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**Contemporary Ocular Motor
and Vestibular Research:
A Tribute to David A. Robinson**

International Meeting Eibsee, 1993

Edited by A.F. Fuchs, T. Brandt, U. Büttner, and D. Zee



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Can the Phasic and Tonic Contributions of Agonist and Antagonist Muscles during Saccades be Identified from the Waveforms of the Post-Saccadic Drift?

Paolo Inchingolo, Paolo Bruno
Dipartimento di Elettrotecnica, Elettronica ed Informatica, University of Trieste, Italy

Introduction

Fine analysis of the eye position following normal horizontal saccades reveals a very small ocular drift, mainly composed of two exponential components (Inchingolo et al., 1993), with either opposite or same directions. Both components vary in size and time constant (TC) with orbital position and saccade direction; usually, they have opposite directions in the two eyes (Fig. 1B-E). In the monkey, the drift TCs range from 20 to 200 ms for one component and from 100 to 500-1500 ms for the other one. Two drift components with similar characteristics are macroscopically evident in monkeys with one eye weakened by botulinum toxin (Fitzgibbon et al., 1991). In this case, one drift component is usually much larger than the other one (Fig. 1C-F), up to 2-3 times the saccadic step size (Fig. 1F). The aim of this work is to try an interpretation of all these drift components and to see if, from their analysis, it is possible to estimate the characteristics of the plant, particularly of a pair of agonist-antagonist muscles, and the neural signals used to control it during saccades.

Analytical interpretation of the post-saccadic drifts

Although the functions of the two TCs (T_a and T_b) and of the two corresponding drift amplitudes (D_a and D_b) with respect to the orbital position and saccade direction are very different for normal and botulinized subjects, in both situations the motion of the eyes can be described theoretically by the following equation in Laplace notation:

$$E/E_d = G_a (1 + s T_{za}) / (1 + s T_a) + G_b (1 + s T_{zb}) / (1 + s T_b) \quad (1)$$

where E_d and E are the Laplace transforms of the desired and the actual eye positions, respectively, and T_{za} and T_{zb} represent the phasic contributions to the eye movement. A saccadic step is normometric when $G_a + G_b = 1$. Both components of post-saccadic drift are suppressed if T_{za} and T_{zb} match T_a and T_b , respectively. Under some hypotheses (e.g. cyclopic neural controls), from the sizes of the saccadic step and pulse and from those of the drifts D_a and D_b it is possible to evaluate all the parameters of Equ. 1 as functions of orbital position and saccade direction. Consequently, these parameters identify the tonic and phasic contributions of two variable lead-lag equivalent elements, contributing to the saccadic movement. Is there a physical correspondence to these theoretical elements in oculomotor system? A hypothesis that they represent the couple of agonist (AgM) and antagonist (AntM) muscles, functionally different each other, behaving as non-linear visco-elastic elements, and controlled by two different neural pulse/step signals has been previously proposed (Inchingolo et al., 1993).

A model study of the oculomotor plant and its premotor circuits

A more or less complex linear model of the oculomotor plant cannot be used to validate or reject this hypothesis, since no one linear model can be compatible with the experimental drift data. Then, we studied analytically and simulated a rather complete non-linear model (for horizontal movements), adherent as much as possible to the anatomo-functional behaviour of the oculomotor plant. The simulated model (Fig. 1A) is an extension and an implementation of that proposed by Robinson (1981).

The orbital tissues and the eye ball The orbital tissues (OTs) have been modelled as two Voigt visco-elastic elements and the eye ball as an inertial mass. During eye motion, other than a tonic elastic force, a sliding visco-elastic force with very large TCs (a zero at about 1s and a pole at 500ms) and a small transient viscous force with a zero at very low TC (20-40ms) are also produced. The sum of these sliding-tonic-phasic forces (F_{ot}) and the phasic inertial force

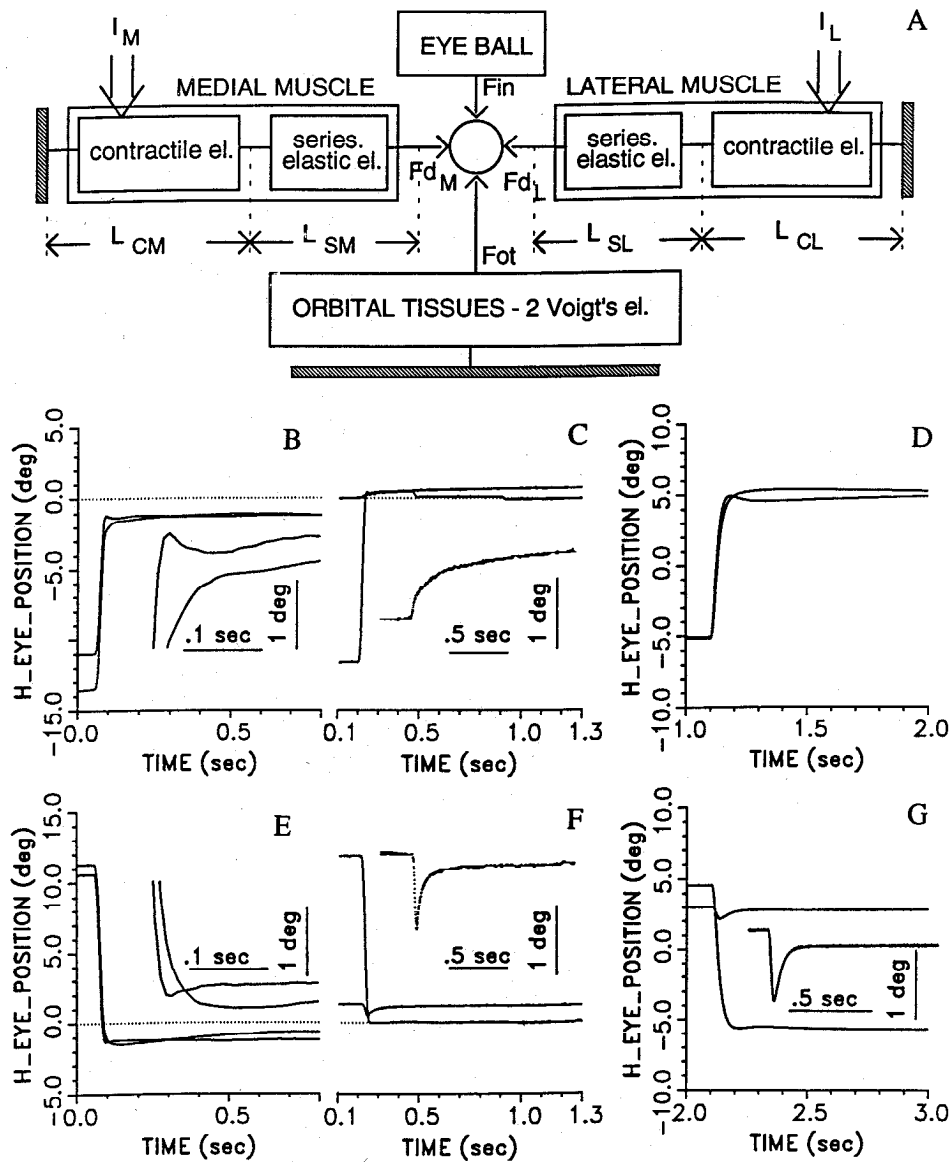


Figure 1: A: model of the oculomotor plant. The current eye position E is determined by the balance of the forces F_{dM} and F_{dL} at the tendons with the forces F_{ot} and F_{in} , developed by the orbital tissues and the eye ball inertia, respectively. For each muscle, E must match the sum of the changes of length of the contractile elements L_C and of the series-elastic elements L_S , which are in turn non-linear functions of innervation I and tendon force F_d at that muscle. B and E: examples of saccades of the two eyes in a normal monkey. C and F: examples of saccades of the two eyes in a monkey with the left eye botulinized. D: example of simulated saccades in a normal monkey. G: example of simulated saccades in a botulinized monkey. All the inserts show the details of the ocular drift.

(F_{in}) are balanced by the forces F_{dL} and F_{dM} at the tendons of the muscles. The model study suggests that a proper (pulse)-slide-step neural command is generated by a *neural inverse model* of the OTs and the ball, to innervate the orbital fibers of the couple of muscles. Any small sliding mis-match between the OTs and their neural model reflects (Fig. 1D) on long-TC drifts (500-1000 ms), as those observed in normal saccades (Fig. 1B and E).

The contractile elements The contractile elements (CEs) of each muscle have been modelled according to their non-linear innervation-tension-length characteristics. The viscosity has been evaluated as a function of CEs velocity, direction of motion (contraction or relaxation) and active force. The CEs behave as single visco-elastic elements with a TC (T_C), changing largely during saccades and with the motion direction (on average, 150-300 ms during contraction and 50-150 ms during relaxation). T_C is also sensibly dependent on the current CEs length (L_C) and velocity. Finally, it is larger in the medial rectus than in the lateral rectus. The model study suggests that most of the tonic and phasic tension developed by the CEs of one muscle is balanced within the muscle itself by a tuned pulse-step component of innervation to the global fibers, generated by a *neural inverse model* of each muscle. This hypothesis is supported by the values of the forces F_{dL} and F_{dM} reported by Collins (1975).

The series-elastic elements The length (L_S) of the series-elastic elements (SEEs) exhibits a fixed value when the eye is steady, and changes with a TC of 20-40 ms proportionally to the viscous force and to the inverse of the active force when it is in motion. The SEEs increase the velocity of saccades and produce a post-saccadic drift backwards, with a TC (T_S) of 20-40 ms. This effect can be balanced by the dumping effect of the small TC of the OTs. So, a low-TC drift either backward or onward can appear in the movements (Fig. 1D), as the first or the second effect is dominant, according to the saccades recorded from normal subjects (Fig. 1B-E). The SEEs functionally separate the muscles from each other and with respect to the OTs and the ball, in the sense that the individual TCs of the CEs of each muscle are partially transferred to the eye motion, when the matching between the CEs and their neural model is altered. In particular, for the unbalance of the AntM, its T_C is transferred almost intact to the eye drift. When the AgM is unbalanced, its T_C is transferred to the eye drift, with a value altered by the corresponding T_S and also by the T_C of the AntM (Fig. 1G). These transfers are particularly evident when the contributions of the OTs can be neglected, that is when the muscles are weak, as in the butuline experiments. So, the long-TC drift of Fig. 1C should be imputed to the AntM and that of Fig. 1F partially to the AgM (the lateral rectus in both cases).

Conclusions.

In conclusion, with respect to the starting hypothesis, the analysis of the the post-saccadic drifts provides a very complex information about the ocular plant components and their neural controllers. This study suggests the causes of the short, medium and large TC components in the drifts. Some conditions appear very interesting and simple, as the direct transfer of the T_C of the AntM in a weak eye. In general, it seems to be possible, although conceptually difficult, to evaluate analytically most of the tonic, phasic and sliding contributions of the muscles, of the orbital tissues and of the innervation components, from the composite post-saccadic drifts. However, much more work, both experimental and theoretical, is still necessary to set up a method for these evaluations and to focus on all the possible limitations.

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