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MODEL SIMULATION STUDIES TO CLARIFY THE EFFECT ON SACCADIC EYE  
MOVEMENTS OF INITIAL CONDITION VELOCITIES SET BY THE VESTIBULAR  
OCULAR REFLEX (VOR)

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## SUMMARY

Voluntary active head rotations produced vestibulo-ocular reflex eye movements (VOR) with the subject viewing a fixation target. When this target jumped, the size of the refixation saccades were a function of the ongoing initial velocity of the eye. Saccades made against the VOR were strikingly attenuated in magnitude while saccades going with the VOR were larger in magnitude. Simulation of a reciprocally innervated model eye movement provided results comparable to the experimental data.

Most of the experimental effect appeared to be due to linear summation for saccades of 5 and 10 degree magnitude. For small saccades of 2.5 degrees, peripheral nonlinear interaction of state variables in the neuromuscular plant also played a role as proven by comparable behavior in the simulated model with known controller signals.

## INTRODUCTION

Under natural conditions, it is well known that different types of eye movements, generated by specialized subsystems of the CNS, may interact temporally in a complex manner. In recent years, the interactions between different types of eye movements has been studied in humans and primates in a number of different ways and the linear summation theory for such movements has been proposed. In particular, data on voluntary saccades with compensatory movements (VOR) in monkeys (Morasso et al (1973)), saccade/vergence interactions in man (Kenyon et al (1980)); Ono et al (1978)), goal-directed saccades and VOR in man (Jurgens et al (1981)) all support the theory of additivity when two types of eye movements combine. Chun and Robinson (1978) postulated switching off of slow command during the execution of quick phase VOR in monkey. Also, earlier work by Nam et al (1981) presented some evidence for the 'Kenyon effect' in saccade and VOR interaction.

In this study, we examined our former hypothesis on linear summation through the interaction between saccade and VOR eye movements by experiments in humans and by computer simulation using a modified version of the eye model described previously by Lehman and Stark (1979). Were the observed phenomenon due to 1) linear summation of VOR with the saccades, 2) peripheral nonlinear interaction of state variables in the neuromuscular plant, i.e., the 'Kenyon effect', 3) nonlinear interaction at ocular motor neurons, the final common path that might have shown nonlinear squelching phenomena, or 4) higher level preprogrammed changes in saccadic magnitude? By combining experimental results with simulation findings, in which the latter has a known controller signal, cases 1) and

2) can be separated from cases 3) and 4), and significant insights can be obtained.

## METHOD

### A. Experimental

Horizontal eye movements were measured using the infrared photo-electric method which has a bandwidth of 1 kHz and a sensitivity of 10 min of arc. Measurements were linear for a range of  $\pm 25$  degrees and frequent calibrations guaranteed that recorded eye movements faithfully reflected retinal orientation.

Horizontal head movements were measured with an electro-mechanical transducer system consisting of mechanical linkages using light-weight universal joints and a sliding mechanism coupled to a low torque special film potentiometer. The linkage was self-aligning with the vertical axis of the head and thus only rotational motion of the subject's head in the horizontal plane was measured by the potentiometer. This system allowed for flexible and natural head movements for the subject.

Data was obtained for five adult subjects. To generate the appropriate VOR, the subject would rotate his head voluntarily at a frequency between 0.8 and 1.5 Hz in a sinusoidal-like motion with a peak amplitude between  $\pm 10$  and  $\pm 15$  degrees relative to the center 'straight-ahead' position. Calibrations were performed on eye movements within  $\pm 25$  degrees of the visual target using 5 equidistant points at a distance of 19 cm from the eye axis of rotation. After separate calibrations for the eye and head movements to the same calibration target, the task of the subject was to follow the jumping targets as quickly as possible while making the sinusoid-like head rotations.

The experimenter instructed the subject to carefully follow the visual target and also gave the subject's various head rotation schemes (eg. faster, slower, larger, smaller so as to obtain data with a variety of head rotations), all the time viewing the eye and head movement recordings. Vision was monocular to avoid vergence effects. The data was classified in terms of the initial velocity conditions as being 'with' (W) or 'against' (A) the VOR.

### B. Simulation

The 'core' eye model algorithm has been described in detail previously (Lehman and Stark, 1979). The corresponding program represented

a simulation of the eye mechanics for horizontal eye movements, i.e. of the lateral and medial rectus muscle, involves the integration of a set of six nonlinear differential equations.

The present program represents a significant extension of the model so as to allow a sinusoid 'VOR' neurological signal---of specified magnitude and frequency---to be the 'base' control signal. A saccade (second order, of 2.5, 5, 10 or 20 degrees magnitude) can then be produced at any time during a run, and consequently for different initial conditions of VOR position, velocity, and acceleration. As presently set up, there is both a left and a right saccade, with the left occurring first.

The main outputs of the program are the eye position and velocity as a function of time. In addition, a number of relevant data parameters are calculated directly by the program, including the initial position and velocity of the system at the start of the saccade, the apparent and relative peak saccadic velocities, and the duration and magnitude of the resulting saccade (based on 'returning velocity' considerations).

## RESULTS

Relative velocity distinguished from apparent velocity. Before presenting the primary results, it is important to distinguish between the apparent peak velocity, which is defined as the velocity with respect to the absolute zero velocity, and the relative peak velocity, i.e., the peak velocity relative to the initial velocity at the start of the saccade. The difference between the two, which is due to the velocity of the compensatory eye movement when the saccade begins, can be up to approximately 100 deg/sec, which is obviously significant relative to typical peak saccadic velocities. As a limiting case, consider the difference between the absolute and relative peak velocities for the small 'correction' saccades (Figures 1 and 2). In particular, notice that for the right-most saccade in Figure 2, which has an amplitude of about 1 degree, the 'apparent' peak velocity is -30 deg/sec, while the 'relative' peak velocity is about 90 deg/sec---quite a difference. Clearly, 90 deg/sec is the appropriate velocity for this positive going, leftward saccade. This difference, of course, is more noticeable for small saccades. Still, it is obvious that there will be significant difference between figures using the two different peak velocity definitions. To see this more explicitly, consider a typical simulation run (Figure 3). Notice that the 'against' saccade, which by definition has a negative initial velocity, has a proportionally smaller 'absolute' versus 'relative' peak velocity. Conversely, for the 'with' saccade, the 'absolute' peak velocity is proportionally larger. Notice also that there is a linear relationship between the initial velocity and the peak velocity measurements. Thus, an 'absolute' peak velocity versus

initial velocity curve can be turned into a similar 'relative' graph just by adjusting the slope in an appropriate manner.

Main effect of VOR velocity as an initial condition. The main effects of the VOR initial conditions can be seen in a qualitative manner (Figures 1, 2 and 3). The magnitudes of the saccades are strikingly different depending upon whether they are on or against the initial condition velocity set by the VOR (Figure 1). The saccades against are attenuated and the saccades with are increased. It is interesting to note that saccades against are attenuated with respect to saccades where the initial condition is at 0 degree velocity (Figure 2). Similar results are found in the simulation traces (Figure 3). These similarities between experimental and simulation traces will be shown in a more qualitative fashion in later figures. Since the simulation results were obtained with a known controller signal (CS), by comparing simulation versus experimental results insights can be gained into the mechanism(s) responsible for the observed eye interaction phenomena. Magnitude of a large number of experimental and simulated saccades following 10 degree target jump can be plotted as a function of the initial eye velocity of the VOR (Figure 4). In addition to the experimental and simulation curves, a line representing the projected system behavior if there was ideal linear summation of the two controller signals is also shown. Notice the strong correlation between the experimental and simulation data and the linear summation line. This provides very strong evidence for the linear summation hypotheses. A similarly strong correlation also existed for 5 degree target saccades (not illustrated).

Hysteresis. A secondary observation was that, in the simulation results, a 'hysteresis' loop is apparent. This 'hysteresis' behavior was due to the initial position and acceleration conditions at the start of the saccade, which should be taken as implicit parameters in the displayed curve. When a 'with' saccade is past the center 'zero' position of the eye, the initial position and acceleration conditions will both tend to oppose eye motion, the former by virtue of the system elasticity and the latter by virtue of system inertia and its resulting deceleration. Thus, this could be called a 'with-against' case. By extension there are also 'with-with', 'against-with', and 'against-against' cases. These simulation results indicate that some of the experimental scatter, which is already not very large, may be due to the initial position and acceleration conditions which are implicit parameters in the graph.

Saccadic magnitude as a function of initial condition velocity and of intended saccadic size. Averaged experimental data for the four different nominal saccade sizes is compared with the projected linear summation case (as solid line) (Figure 5). Notice that, in general, the slope of the experimental data is slightly lower. Part of this difference could be

directly due to the fact that average VOR velocity would be a better representation than the initial velocity used. Normalized magnitude is plotted versus the target magnitude so as to compare the experimental magnitude data with the expected data based on linear summation for initial conditions of 40 and 80 degrees per second (Figure 6). Again we see that linear summation accounts for a bulk of the effects. However, experimental results show less effect than that expected from linear summation. This could be due to the assumption that initial condition velocity lasts throughout the saccade; there might be changes during the saccade that would alter the summation calculations.

Saccadic velocity as a factor of initial condition velocity. Additional evidence for linear summation can be found through the analysis of initial condition velocity and apparent peak velocity relationships. Experimental data were compared with data from simulation using the hypothetical linear summation model (Figure 7). The simulation results also show the 'hystereses' effects of initial eye position and acceleration (also seen in Figure 4). Notice that the apparent peak velocity is graphed versus the initial VOR velocity. For reasons explained above, the relative peak velocity could also have been plotted. In the latter case the linear summation hypothesis would give a horizontal line. Naturally, the experimental and simulation data would change in a corresponding manner. Differences between the experimental and simulation data were partly due to this difference of reference.

Main sequence relationships. The relationship between the saccadic magnitude, duration and apparent peak velocity (Figure 8) shows further evidence of interaction. Experimental and simulation data on apparent velocity versus magnitude show different relative slopes for each saccade size, crossing the normal main sequence (solid line) with a significant shift in some cases. The amount of shift between the apparent and relative peak velocity, which corresponds to the initial condition velocity, could explain some of this shift. Mean values and 'with' and 'against' for 5 and 10 degree saccades fall on the main sequence. For 2.5 and 20 degree saccades, while the mean values fall on the main sequence, the with and against initial condition velocity set by VOR lie off the main sequence. The reason for the shift away from the main sequence might be non-main sequence effects of VOR velocity and indicates there are non-linear phenomena with these very small and very large saccade sizes.

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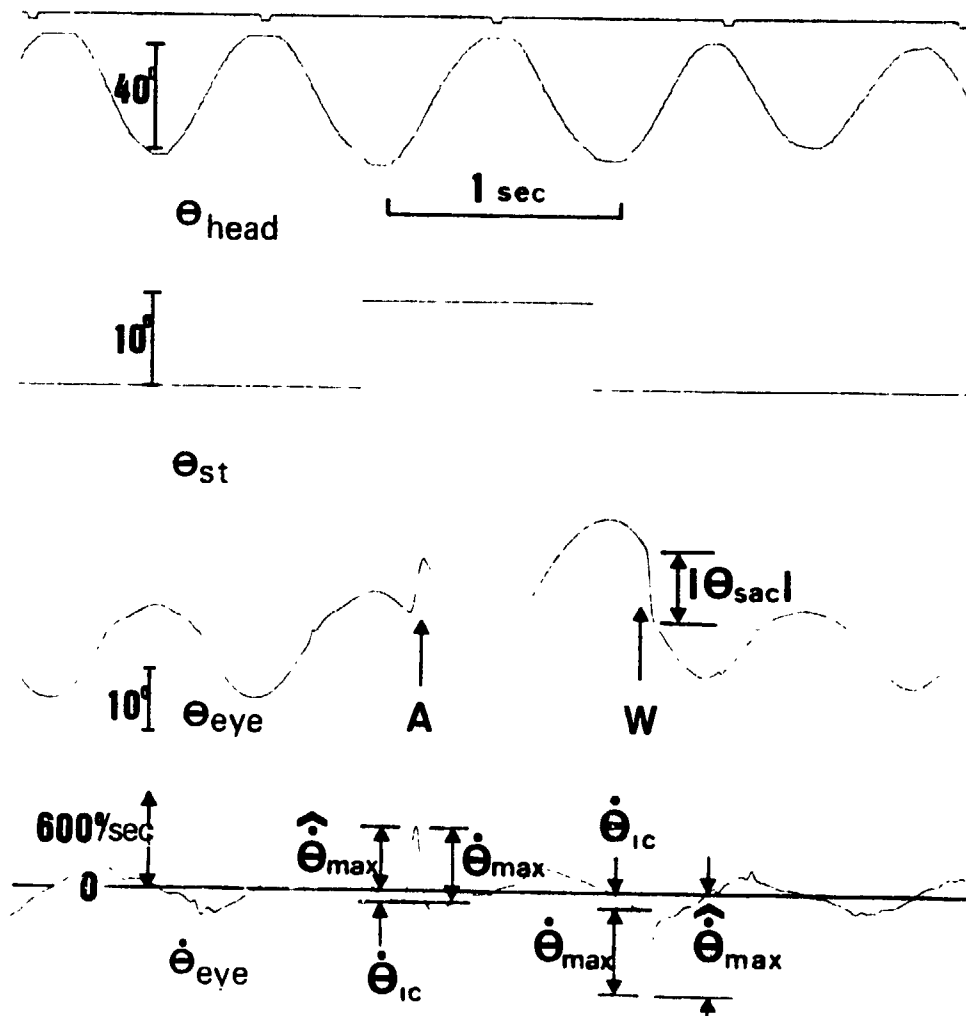


Figure 1. Recordings of head position ( $\theta_{\text{head}}$ ), visual target ( $\theta_{\text{st}}$ ), eye position ( $\theta_{\text{eye}}$ ) and eye velocity ( $\dot{\theta}_{\text{eye}}$ ). In eye position trace, A and W stand for against and with VOR, and saccadic magnitude ( $|\theta_{\text{sac}}|$ ) and duration are measured from saccadic portion. In eye velocity record,  $\dot{\theta}_{\text{ic}}$  = initial velocity of VOR eye movements at the instant of saccadic occurrence,  $\dot{\theta}_{\text{max}}$  = apparent peak velocity.

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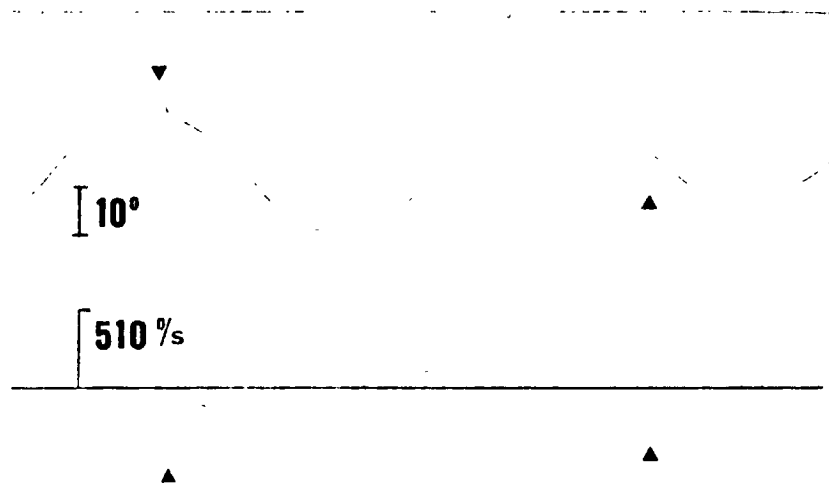


Figure 2. Eye position and velocity record illustrating apparent and relative peak velocity.

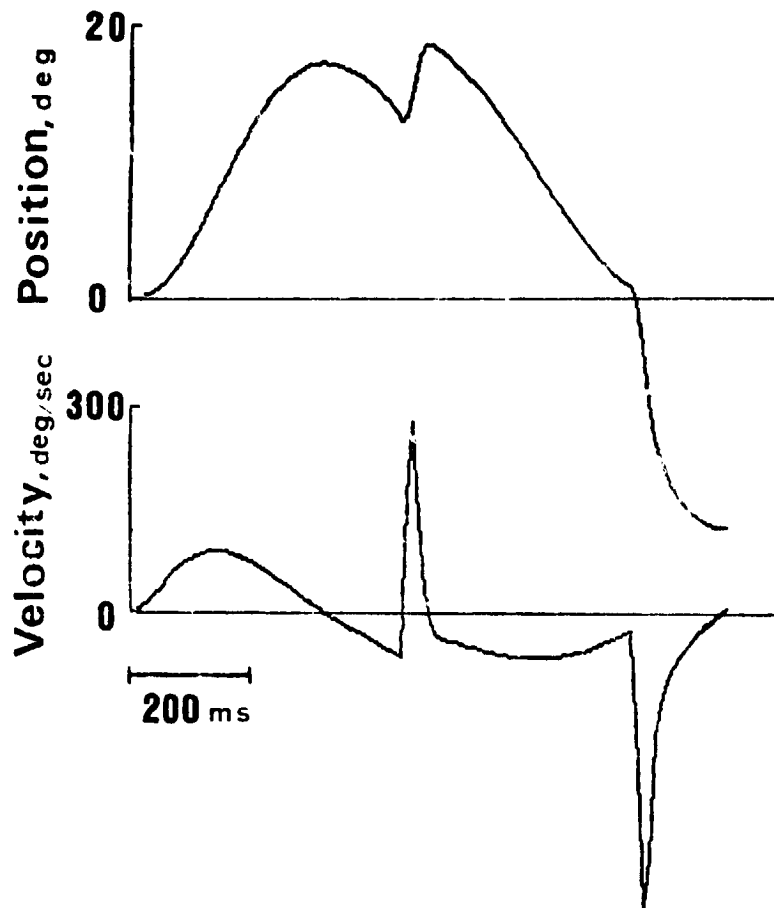


Figure 3. Computer simulation trace for 5 degree saccade and 1 Hz, 35 degree sinusoid VOR controller signal.

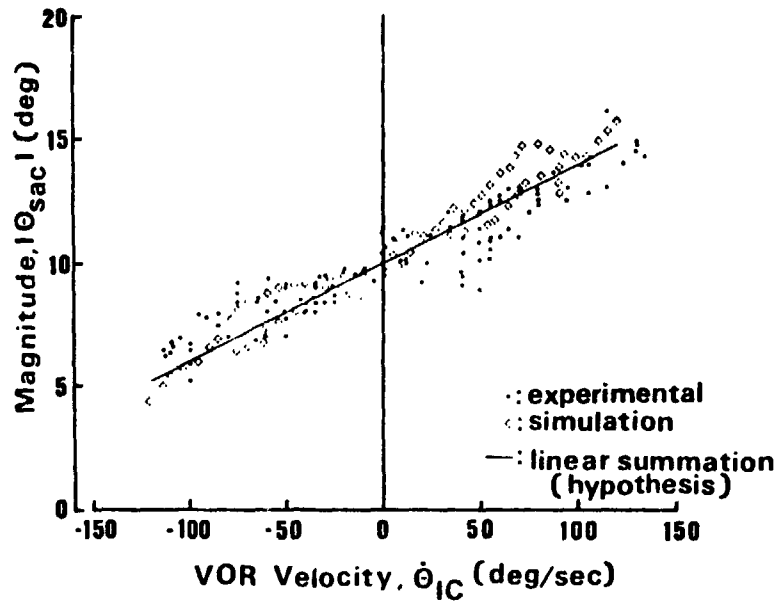


Figure 4. Magnitude vs initial condition velocity relationship for 10 degree target.

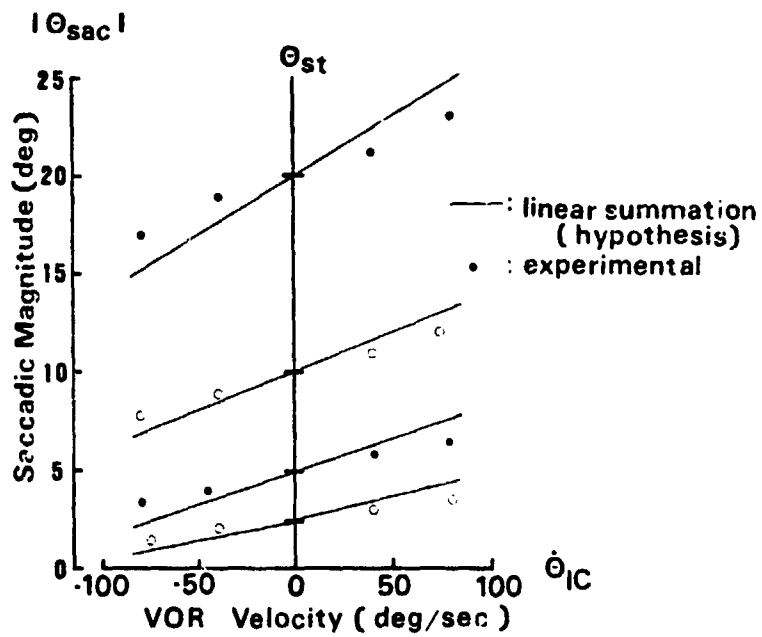


Figure 5. Averaged magnitude vs initial condition velocity relationship for four nominal target jump.

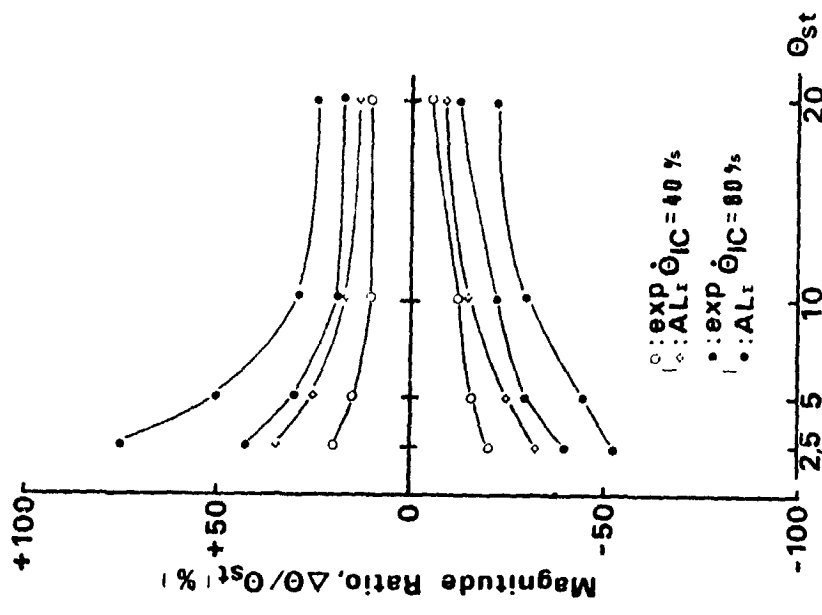


Figure 7. Apparent peak velocity vs initial condition velocity relationship for 5 degree target.

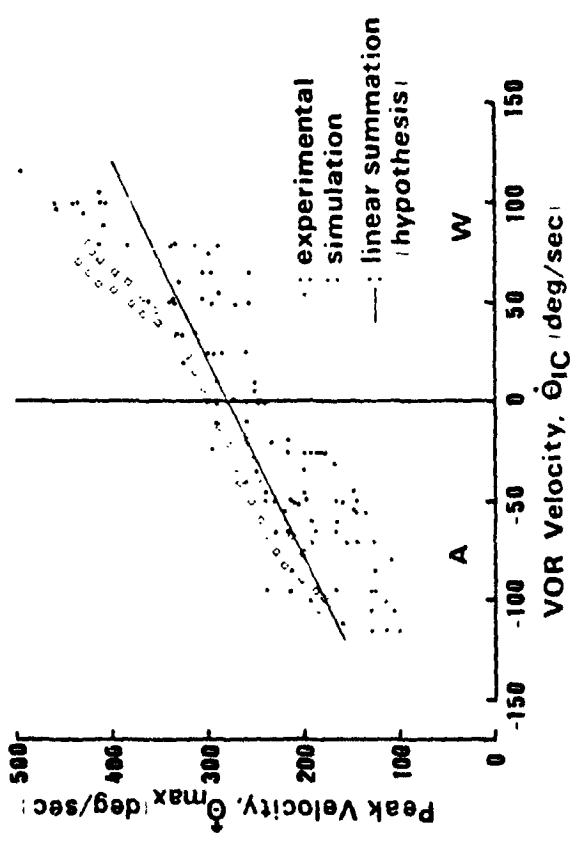


Figure 6. Normalized magnitude vs four nominal target.

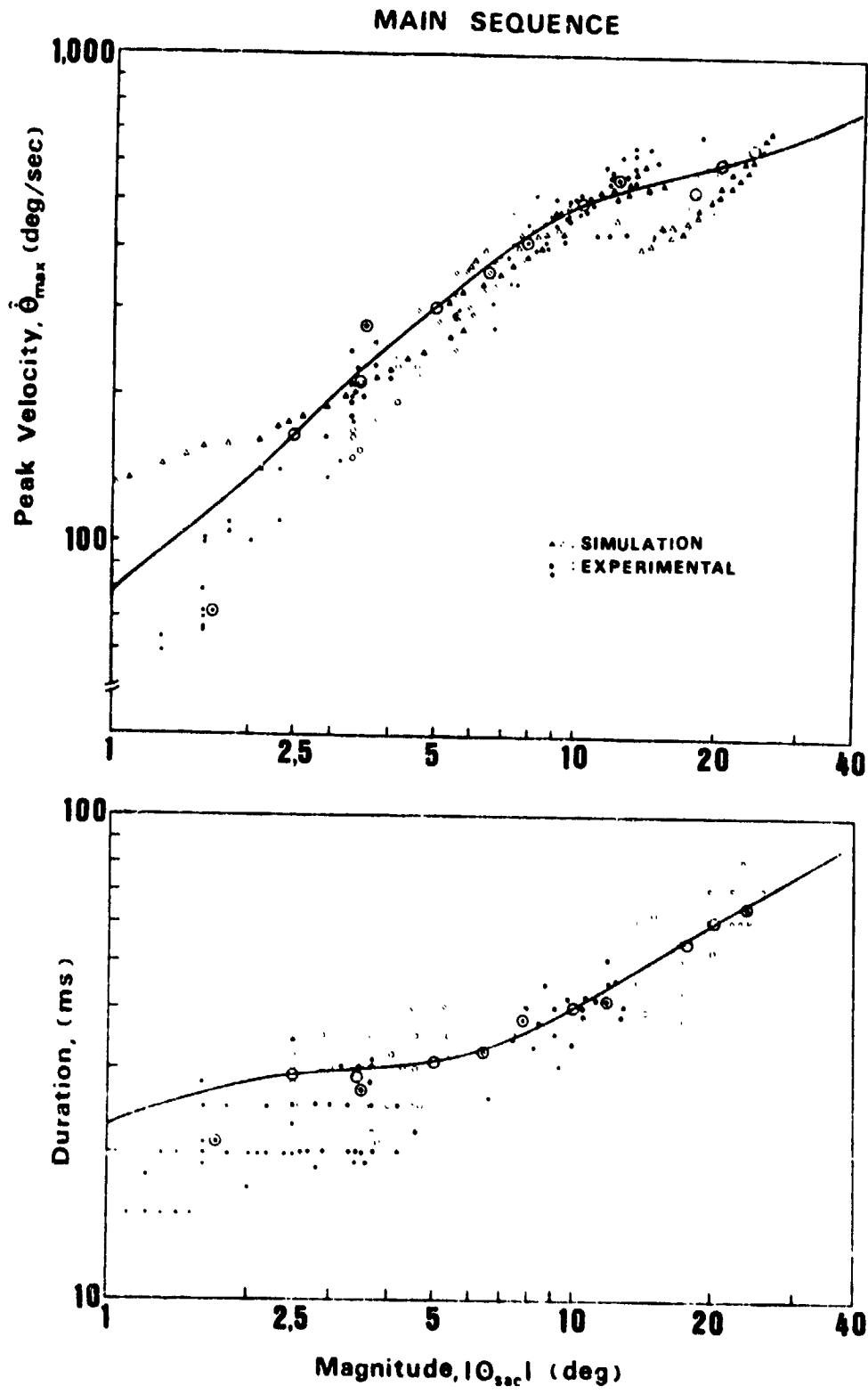


Figure 8. Main sequence relationship for apparent peak velocity, duration vs magnitude.