Discriminating external and internal causes for saccade initiation in freely flying Drosophila

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2m diameter

0.5 Straw height
Saccades

“body saccades”

smooth turn
What triggers saccades?

Saccades as obstacle avoidance:

(fly-centric view)
What triggers saccades?

Saccades as obstacle avoidance:

(fly-centric view)

orientation vs. time in tethered experiment

Fruit flies saccade “spontaneously” even with featureless stimuli
(Drosophila: ~0.3 saccades/sec)
What triggers saccades?

What triggers (this) behavior?

- internal states (metabolic/neural)
- stateless “random” decisions
- external visual stimulus
What triggers saccades?

What triggers (this) behavior?

- internal states (metabolic/neural)
- stateless “random” decisions
- external visual stimulus

Not distinguishable if the internal states are not observable

$\xi(t)$

internal state

“random” number generator

“random” sequence
What triggers saccades?

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What triggers saccades?

What triggers (this) behavior?
- internal states (metabolic/neural)
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- external visual stimulus

Summary of our analysis
- We will bound the contribution of the various factors:
  - 90% visual stimulus
  - 10% internal states + stateless random decisions

- We will show that the visual stimulus can be compressed down to a 1D feature z.
Nomenclature

- **states**
  - external, observable (spatial configuration)
  - internal, unobservable

- **stimuli**
  - all information available for decision making

- **features**
  - “features”: behaviorally relevant functions of the stimulus

- **behavioral models**
  - causal explanation of behaviors given states and features

- **behaviors**
  - observable behaviors
Behavioral pathway studied in this work

- states
  - stimuli
    - features
      - behavioral models
        - behaviors

- internal
  - hunger
    - visual stimulus
      - feature “z”
        - rate-variant Poisson processes
          - landing

- external
  - spatial configuration
    - odor
      - ?

- ?
  - saccades
We assume that the stimulus can be compressed down to a 1D feature $z$.

The functions $f_R$ and $f_L$ give the instantaneous rates $r_L(t)$ and $r_R(t)$ as a function of the feature $z$.

Saccade events are generated based on the instantaneous rate by interacting Poisson processes.

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$$r_L(t) = f_L(z(t))$$

$$r_R(t) = f_R(z(t))$$

$z$: relevant feature of the stimulus that explains the behavior.
We assume that the stimulus can be compressed down to a 1D feature $z$.

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Saccade events are generated based on the instantaneous rate by interacting Poisson processes.

The left saccade rate is $r_L(c) = f_L(z(c))$ and the right saccade rate is $r_R(c) = f_R(z(c))$.

$z$: relevant feature of the stimulus that explains the behavior

c: spatial configuration
Model

\[ \xi(t) \]

other unmodelled processing

interacting Poisson processes

\[ r_L(t) = f_L(z(t)) \]
\[ r_R(t) = f_R(z(t)) \]

left saccade rate \( r_L(c) = f_L(z(c)) + r_0 \)
right saccade rate \( r_R(c) = f_R(z(c)) + r_0 \)

c: spatial configuration
Inference

Optimization problem

given: - the average saccading rates \( r_L(c) \) and \( r_L(c) \)

find: - the best 1D feature \( z(c) \)
- the feature-to-rate functions \( f_R \) and \( f_L \).

Model

left saccade rate \( r_L(c) = f_L(z(c)) + r_0 \)
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\( c \): spatial configuration
Predictions of simple functional models

**Functional model**

Simple thresholding + noise

Predicted event rate as a function of feature $z$

$$y(t) \xrightarrow{\text{stimulus}} \text{visual processing} \xrightarrow{\text{feature}} z(t) \xrightarrow{\text{thresholding}} \text{rate} \xrightarrow{\text{stochastic trigger}} \text{event}$$

$$f_r(z) \quad f_L(z)$$
Predictions of simple functional models

Functional model

Simple thresholding + noise

Predicted event rate as a function of feature z

$y(t)$
stimulus

visual processing

$z(t)$
feature

thresholding

rate

stochastic trigger

event

rate $f_R(z)$

rate $f_L(z)$

feature $z$
Predictions of simple functional models

Functional model

Simple thresholding + noise

Parallel random trigger generation

Predicted event rate as a function of feature z
Predictions of simple functional models

**Functional model**

Simple thresholding + noise

Parallel random trigger generation

Unmodelled feature

Predicted event rate as a function of feature $z$
Results
Results

observed event rates as a function of estimated $z$
Results

observed event rates as a function of estimated $z$

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**Results**

<table>
<thead>
<tr>
<th>Feature</th>
<th>$z$ (a.u.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Event rate $r^k_3$ (sac./s)</td>
<td></td>
</tr>
</tbody>
</table>

- ... + random process
- ... + another feature $z'$

thresholding + noise
observed event rates as a function of estimated $z$

Results

thresholding + noise

$\mathbf{f}_L(z)$

... + random process

$\mathbf{f}_R(z)$

... + another feature $z'$

Event rates $r_i^k$ (sac./s)

$z$ (a.u.)
Results

observed event rates as a function of estimated $z$

- Event rates $r^k(z)$
- $f_L(z)$
- $f_R(z)$

Baseline rate = ~0.4 saccades/sec

Symmetry

Thresholding + noise

... + random process

... + another feature $z'$
Results

observed event rates as a function of estimated $z$

Results

$f_L(z)$

$z$ (a.u.)

thresholding + noise

93% of the data falls on a monotone function

... + another feature $z'$

Baseline rate $= \sim 0.4$ saccades/sec

$z$ (a.u.)

(same data, with error bars)

... + random process

Event rates $r^k_i$ (sac./s)

Event rates $r^k_i$ (sac./s)
Feature field

observed event rates as a function of estimated $z$

$z$ as a function of configuration

Event rates $r^k$ (sac./s)

$z$ (a.u.)
Comparison with another saccade detector

Geometric detector, working with $x,y$ data

Alternative detector, working with angular velocity
We assume that this feature can be obtained by a linear function of the optic flow:

\[ z = \int_\theta A(\theta) \cdot \text{OF}(\theta) \, d\theta \]

and then we fit \( A(\theta) \).
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**estimated feature field**

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**least squares solution**

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**norm regularization**

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**derivative regularization**

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**curvature regularization**
From feature field to computational structure

Estimated feature field

Assuming bilateral symmetry and harmonic function
From feature field to computational structure

Estimated feature field

Assuming bilateral symmetry and harmonic function

Setting to zero the contribution of the caudal region:
From feature field to computational structure

Estimated feature field

Assuming bilateral symmetry and harmonic function
Evidence of inverse optomotor response?

These results match with the results in Tammero et al. 2004; but found from free-flight data rather than direct stimulation.
Conclusions

What triggers saccade?
- Internal states 10% (0.4 saccades/sec)
- Stateless random process
- Visual stimulus 90%

What function of the visual stimulus?
- In 93% of this environment, the effect of the stimulus can be compressed to a 1D feature $z$.

What is this feature?
- It is well approximated by a linear function of the optic flow (but this step is not well conditioned)

$$z = \int_{\theta} A(\theta) \cdot OF(\theta) \, d\theta$$