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DISSOCIATING THE IMPACT OF SENSORY AND MOTOR NOISE IN HUMAN SACCADES

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ABSTRACT

Eyes rarely land exactly on target. Here we investigated to which extent sensory (visual) or motor (execution) noise in neural signals determines the imprecision of saccades. We compared the variability of saccades recorded in human subjects to the predictions of a stochastic feedback optimal model of the oculomotor system. From the spatiotemporal development of the variability along the trajectories, we derived plausible estimates of the noise in sensory and motor signals.

KEY WORDS

Modeling, psychophysics, simulation, sensorimotor systems, saccades, noise.

1. Introduction

Noise in motor signals has been proposed as the main determinant of movement kinematics [1]. Motor commands would minimize the impact of this motor noise on the terminal positional variability. Moreover, optimal estimation models have suggested that noise in neural signals explains how sensory feedback is taken into account to control and refine movement [2,3,4]. Thus, deriving accurate estimates of the noise in sensory and motor signals is fundamental in assessing the validity of these models.

Recently, estimates of the sensory or motor noise explaining terminal variability of the eye position have been proposed [5], on the basis of the Harris & Wolpert model [1]. Motor noise was estimated to contribute to about 40% of the terminal saccadic variability. However, these studies have hypothesized a simple 'ballistic' feedforward control, whereas several lines of evidence show that saccades are generated in a closed loop. For instance, a pharmacologically slowed or wrongly initiated saccade eventually reaches its goal [6,7]. Furthermore, many anatomical pathways potentially subtending this feedback control have been discovered from the brain stem to the higher-order oculomotor control sites [8,9,10].

Since feedback is bound to reduce the impact of motor noise on endpoint variability, previous studies discarding it may have incorrectly estimated the impact of motor vs. sensory noise on saccadic precision.

Here we fitted a stochastic feedback optimal model to the saccades recorded in human subjects, in order to derive better estimates of neural noise in sensory and motor signals.

2. Body of Paper

MATERIAL AND METHODS

Subjects

Eight human subjects with normal or corrected-to-normal vision and no history of neurological or ophthalmological disorder participated to the study. All participants except the two authors were naive to the purpose of the study.

Setup

Subjects were seated in a dark room in front of a back-projection screen, the head immobilized by a bite bar with dental impression. Viewing distance was 50 cm. Stimuli were displayed with a 120 Hz video projector. Eye movements were recorded at 250 Hz using a head-mounted infrared eye tracking system. The task was completed in monocular vision, the left eye covered with a black patch.

Task

We analyzed center-out saccades to visual targets. Each trial started with the presentation of a fixation point displayed in front of the subject's right eye.

When ready, the subjects pressed a key that triggered the eye tracker drift correction. The a target (a filled green square, $0.61^\circ \times 0.61^\circ$) was presented, at 6, 12 18 or 24° horizontally. The extinction of the fixation point served as the go signal to initiate a saccade. In one third of the trials, the target was extinguished during the saccade; as this manipulation did not significantly affect variability, these trials were pooled with the others.

Trials were aborted if an eye blink or an anticipation was detected.

The experiment comprised 96 saccades of each amplitude, thus at least 384 trials. They were completed in two separate sessions; the longest recorded session (including aborted trials) lasted 215 trials.

Data analysis

The eye position trace was digitally differentiated, then the eye velocity trace was segmented using start and stop thresholds fixed at 10% of the peak velocity. Fatigue effects were compensated by fitting a quadratic equation to the peak velocity across each experimental session and rescaling the movement time accordingly. Saccade endpoints were centered then nasal and temporal saccades of same amplitude were pooled. A Hotelling T2 test was used to exclude endpoints at a threshold of 10^{-4} . This procedure led to the rejection of 2.8% of the data.

Then saccades trajectories were uniformly sampled at nine points either in space or time and the covariance of these sampled positions was computed.

Model

We modeled the eye as third order linear system with time constants 224, 13 and 1 ms [11, 1, 2]. Pairs of extraocular muscles were modeled as torque generators; the action of oblique muscles was not taken into account. Multiplicative Gaussian noise of SD σ_M was hypothesized in the motor signals. Additive Gaussian noise of SD σ_A was added to the motor commands to take into account the effect of extraocular muscle co-contraction. The muscle excitation signal was fed back to the controller with a delay of 20 ms, approximating the time delay of the loop linking the superior colliculus to the oculomotor nuclei [10]. Multiplicative noise (SD: σ_M) was also added to this efference copy.

An approximation of the optimal feedback controller for the eye was obtained using the procedure described in Todorov [12]. Basically this method starts by computing the optimal controller for a plant with only additive noise, then iterates to converge towards an approximation of the optimal controller in presence of both additive and signal-dependent noise. We refer the reader to ref. 12 for a detailed description. For each amplitude we determined the optimal control and estimation laws. Saccade amplitudes and durations used in the optimization procedure were set to the corresponding average in our experimental data. Then 400 trials were simulated according to the following Monte-Carlo procedure. For an actual target at T° , the planned target was randomly chosen in a Gaussian distribution centered on the average experimental endpoint for this target with scale parameter σ_V . This variability was hypothesized to include both the localization and visuomotor transformation noise. The saccade was then simulated with a time step of 1 ms, adding noise to the sensory and motor signals. The positional data was undersampled at 250 Hz (with random offset to simulation start time) and then analyzed using the same methods as for our experimental data. The quality of the fit was then assessed by computing the overall quadratic error to the subject average at mid-point and the end of the trajectories in both space and time. As the off-diagonal component (covariance between horizontal and vertical) was negligible, we only analyzed the variance along the two cardinal axes.

This procedure was repeated for various values of the free parameters, in order to compute the error landscape

and appreciate the impact of all parameters. A precise value of the global minimum was found by the Nelder-Mead simplex method as implemented in Matlab (fminsearch). This was first done for variance orthogonal to the trajectory, in order to derive the estimate of the additive noise component σ_A . Then this parameter was fixed and the procedure repeated for the horizontal variance.

RESULTS

Experimental positional variance in time and space

The endpoints of saccades of the four recorded amplitudes are displayed on Figure 1-A and B for two representative subjects. The anisotropy of the endpoint distribution is moderate, and variance is not systematically larger on the horizontal. Note that the effect of multiplicative motor noise should principally be visible along the axis of movement.

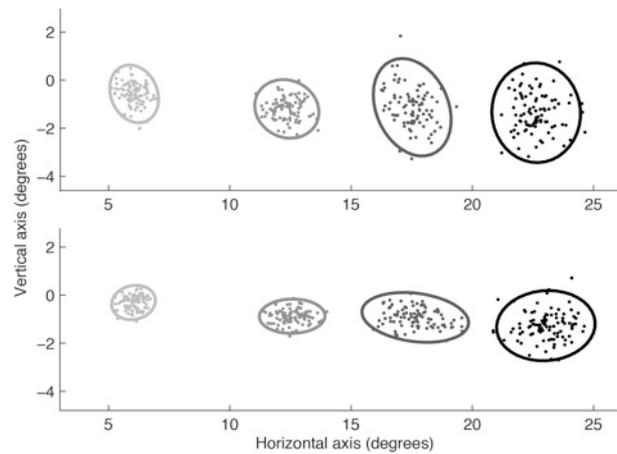
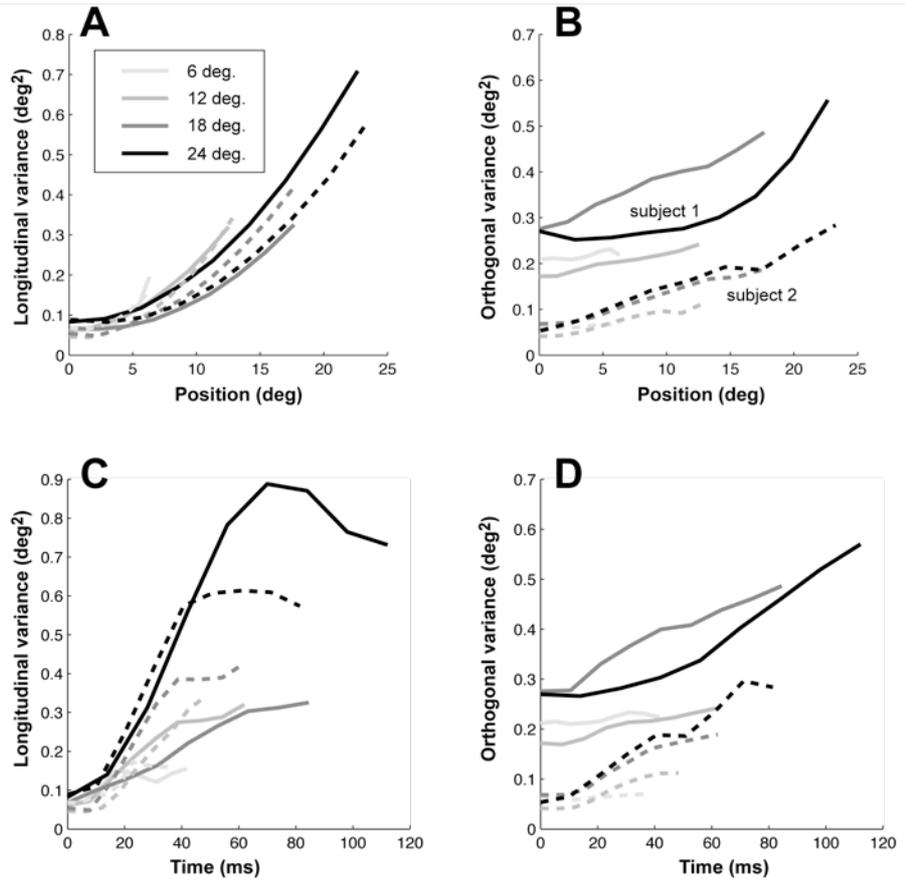


Figure 1. Endpoints of saccades for two representative subjects.

The development of the saccadic positional variability is shown on Figure 2 at nine points uniformly distributed along the trajectory in time and space. The results for the same two subjects are displayed Figure 2-A and B. It is clear from these plots that variance does not increase linearly with time as in a feedforward control system: for saccades over 6° , detrimental effects of motor noise on the initial kinematics of the saccade are mitigated later on along the movement. The orthogonal variance tends to grow more linearly, but the population average also shows a saturation (see Figure 4).

Figure 2. Variance along the trajectory for two representative subjects. A, C: longitudinal variance as a function of position along the trajectory in space (A) or time (C). B, D: Same for variance orthogonal to the movement. Solid: subject 1, dashed: subject 2



Model trajectories

The trajectories generated by the model are represented on Figure 3-AB for two of the four saccadic amplitudes we recorded. Noise parameters were set to the best fitting values (see below). The feedback control law produces saccades with correct kinematics; for a comparison the saccades of a human subject are shown on Figure 3-CD.

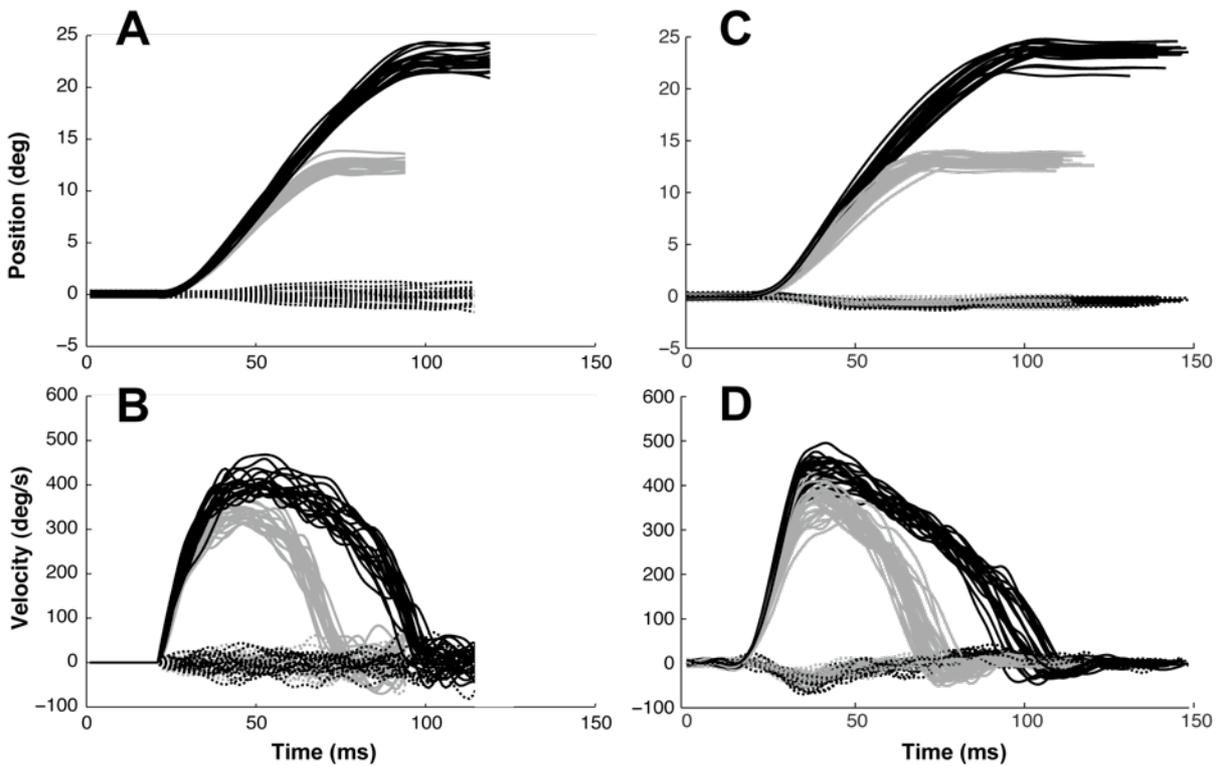


Figure 3. Displacement (A) and velocity (B) of the model trajectories. Saccades of subject 1 are shown in C, D for comparison.

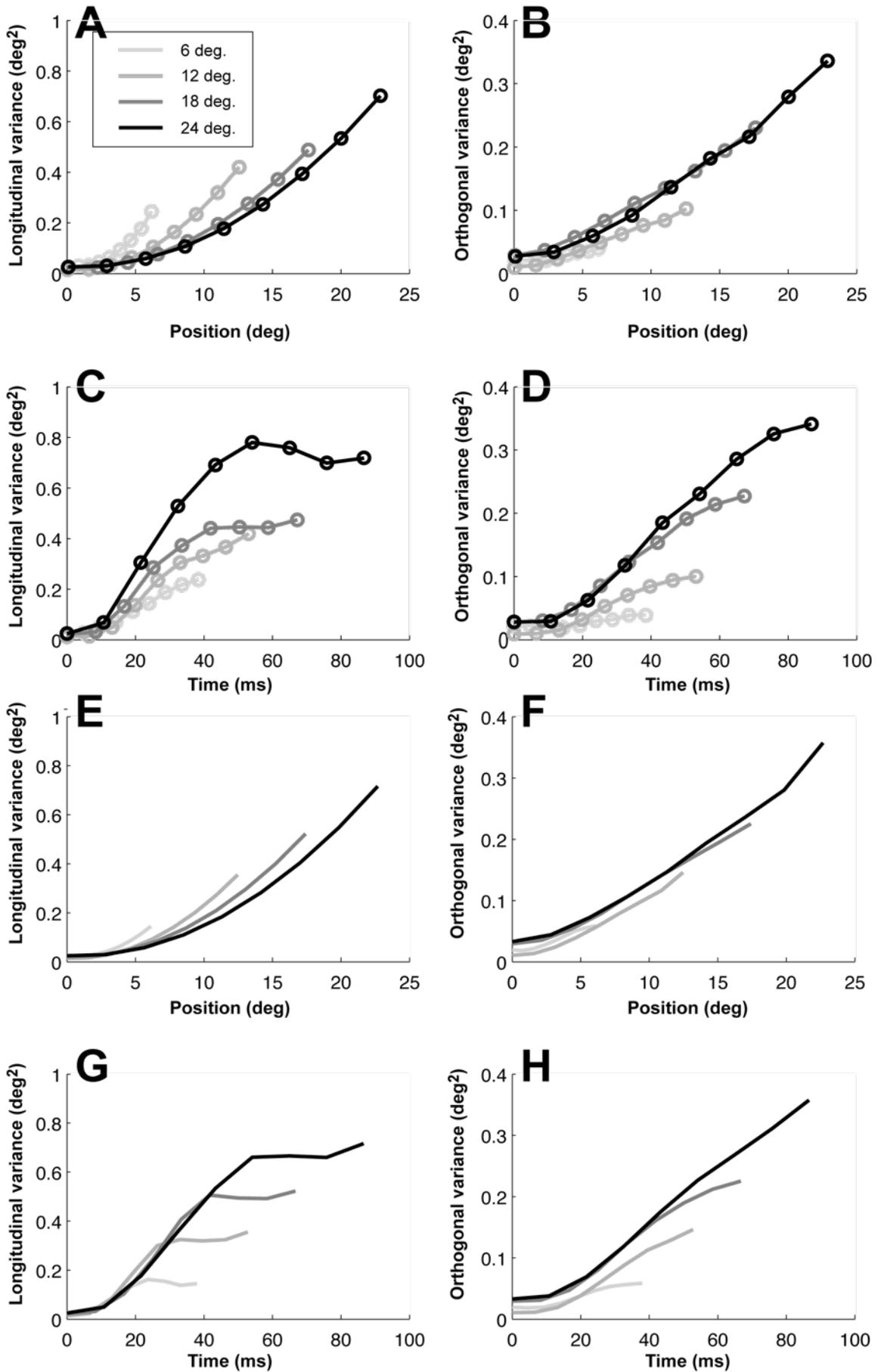


Figure 4. Development of the positional variability in time and space: A-D: Average experimental values for 8 subjects (measurement variability removed). E-H: Model results. Shading identifies the saccade amplitude.

Parameter estimation

Measurement noise was estimated with the covariance between saccade start and end points; this value (logically stable across saccadic amplitudes, average $\sigma^2_{Ex}=0.038$, $\sigma^2_{Ey}=0.064$) was first removed from the positional variance. Noise in visual and motor neural signals was then estimated by fitting the model to the average human data. Visual noise was modeled as multiplicative noise: $V_{noisy}(t) = V(t) \cdot (1 + \sigma_V \varepsilon(t))$, where ε is a white noise process of unit variance. Since there is not a very good agreement in the literature as regards the value of σ_V , we preferred to let this parameter free. Motor noise was assumed to be a combination of multiplicative and additive noises: $M_{noisy}(t) = M(t) \cdot (1 + \sigma_M \varepsilon'(t)) + \sigma_A \varepsilon''(t)$. The noise in the efference copy (internal feedback) was assumed multiplicative with σ_M . To avoid local minima and get a feeling for the incidence of the three parameters σ_M , σ_A and σ_V , we performed an exhaustive search on a grid sampling the parameter space. Then we ran a simplex minimization that converged towards the following parameter values: $\sigma_V=0.028$, $\sigma_M=0.20$, and $\sigma_A=5 \cdot 10^{-3}$.

Model variance in time and space

The spatial and temporal development of the variance along the trajectory for the model simulations as well as for the average subject is shown on Figure 4. The model is able to capture most of the time course and space distribution of the positional variance found in the experimental data. Here we used three free parameters for the optimal stochastic feedback controller to correctly reproduce both saccadic mean trajectories as well as their variance.

3. Conclusion

Our experimental results complement and extend those by van Beers [5] and West et al. [13]. This characterization of the development of positional variance across time and space allowed us to derive estimates of neural noise in sensory and motor signals in the oculomotor control system. We believe these estimates to be more accurate since they take into account both more data than endpoint scatter and the existence of a feedback loop. A key point here is that contrary to feedforward models, here 'apparent noise' (from the global trajectory average) is correlated in time since part of this 'noise' is actually feedback corrections to previous noise in afferent or efferent signals.

Trials with or without intrasaccadic display of the target did not exhibit any difference in the spatiotemporal development of variance; thus visual feedback during the saccade was not considered. It may be used to control longer saccades [14].

The model fit is globally adequate; the positional variability at mid-point of the movement duration is slightly overestimated though. We are currently investigating whether this can be due to trial-to-trial variability in command (or muscle) gain. It should also be acknowledged that these estimates were derived

from average variability; still more precise values (and their distribution in the population) can be obtained by individually fitting the model to each subject.

We observed that our estimation of the visual noise is quite robust to the details of the model (delays, feedback noise different from motor command noise...); our simulations indicate that visual noise markedly dominates motor noise for large saccade amplitudes ($>16^\circ$) whereas the contrary is true for short amplitudes. This is at variance with van Beers [5] who concluded to a fairly constant variance ratio. Experimental verification of this prediction is under way.

These estimates of neural noise magnitude will allow us quantitative tests of whether visual feedback is optimally integrated with internal model prediction in saccadic eye movements. A possible role of proprioception could emerge from these experimental results; further modeling studies will take this additional sensory input into consideration.

Acknowledgements

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