so that each contracts appropriately, that is, what is the transformation from a retinal to a muscular representation of a location in space?

c) What transformation converts information about the location of the new target from a spatial representation in the superior colliculus into a temporal representation, that is, the 'pulse-step' firing of the motor neurons?

3.2. Translating Target Location from Retinocentric to Head-centered Representation.

The deep layers of the superior colliculus can be considered as a two-dimensional array onto which the retinal image is mapped, after some processing. The location of a peak of activity, in this array, represents the location of the new target with respect to the current direction of gaze. Therefore, the output from the superior colliculus specifies the <u>change</u> in the direction of gaze, irrespective of the current gaze direction.

However, since the eyes are located in the orbit, and the force required to deviate the eye increases nonlinearly with the deviation from a 'forward' direction of gaze, the motor neuron output must depend not only on the desired change in direction of fixation but also on the current direction of fixation. Therefore, the retinocentric representation, in the colliculus, of target location must be translated into a head-centered representation at the motor neurons. This raises the question about the representation of the visual field at the level of the motor neurons.

A possible representation is a two-dimensional map of the visual field, but a head-centered one rather than a retinocentric one. An activity peak in this array would code the desired final position of the eyes relative to the head, thus taking into consideration both the current direction of fixation and the change in direction, as desired. However, in such a head-centered representation of the visual field, each shift of the eyes would require a shift in the projection from the colliculus to the motor neurons, as shown in Fig. 1. Figure 1a shows the projection of the collicular array onto the motor neuron array for a particular direction of fixation. 'A' is the collicular representation of the fovea. 'B' is the representation of the location of the new target. Shifting the gaze to the new target (Fig. 1b) shifts its representation on the collicular array but does not shift its representation on the motor neuron array, because the head has not moved. Therefore, the projection from the

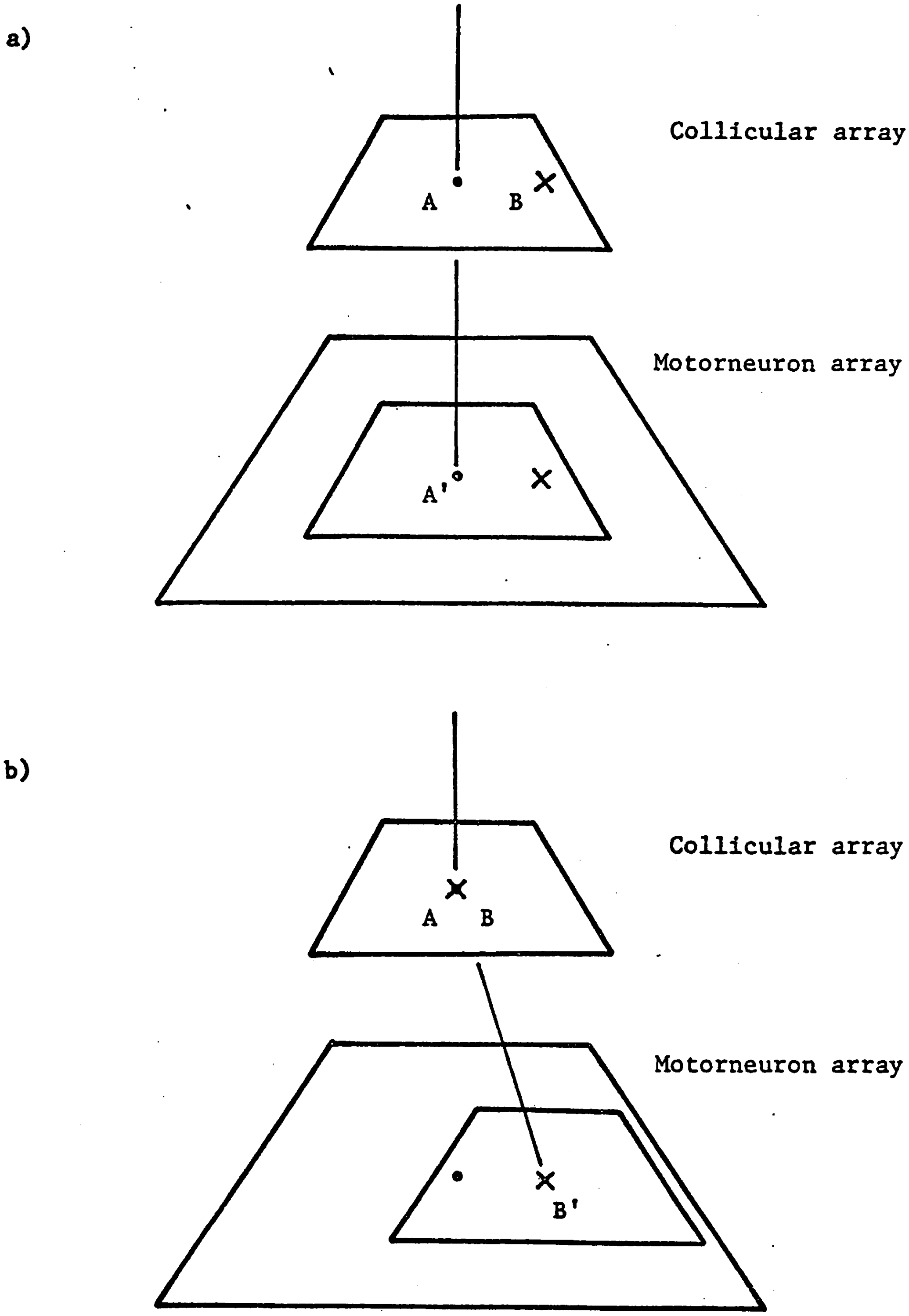

Fig. 1. Illustrating the Projection from the Collicular to the Motorneuron Array a) before and b) after an Eye Movement. A' and B' represent the targets fixated before and after the eye movement.

colliculus to motor neurons has to shift as shown. Neurally, this implies a change in the axon branch used with each shift of the eyes. This probably does not occur, though there is some evidence to the contrary (Chung et al., 1970).

On the other hand, neurophysiological data (Schiller and Koerner, 1970; Fuchs and Luschei, 1970) show that, in the motor nuclei, the location of the new target is represented by the rate-of-firing of a population of neurons, with no apparent spatial ordering. The rate-of-firing of each neuron, in a nucleus, increases with the degree of contraction of the corresponding muscle, and is linearly related to the eye deviation caused by contraction of that muscle. For greater deviations, the number of motor neurons active is greater.

This suggests that there is <u>no</u> transformation of the entire visual field from a retinocentric to a head-centered representation. (However, the possibility of the existence of such a transformation cannot be entirely ruled out.) Instead, it is information about only a single point in the visual field, the location of the new target, that is transformed into head-centered coordinates, altering the firing of the motor neurons to that corresponding to the new deviation.

The system can be conceived of as an integrator, whose current output value corresponds to the current position of the eyes in the head, and which receives as input the signal for the desired change in firing rate.

Figure 2 presents a block diagram of this transformation. The deep layers of the superior colliculus produce a change-in deviation signal, $\vec{\delta\theta}$, indicating the location of the new target relative to the current fix-

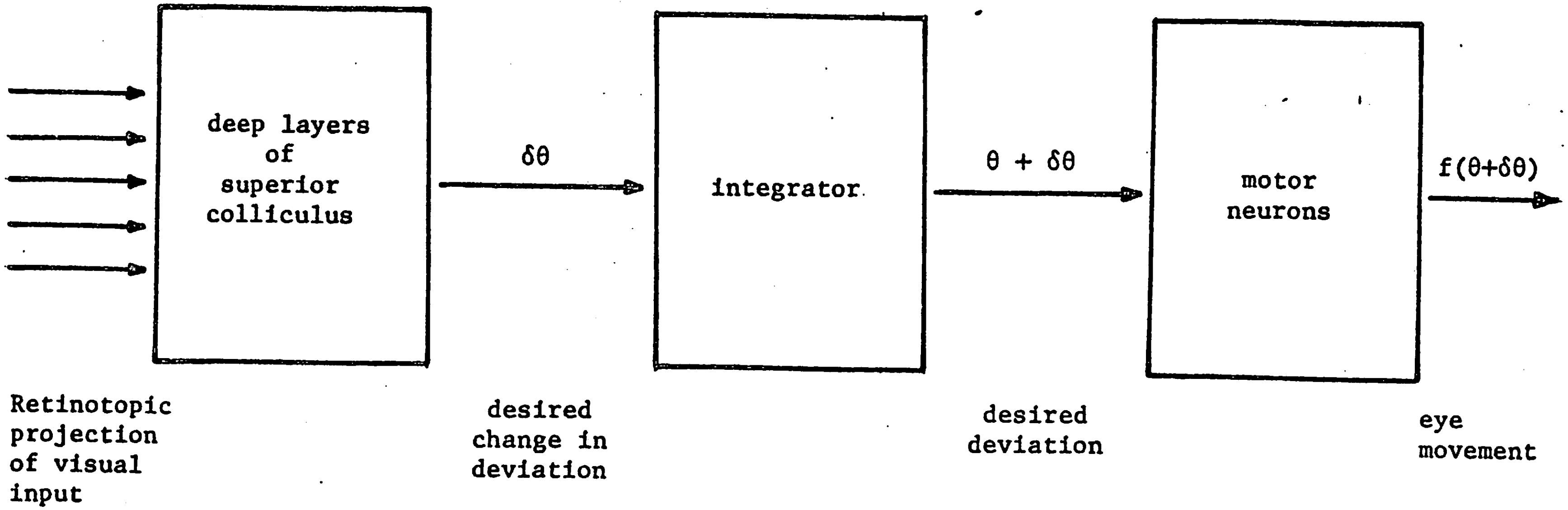

Fig. 2. The Transformation from a Retinotopic to a Head-centered Representation

ation point. The initial output, Θ, of the integrator is the current diviation of the eyes. $(\Theta + \partial\Theta)$ corresponds to fixation of the new target.

A randomly interconnected network of neurons with excitatory interconnections acts as a leaky integrator, a perfect integrator, or an unstable system, depending on the amount of positive feedback within the system. In this system, the leaky integrator is the most likely alternative (Collewijn, 1972). If a leaky integrator is to produce a constant output, corresponding to current eye position, it requires constant input. This input is probably supplied by the muscle spindle afferents of the extraocular muscles. The existence of these spindles has been demonstrated (Skavenski, 1972) but they do not take part in any oculomotor reflex. A change-in-deviation signal, $\partial\Theta$, causes a transient increase of the integrator output. This alters motorneuron firing, thus moving the eyes. The altered feedback from the muscle spindles holds the integrator output at the new value of $(\Theta + \partial\Theta)$.

The motorneuron pool can be considered to consist of a set of idealized linear threshold elements (Fuchs and Luschei, 1970). If the output firing rate of the n-th motorneuron is y_n, and its input is x_n, its behaviour can be represented by

$$y_n = a_n . x_n - b_n , \qquad (1)$$

where the gain a_n and the threshold b_n differ for different neurons. As the input to the motorneuron pool increases, the number of neurons activated increases. At the same time, the firing rate of currently active neurons also increases. Thus the total activity of the motorneuron pool increases nonlinearly for a linear increase in input, as shown diagrammatically in Fig. 3. This corresponds to the nonlinear increase in the

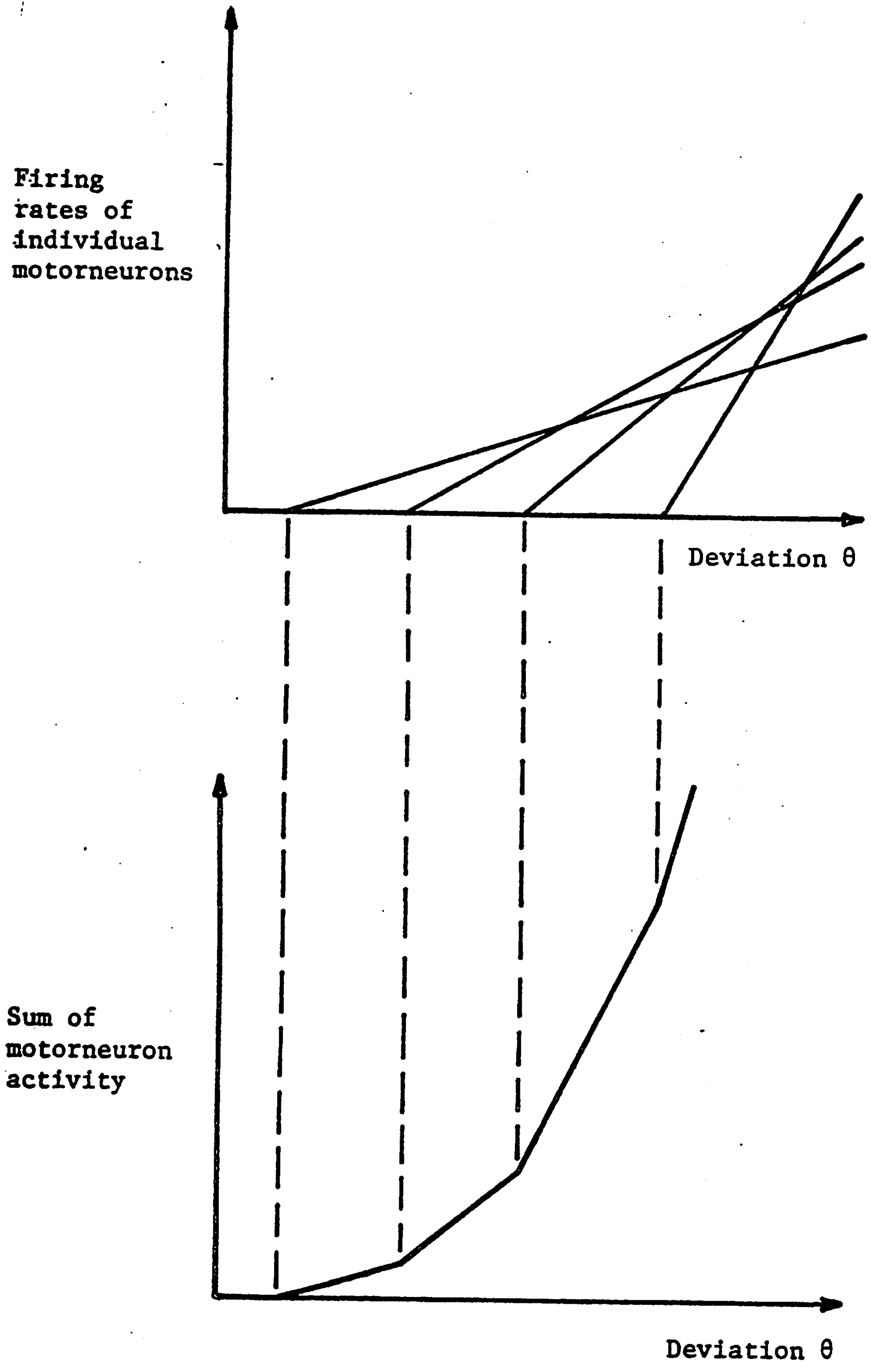

Fig. 3. Nonlinear Increase of Total Neural Activity Resulting from a Summation of Activity in Neurons with Linear Threshold Characteristics

force required to hold the eyes in an increasingly deviated position.

3.3. Translating Target Location from a Retinal to a Muscular Representation

Target location information from the superior colliculus must be distributed to the six muscles of each eye, so that each contracts appropriately. At the colliculus, target location is specified by the location, in the collicular array, of a peak of neural activity. At the motor nuclei, a high level of activity in one nucleus causes a greater degree of contraction of the corresponding muscle. Thus the relative levels of activity in the different nuclei determine the degree of contraction of the muscles, and thus also determine the direction of gaze.

Consider a one-dimensional array of neurons, whose output projects to two pools of neurons (Fig. 4). A peak of activity exists at only one location in this array. It is desired that the relative activity in the two pools reflect the location of the peak in the array, that is, if the peak is far to the left in the array, the neuron pool to the left should be the more active.

Neuroanatomically, there are two possibilities. One is that each neuron in the array projects to only one of the pools. Nevertheless, any small region of the array innervates both the pools, with a fraction of neurons innervating one pool and the rest the other. The fraction of neurons innervating one pool, as a function of location along the array, is a monotonic function, as shown in Fig. 4. The other possibility is that each neuron can project to both pools, but how heavily it projects to one pool (e.g., how many synaptic terminals it possesses, or how effective each synaptic terminal is) is again a monotonic function of the

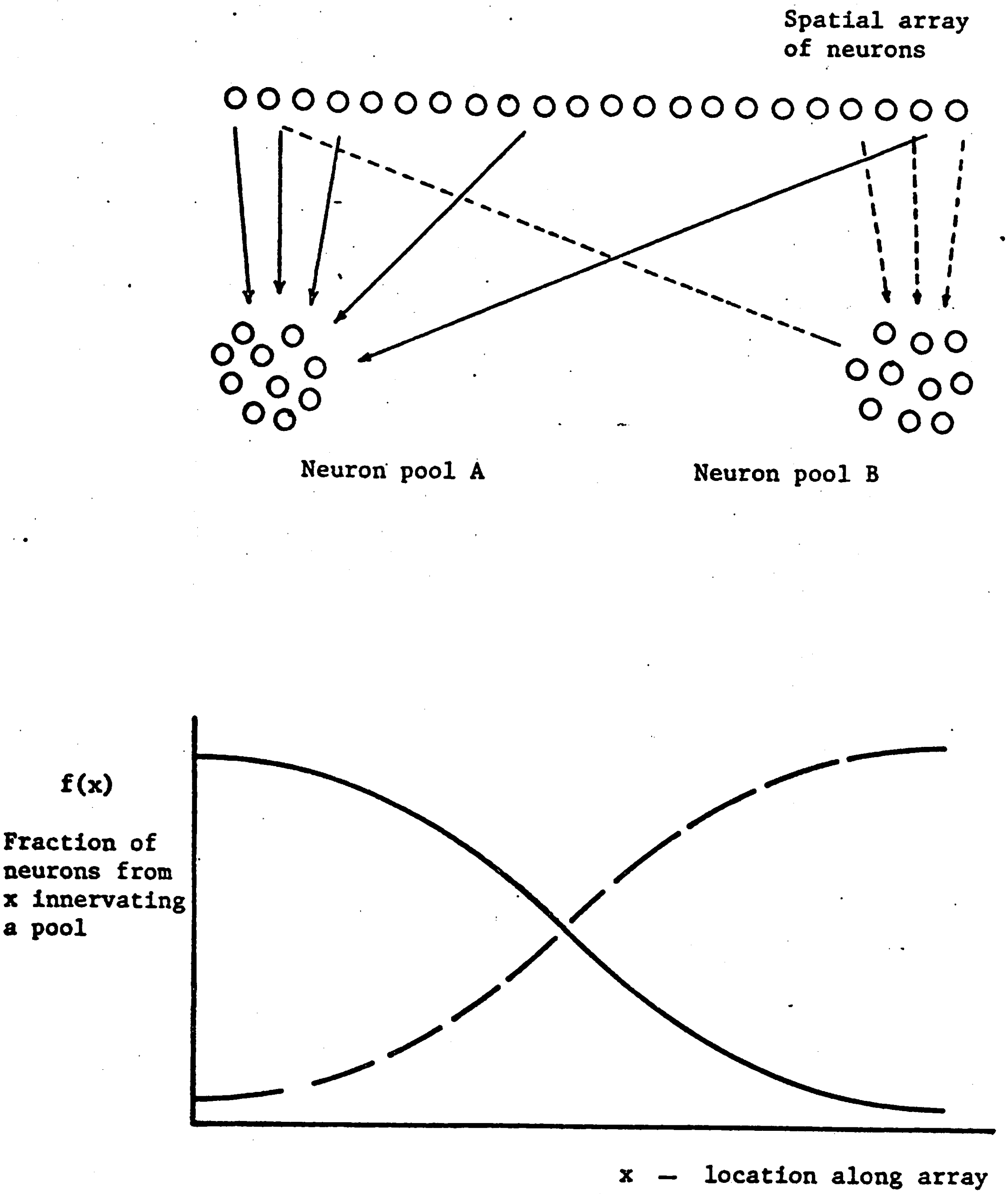

Fig. 4. Spatial Redistribution of Locus Information based on Differential Projection Densities

location of the neuron in the array, as in the previous case (Pitts and McCulloch, 1947).

For the oculomotor system, the collicular projection must be discussed in terms of a two-dimensional array (in colliculus) projecting to the various motorneuronal pools of the extraocular muscles. Two of the six extraocular muscles, the superior oblique and the inferior oblique, cause rotation of the eye instead of deviation, and are closely tied to the vestibular system for stabilization of the eyes in the head. The other four extraocular muscles deviate the eye along various directions (though some component of rotation may be introduced at large deviations).

Therefore, the formal requirement is that the net input to a motorneuron pool, from any location of the collicular array, increase monotonically along the coordinate corresponding to the direction of eye deviation caused by contraction of the corresponding muscle. This monotonic relation between location on the collicular array and density of projection to a specific motorneuronal pool may be achieved in different ways, as suggested by the example above. However, if the above hypothesis about the translation from retinal to muscular representation is correct, it permits us to make a verifiable prediction about these differential projections. A spatially localized lesion, in the deep layers of the superior colliculus, should, according to the hypothesis, cause different amounts of degeneration in the neuropil surrounding the different motor nuclei of the extra-ocular muscles. The most clearly defined system for such an experiment is the projection to the abducens nucleus (Nuc.VI) which causes lateral deviation of the eyes through contraction of the lateral rectus. The abducens nucleus does not innervate any other extraocular muscle. The hypothesis predicts a spatial map of projection density,

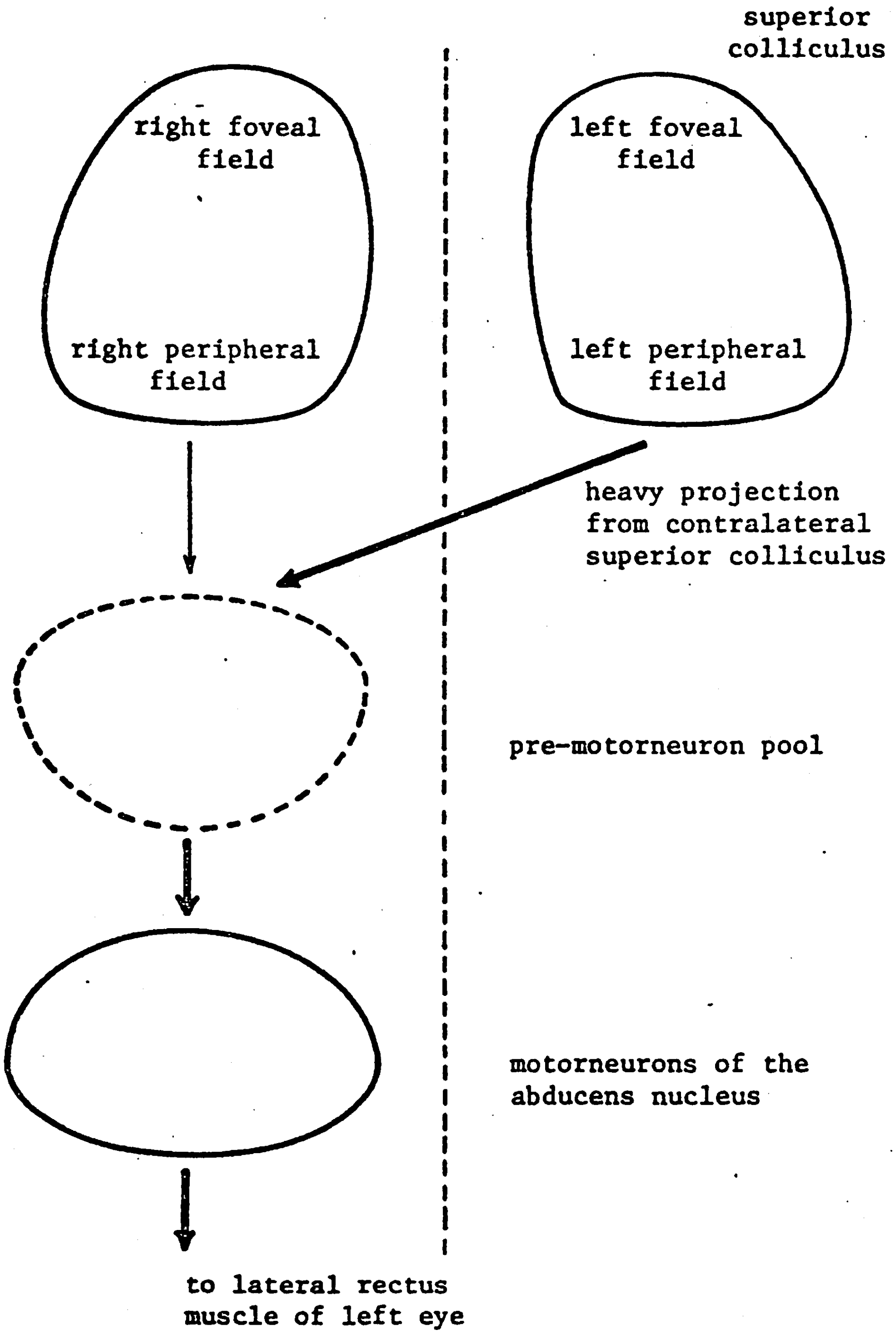

Fig. 5. Predicted Differential Densities of the Neural Projection from the Superior Colliculus to the Regions surrounding the Abducens Nucleus

with the heaviest projection to, say, the left abducens nucleus from that region of the collicular array representing the left visual field (Fig. 5).

3.4. Generation of the 'Pulse-Step' in Motorneuronal Firing

In Sec. 3.2, we showed that a desired change in eye deviation could be transformed to a change in the level of motorneuron firing. However, the inertia of the eyeball and the response time of the extraocular muscles require an initial input kick if rapid eye movements are required. This is reflected, in motorneuronal firing, by an initial burst whose duration corresponds to saccade amplitude, followed by a steady level of firing corresponding to the direction of fixation of the eye.

A number of suggestions have been made about the neural mechanism that may generate this initial pulse. Barmack (1972) points out that the motorneuron membrane itself has the capacity to differentiate the input. Thus a step input produces an initial spike in the EPSP followed by a steady potential. However, the duration of this spike is small compared to the duration of the burst of increased firing, though it does vary directly with the amplitude of the input step.

Robinson (1971) hypothesizes a pulse-generating mechanism where the duration of the pulse is controlled by the amplitude of the desired-deviation input. Figure 6 shows how a 'step' input (the desired change in eye deviation), through two parallel pathways, produces the pulse-step input to the motorneurons. The pulse duration is proportional to the step amplitude. However, Robinson does not detail the nature of this pulse-generator.

Llinas (1972) shows that activity in the cerebellum, a structure

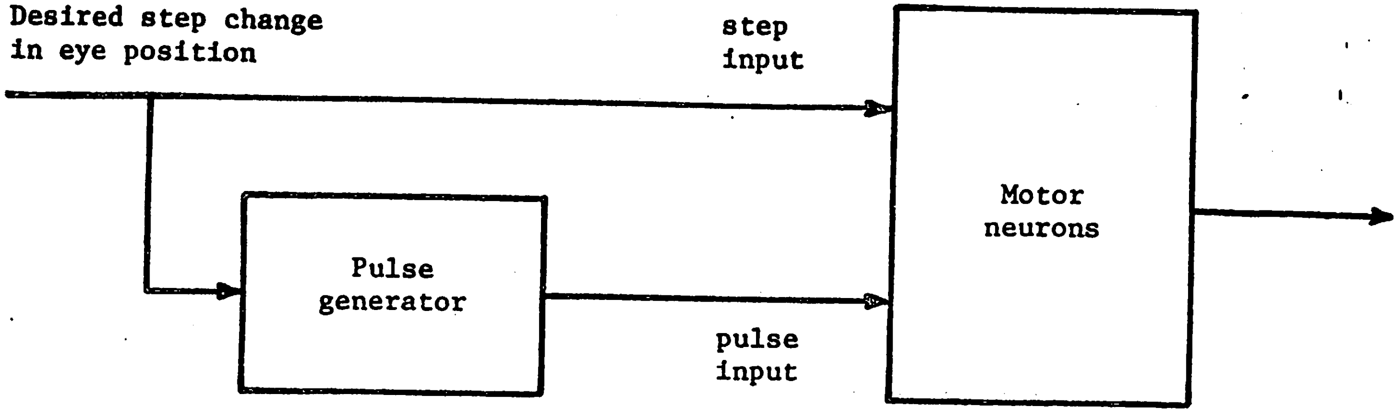

Fig. 6. Illustrating the Pulse-Step Input to the Motorneurons required to overcome the Inertia of the Eye

closely concerned with the control of movement, is directly related to saccadic activity -- the larger the amplitude of the saccade, the less the firing of Purkinje cells, the output elements of the cerebellar cortex. He further points out that the cerebellum does not initiate movement, but is involved in modulating or stopping movement.

In Fig. 7, we show how the cerebellar cortex may control a pulse generator such as is suggested by Robinson. A reverberatory, positive feedback network (such as that described by Boylls (1974), in a model of the cerebellum) is activated by a step input. The amplitude of the step input may determine the rate at which this activity builds up. Measurements of saccade amplitude versus latency suggest that the latency of eye movement is greater for small saccades. The output of this network drives the motorneurons of the extraocular muscles. At high levels of network activity, the activity in the motorneuron pool reaches saturation. Meanwhile, the cerebellar cortex generates an output whose amplitude is inversely proportional to the amplitude of the input step. (Llinas suggests that this may be because of increased feedforward inhibition on the Purkinje cell for larger input amplitudes.) This output, which is inhibitory, suppresses activity in the positive feedback network. A large inhibitory input, corresponding to a small saccade, causes rapid decay of network activity, while the decay is slower for the small inhibition corresponding to large saccades. This modulates the duration over which the motor neurons are held at saturation levels of activity, that is, the high-frequency burst of motorneuron firing that provides the initial kick to overcome the inertia of the eye and the accompanying viscous drag.

4. Discussion

Figure 8 summarizes the three translation mechanisms in a block

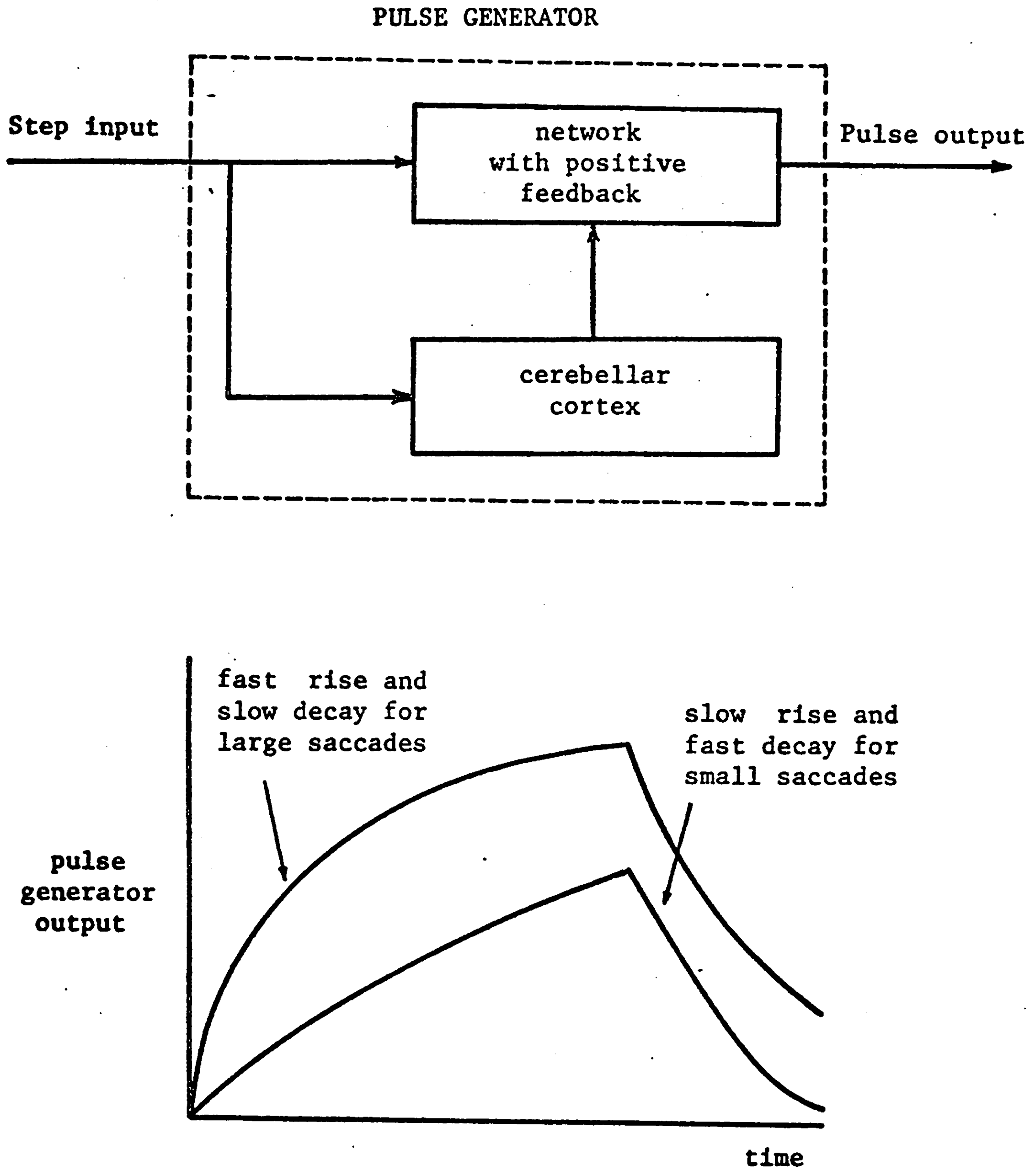

Fig. 7. Generation of an Output Pulse of Duration proportional to the Amplitude of the Input Step

diagram, where each block is a distributed network of neurons and the projection from one block to the next is also distributed.

The spatial redistribution of locus information, as discussed in Sec. 3.3, is hypothesized to be the first transformation. The differential projection from the deep layers of the superior colliculus to the brainstem regions surrounding the various motor nuclei controls the relative inputs to these regions depending on the location of the activity peak in the collicular array.

An intermediate 'summation' network has been hypothesized to take into account possible intervening stages between the collicular output and the input to the cerebellum and to the pre-motorneuronal integrating mechanism. A summation stage would be a network of neurons such that the output of each neuron is affected equally by all the inputs to that network. A randomly interconnected network of neurons would provide a close approximation to these desired characteristics. It can be inferred that the deep layers of the colliculus must be acted on by an 'erase' mechanism after every decision to alter the direction of gaze. Therefore, the duration of the input to the summation stage is fixed (depending on the latency of the erase mechanism) but the intensity of the input (e.g., the number of active fibres) is a function of the location of the activity peak on the collicular array.

The integrator, as described in Sec. 3.2, is a network of neurons with excitatory interconnections, with a leaky integration response. The input to the integrator, from the summation network, is proportional to the desired change in direction of gaze. Spindle input from the extraocular muscles maintains a constant output from the integrator,

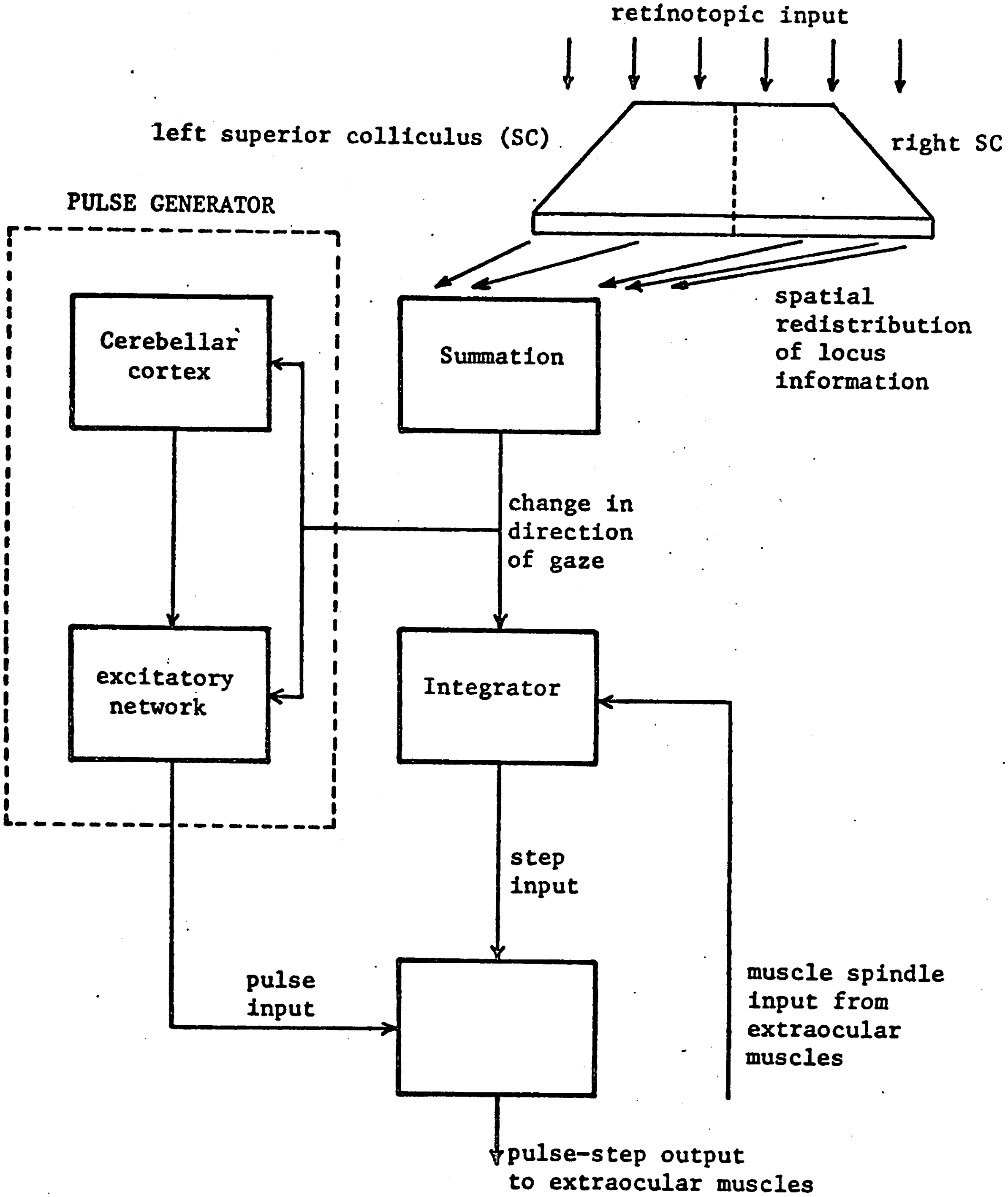

Fig. 8. The Spatio-Temporal Transformations involved in Decoding a Retinotopic Eye-Movement Command

and thus maintains a tonic activity in the motorneurons, holding a direction of fixation.

The pulse-generator (Sec. 3.3) receives change-in-deviation input from the summation stage and generates a pulse of corresponding duration, driving the motorneurons at their maximal firing rate and supplying the initial kick to move the eyeball.

4.1. Model Testing and Extensions of the Model

Translation of target location from a retinal representation in colliculus to a muscular representation, through differential projections, may be tested neuroanatomically as suggested in Sec. 3.3.

The existence of a leaky integrator and its dependence on muscle spindle input can be tested by altering or eliminating muscle spindle activity. Selective destruction of afferent fibres is difficult but may perhaps be achieved by chemical methods. Vibrator activation of spindle fibres is another possibility. Lack of constant output from the integrator will cause motorneuron activity to die away, letting the eyes drift back to a central position.

Sectioning collicular pathways to the brainstem removes the change-in-deviation input to the integrator but leaves the spindle input intact. For such a system, fixation will be held at any position the eye is passively moved to.

The integrator receives information about the absolute position of the eye in the orbit. This implies either that there is no gamma system that resets spindle length, or else that the integrator receives gamma output as well as spindle output.

The pulse generator has been modelled such that the duration of the output pulse corresponds to the desired change in deviation. The relevance of the cerebellar cortex to the control of pulse duration may be tested by stimulation or lesion techniques. Cerebellectomized animals have been shown to generate dysmetric saccades (Kornhuber, 1971).

This model of the pulse generator does not take into account the fact that, with increasing initial deviation Θ, there is a nonlinear increase in the force required to make a saccade, $\partial\Theta$. (Earlier, we took into account the nonlinear increase in force required for steady fixation at increasing deviations.) Information about initial eye position is available from the muscle spindles, and these are known to project to the cerebellum (Fuchs and Kornhuber, 1970) where control of the pulse generator is hypothesized to occur (Sec. 3.4). The integrator was also shown to require spindle input (Sec. 3.2). Both the integrator and the pulse generator require excitatory networks suggesting that the excitatory network of the pulse generator may also be the integrator, with an early pulse output in response to the excitatory summation input and the inhibitory cerebellar cortex input, and a late step response held constant by the spindle input.

The location of such an integrator can be investigated by testing cerebellectomized animals in the dark. If the integrator lies in the cerebellum, the animal will be unable to hold any deviated eye position, besides showing dysmetria in saccade behavior. An ability to fixate a visual target even after the target has been turned off implies that the integrator is unaffected by cerebellectomy.

5. Summary

This chapter has dealt with the many translation mechanisms that must exist to recode retinal representation of the visual field into a muscular representation that allows visual grasp of a new target. It involves spatial transformation so that information from any location in the colliculus is available to the motorneurons innervating all the extraocular muscles. It also involves the temporal response of neural nets so that the location of a peak of activity in the colliculus determines the duration and intensity of motorneuron firing, thus moving the eye to the new target and holding it there. The different stages in these translation mechanisms have been modelled qualitatively by distributed neural nets. Some predictions have been made about expected neuroanatomical projections, and experiments have been suggested to test the validity of parts of the model.

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