NEURAL CORRELATES OF FORWARD AND INVERSE MODELS FOR EYE MOVEMENTS: EVIDENCE FROM THREE-DIMENSIONAL KINEMATICS

A Brief Communications by Fatema F. Ghasia, Hui Meng, and Dora E. Angelaki

Presentation by Karen Batch, Amin Edraki, and Alec Langlois

GOAL OF THE PAPER

Neuroscientists have conceived of two models to account for motor control

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Their representation in the neurons is unclear, but there are potential candidate cell types

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This paper seeks to further elucidate the neuron cell types that represent the two models

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They examine the correlation between neural signal and physical movement to identify cell types with each model

KEY TERMS

- Internal Model
  - Forward model
  - Inverse model
- Efference Copy
- Burst-Tonic Cells
- Eye-Head Neurons
- Listing’s Law
- Half-Angle Rule

INTERNAL MODELS

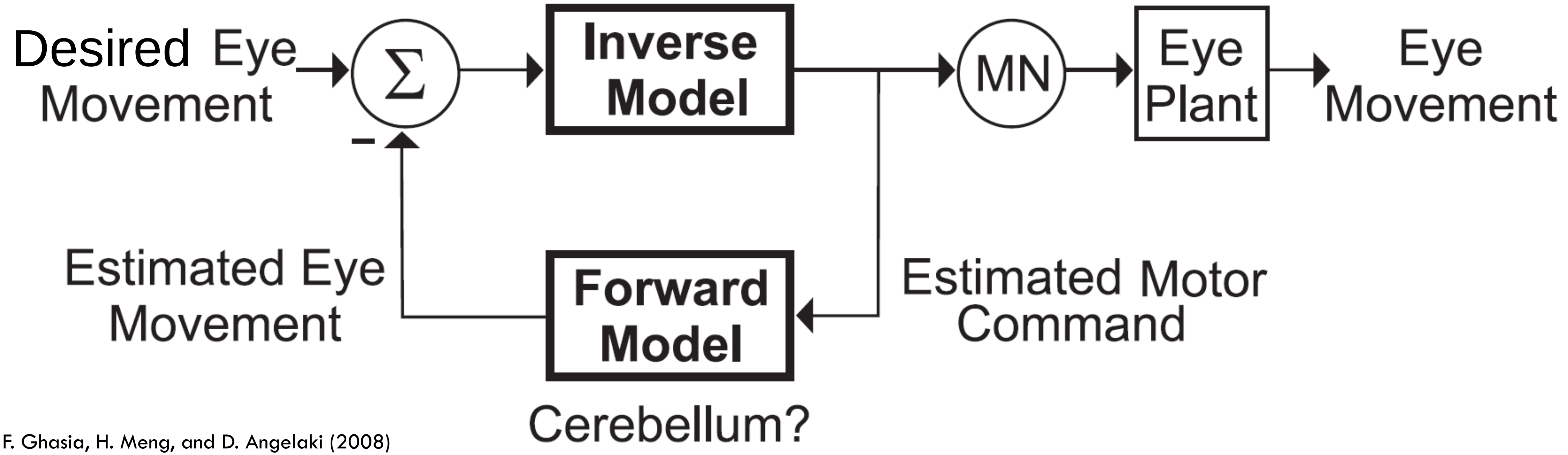
Forward model

Predicts the consequences of the motor command on behaviour by constructing an efference copy of the actual movement

Inverse model

Thought to convert desired action into appropriate motor commands

INTERNAL MODELS



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EFFERENCE COPY

- An internal copy of an outflowing, movement-producing signal generated by the motor system
- Can be collated with the sensory input that results from movement, enabling a comparison of actual and desired movement
- Together with internal models, efference copies can serve to predict the effects of an action

BURST-TONIC (BT) CELLS

Neurons found throughout the brainstem thought to represent the output of the inverse model of a motor command

BT cell dynamics during pursuit and the vestibulo-ocular reflex (VOR) are identical to those of extraocular motoneurons

EYE-HEAD (EH) NEURONS

A premotor cell type that is the target of Purkinje cell inhibition from the cerebellar flocculus/ventral paraflocculus

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Exhibit properties that could be consistent with the half-angle rule

LISTING'S LAW

The eye does not achieve all possible 3D orientations

All eye positions can be reached by starting from one specific "primary" reference orientation

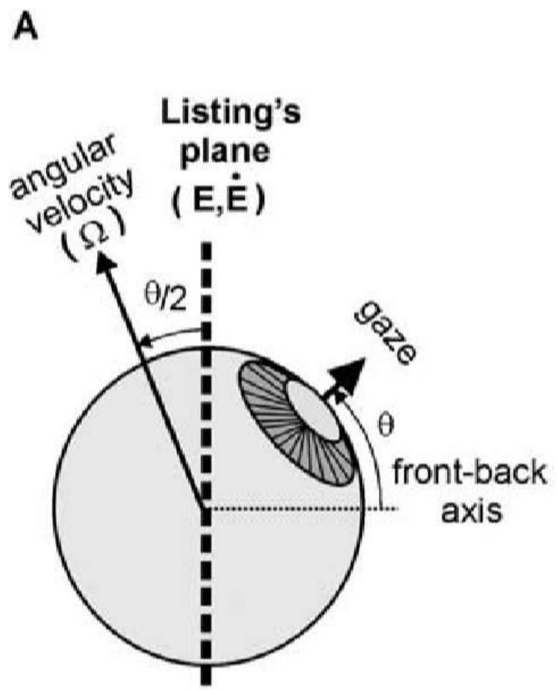
The eye then rotates about an axis that lies within the plane orthogonal to the primary orientation's gaze direction (Listing's Plane)

HALF-ANGLE RULE

The eye must rotate about an axis of rotation that tilts out of Listing's Plane

Such axes lie in a specific plane associated with a non-primary position

This plane's normal lies halfway between the primary gaze direction and the gaze direction of this non-primary position



F. Ghasia and D. Angelaki (2005)

MATERIALS AND METHODS

Data

Collected from five monkeys (2 maccaca fascicularis and 3 maccaca mulatta)

Electrode Penetrations

Nucleus prepositus hypoglossi

Medial/superior vestibular nuclei

Interstitial nucleus of cajal

Cells scattered between the abducens and oculomotor nuclei

MATERIALS AND METHODS

Cell classification

- BT
- EH
- PVP

Main protocol

- Horizontal and vertical pursuit at different eccentricities

Saccades and fast phases removed

Neural activity recording during roll VOR

MATERIALS AND METHODS

- Response gain: $\frac{spike/sec}{degree/sec}$
- Plotting response gains as a function of target eccentricity
  - The slope: how does the firing rate change as a function of eye position
- Comparison of these slopes to the “predicted slopes”
  - Predicted slopes: slope of eye velocity as a function of target eccentricity×sensitivity of the cell to torsional eye velocity ($\frac{spike/sec}{degree/sec}$)

MATERIALS AND METHODS

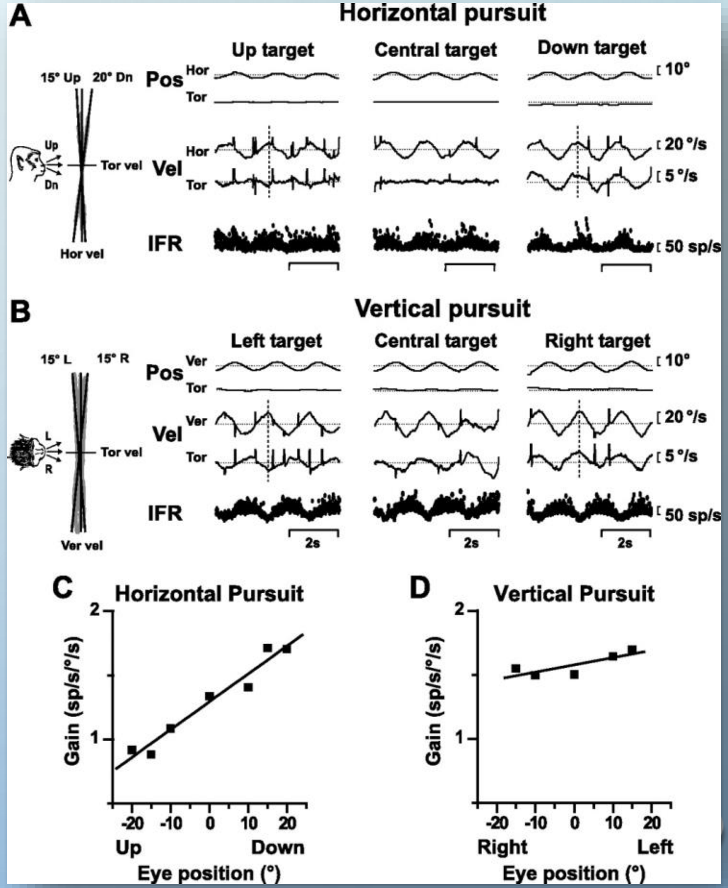
Kruskal-Wallis Test: determines whether the medians of two or more groups are different

Wilcoxon Test: It will test the hypothesis that the scores for two variables were drawn from the same distribution

Spearman Rank Correlation: "assesses how well the relationship between two variables can be described using a monotonic function"

MAIN FINDINGS (BACKGROUND)

- RESPONSE TO PURSUIT WAS RECORDED IN 125 NEURONS, CLASSIFIED AS EH, PVP, AND BT
  - NEURONS FROM THE PREPOSITUS/VESTIBULAR NUCLEI, INTERSTITIAL NUCLEUS OF CAJAL, AND PERIOCULOMOTOR REGION, WITH REGIONS DIFFERING SOMEWHAT IN COMPOSITION
- CONFIRMED TORSIONAL VELOCITY DURING PURSUIT OF ECCENTRICALLY-POSITIONED TARGETS
- SLOPE OF RESPONSE GAINS VS. EYE POSITION DESCRIBES CHANGE IN PEAK FIRING RATE AS A FUNCTION OF EYE POSITION



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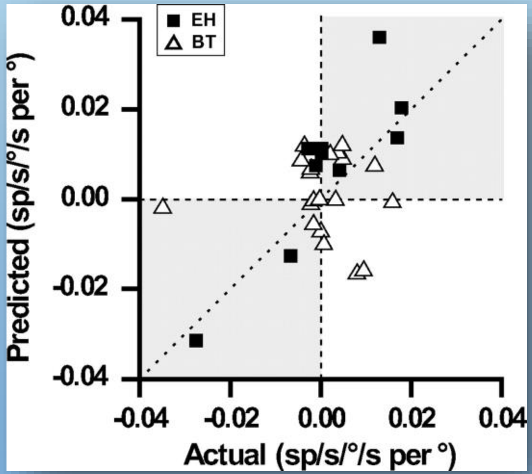
MAIN FINDINGS



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BT cell firing rates showed no correlation with predicted eye position

- Indicates low sensitivity to torsional eye velocity, does not code for half-angle rule, likely part of inverse model

EH Cell firing rates showed correlation with predicted eye position

- They are sensitive to torsional eye velocity, may code for half-angle rule, may be output of forward model

WHY IS THIS SIGNIFICANT?

PROPOSED THAT SIMILAR TO MOTONEURONS, BT CELLS REPRESENT THE OUTPUT OF THE INVERSE MODEL

UNLIKE MOTONEURONS, BT CELLS DO NOT PRODUCE THE EYE MOVEMENT

THE PRIMARY FUNCTION OF BT CELLS IS TO DISTRIBUTE AN EFFERENCE COPY OF THE MOTOR COMMAND ELSEWHERE IN THE BRAIN

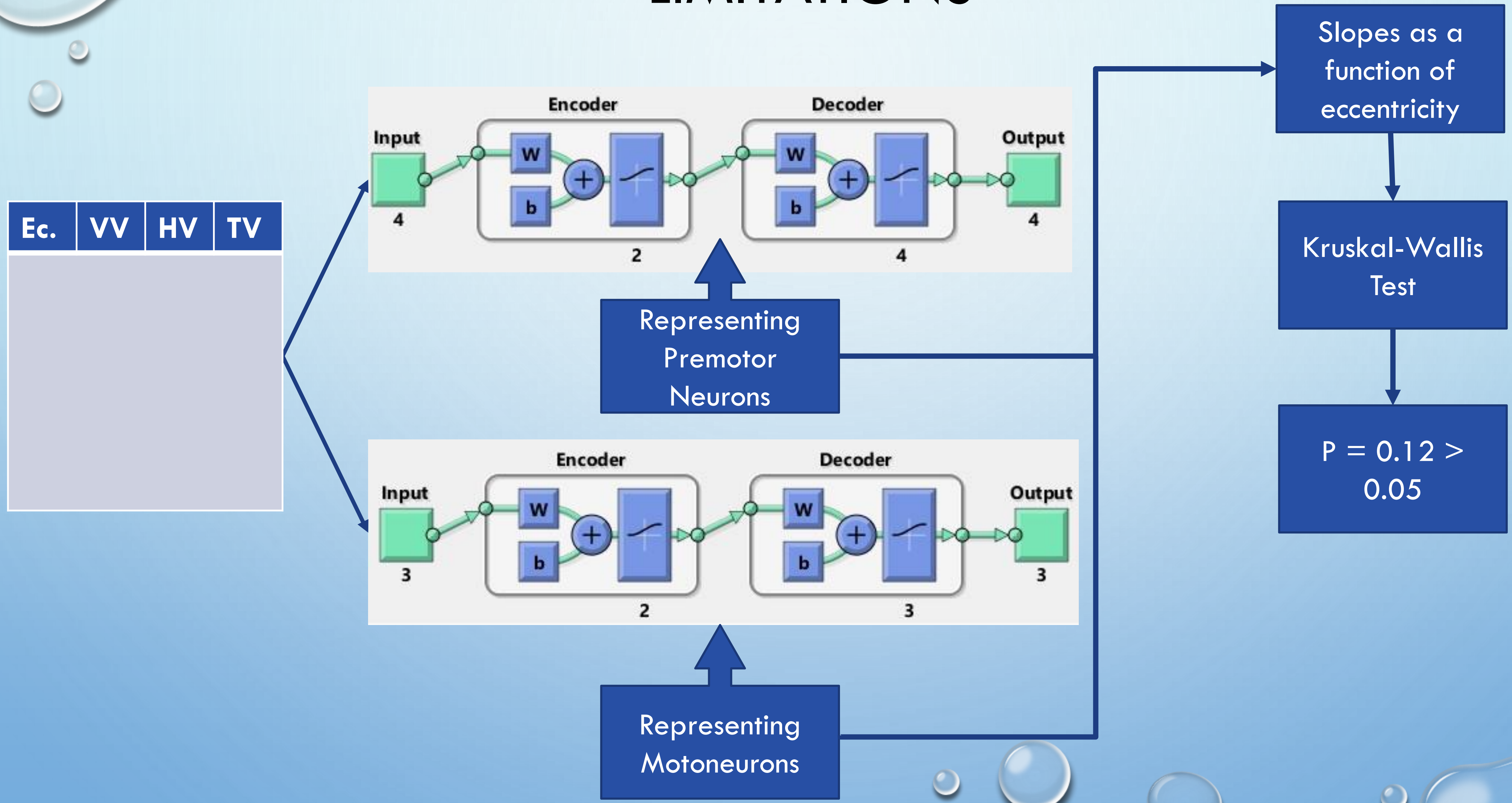
WHY IS THIS SIGNIFICANT?

The findings showing that EH responses might be consistent with coding the half-angle rule during pursuit provide strong support that the cerebellum might be constructing a forward model

This forward model is important for

- Refinement of the motor command
- Motor adaptation
- Appropriate 3D ocular kinematics

LIMITATIONS



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FUTURE DIRECTIONS

- ✓ Evaluate the hypothesis for non-half-angle behaviour — i.e. Rotational VOR
- ← Role of cerebellar-target neurons in relation to this hypothesis

QUESTIONS?