Neural Basis of Saccade Selection & Control

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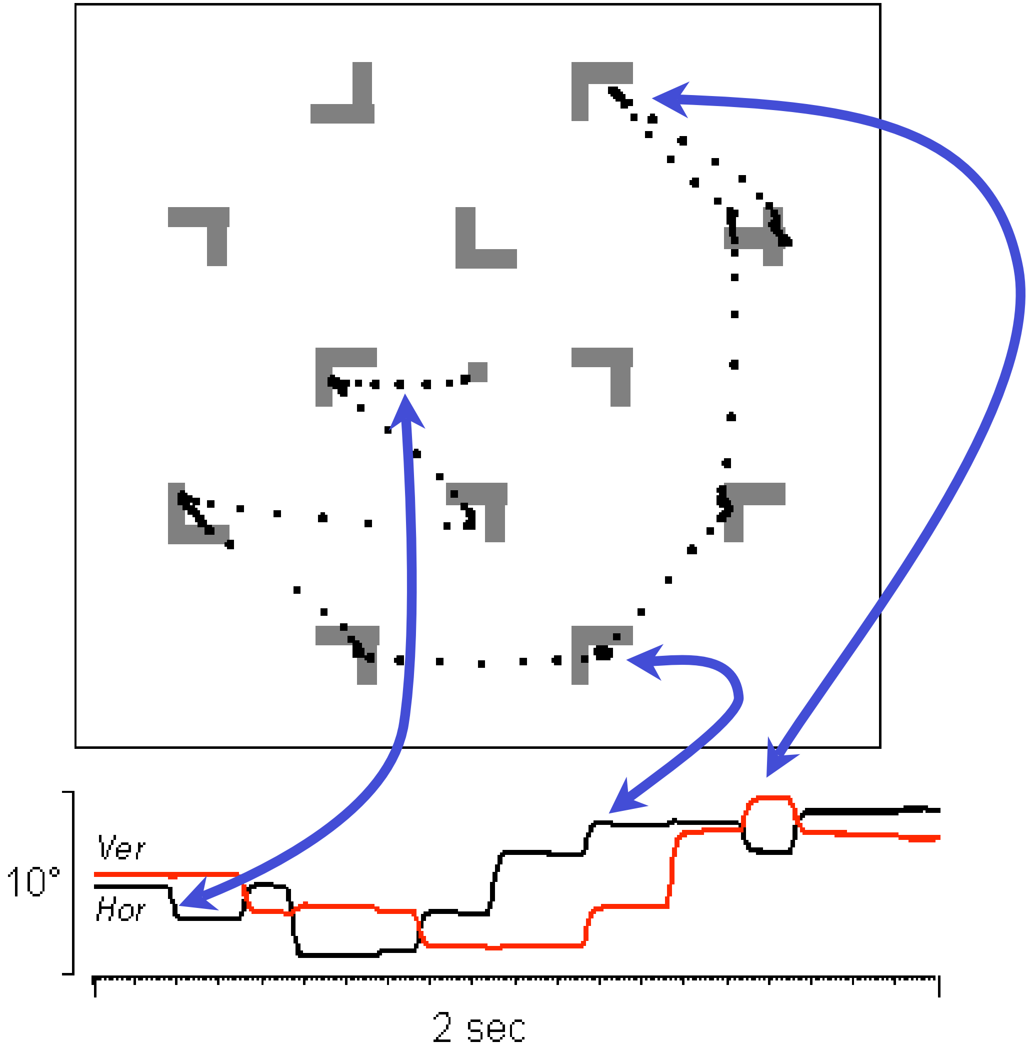
Borsellino College, Trieste, October 2004

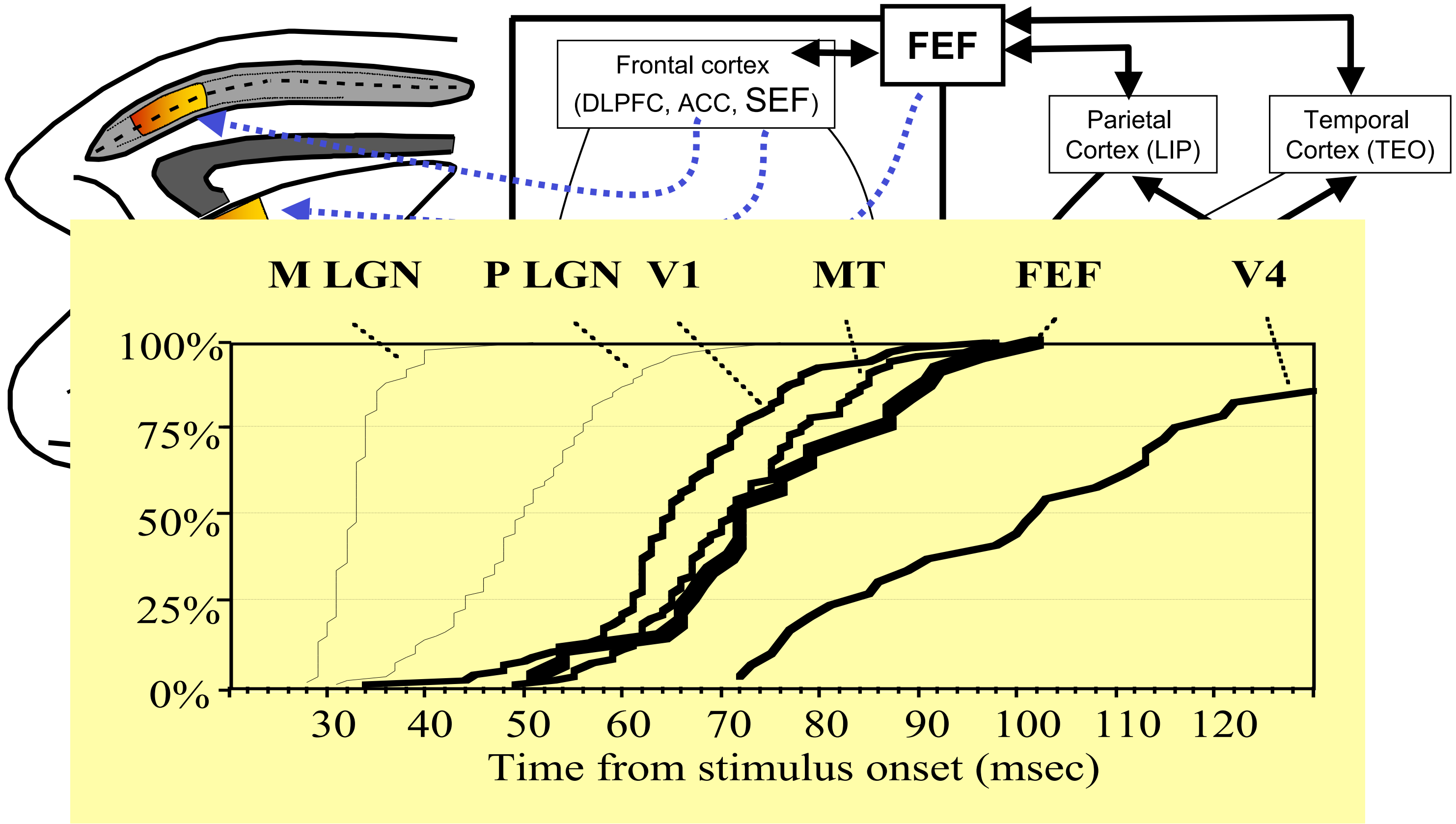
How does the brain choose where to look?

How does the brain control when to move?

How does the brain correct errors?

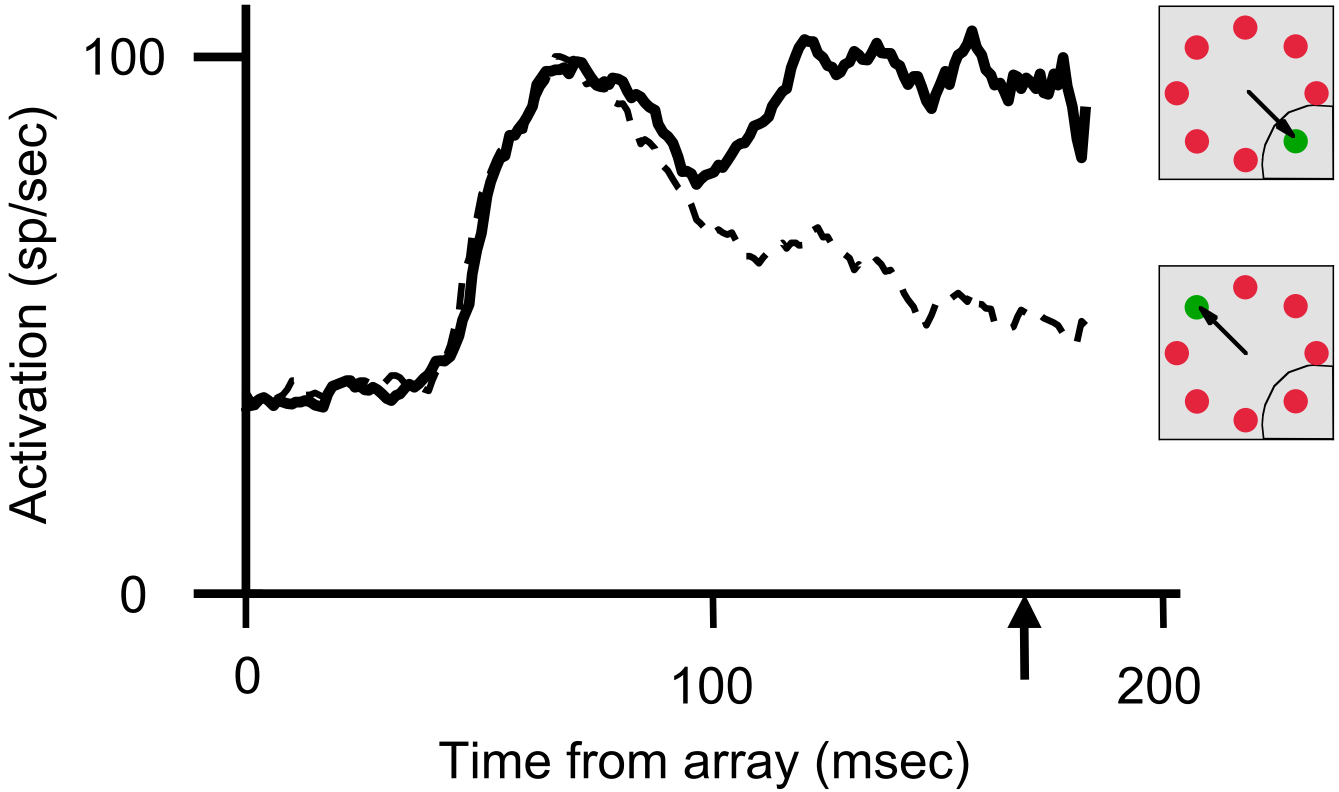


Saccades are produced by a distributed network



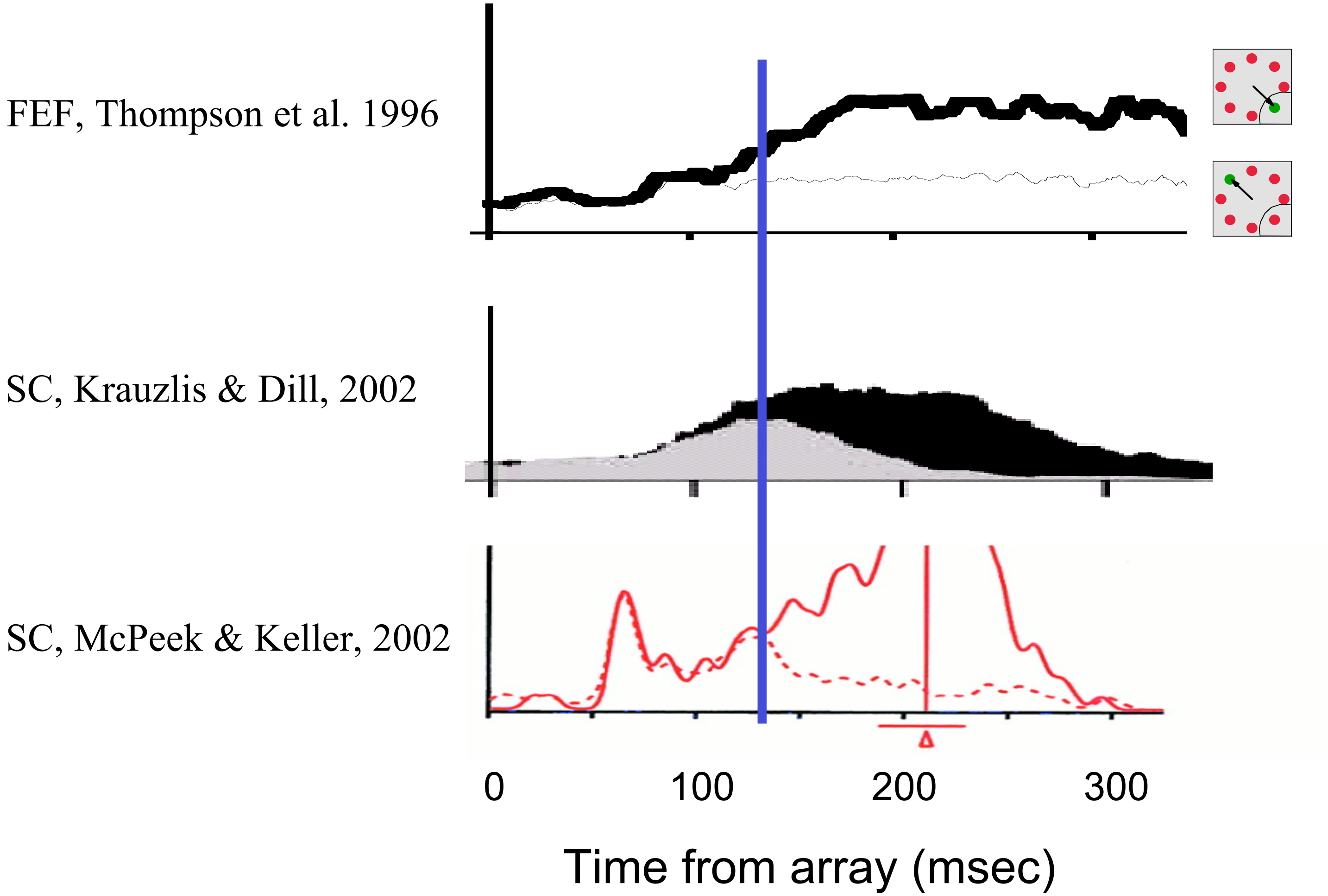
Munoz DP, Schall JD (2003) Concurrent distributed control of saccade initiation in the frontal eye field and superior colliculus. In *The Oculomotor System: New Approaches for Studying Sensorimotor Integration*. Edited by WC Hall, AK Moschovakis. CRC Press, Boca Raton, FL. Pages 55-82.

FEF neurons select the target during singleton visual search



Thompson, Hanes, Bichot, Schall (1996) Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search. *Journal of Neurophysiology* 76:4040-4055.

Target selection happens in a network including at least FEF, SC, LIP, thalamus and basal ganglia

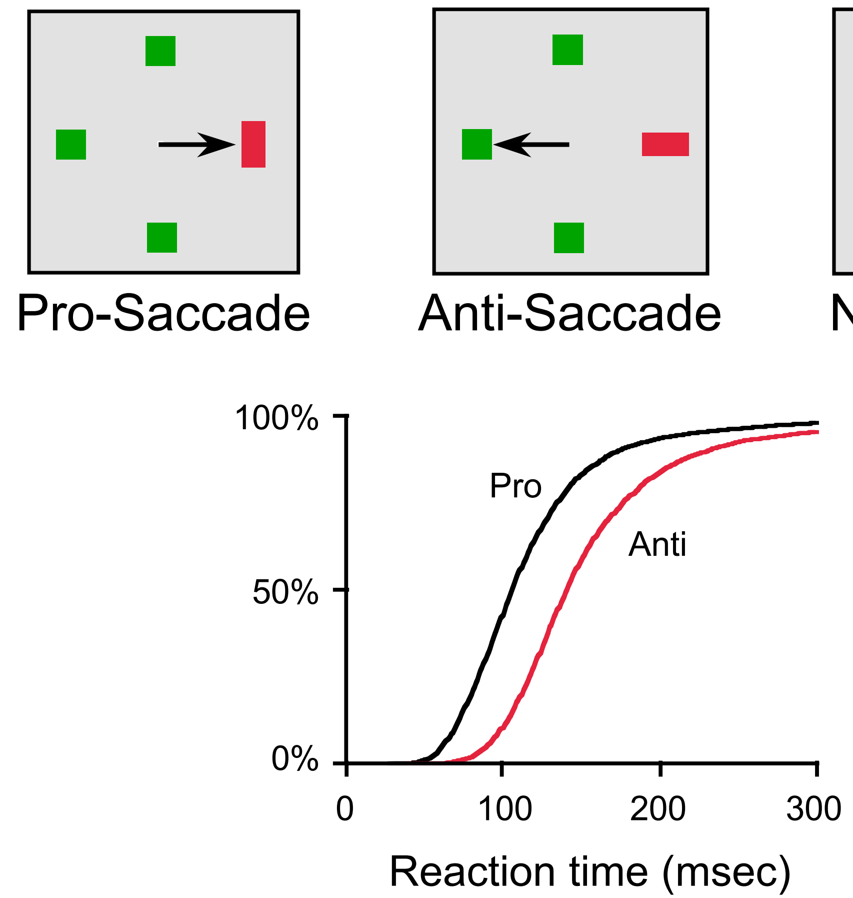


What is this selection process?

- Visual selection (attention)
- Saccade preparation

Experimental dissociations necessary to answer

An explicit dissociation of stimulus selection and saccade selection.



Sato & Schall, (2003). *Neuron* 38:637-648

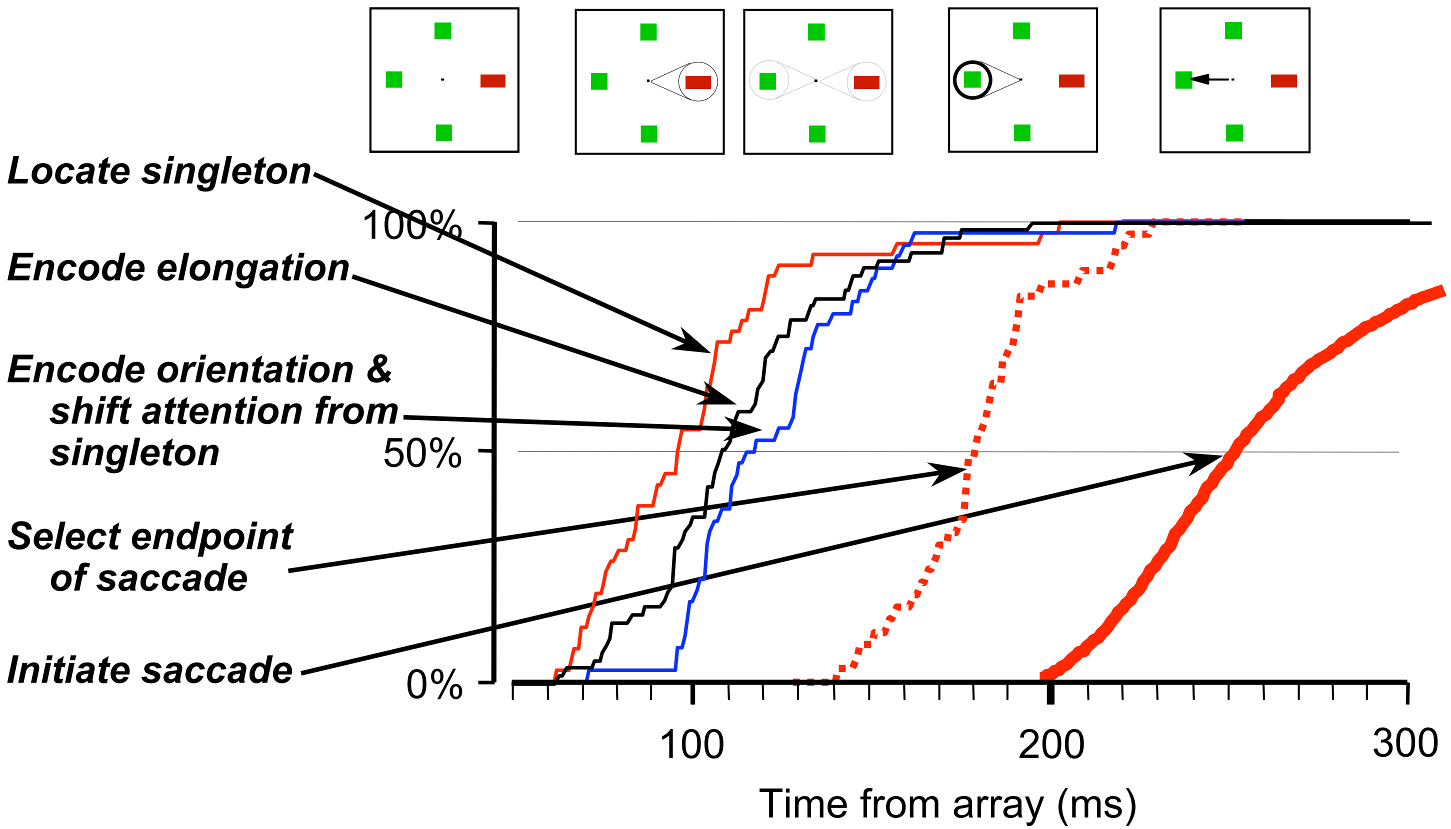
This task requires

- localization and categorization of the singleton
- selection of the endpoint of the saccade
- preparation and execution (or not) of the saccade.

Can these processes be dissociated?
Are they instantiated by different neurons?
Do they occupy different amounts of time?

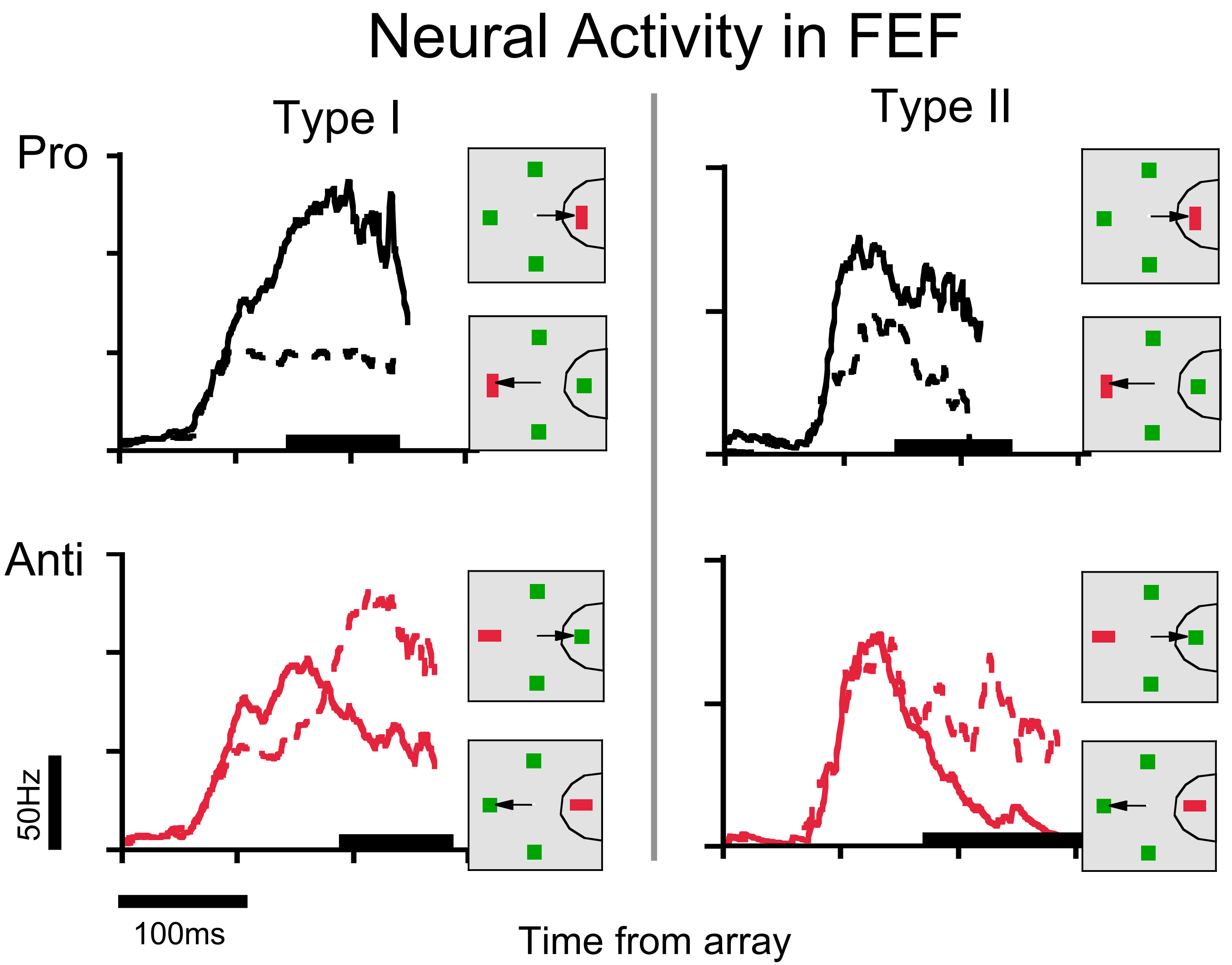
> "[Since] we cannot break up the reaction into successive acts and obtain the time of each act, of what use is the reaction time?"
> – R.S. Woodworth (1938) in *Experimental Psychology*

Consider the sequence of events in an anti-saccade trial

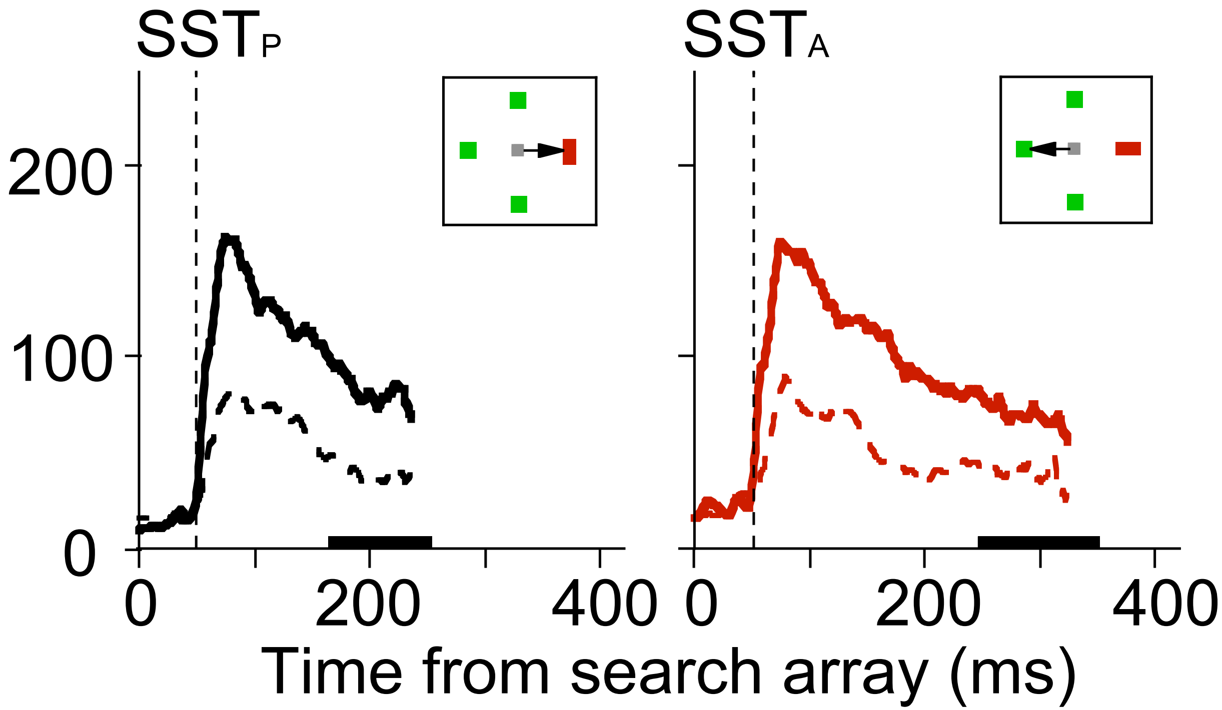


Do FEF neurons select the singleton in anti-saccade trials?

Most do, but some don’t.

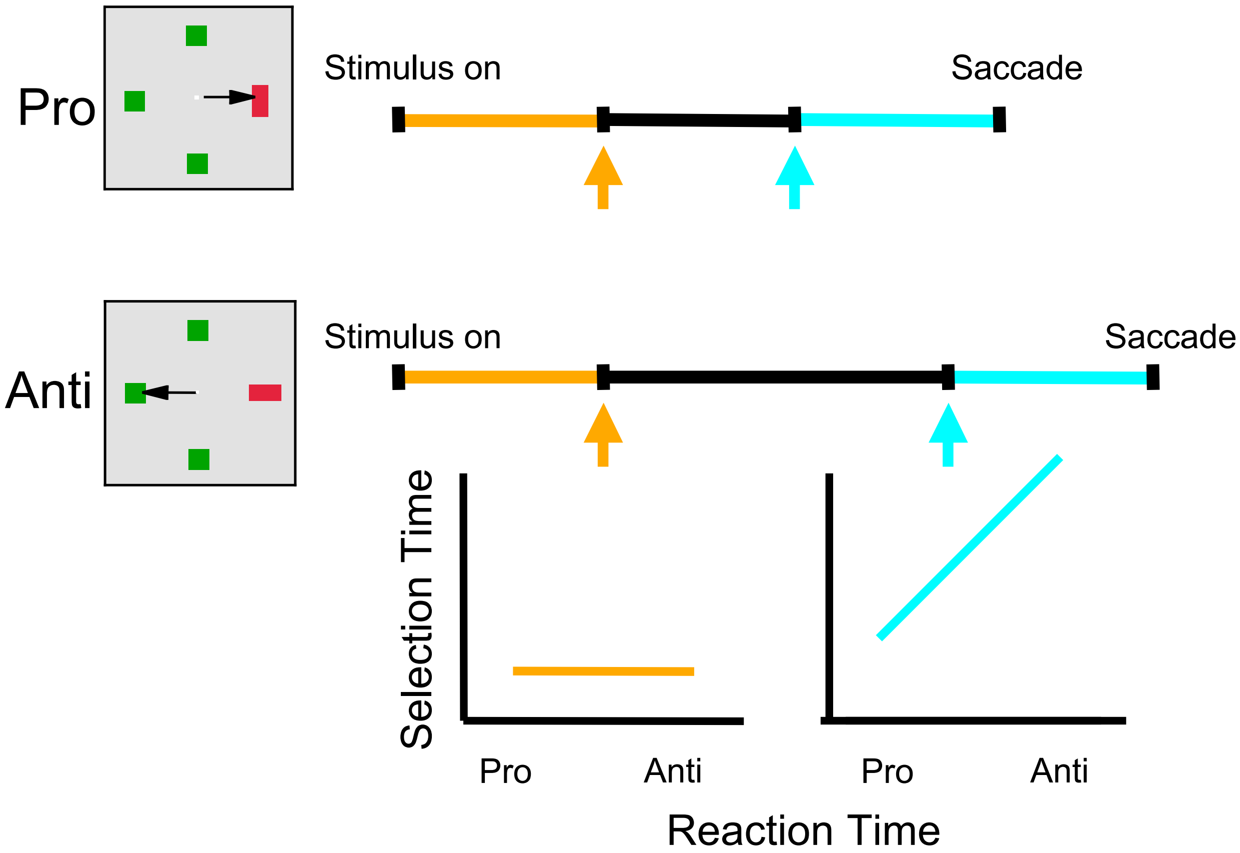

Neural Activity in FEF
Type I
Type II
Pro
Anti
50Hz
100ms
Time from array

A few FEF neurons select the singleton until the saccade in anti-saccade trials.



How does the stimulus-response compatibility affect the selection time of FEF neurons

Stages of processing



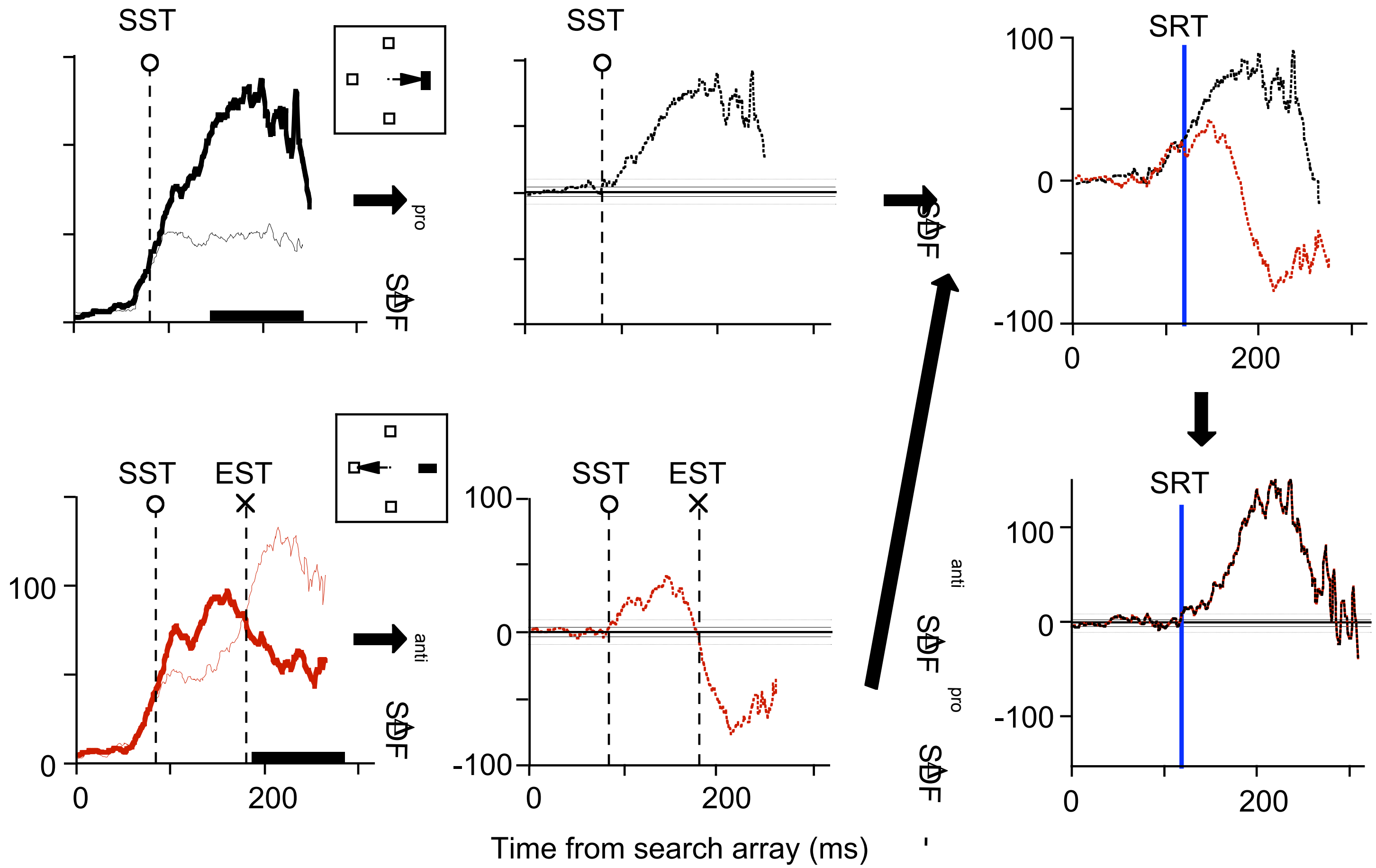
Measure the following times:

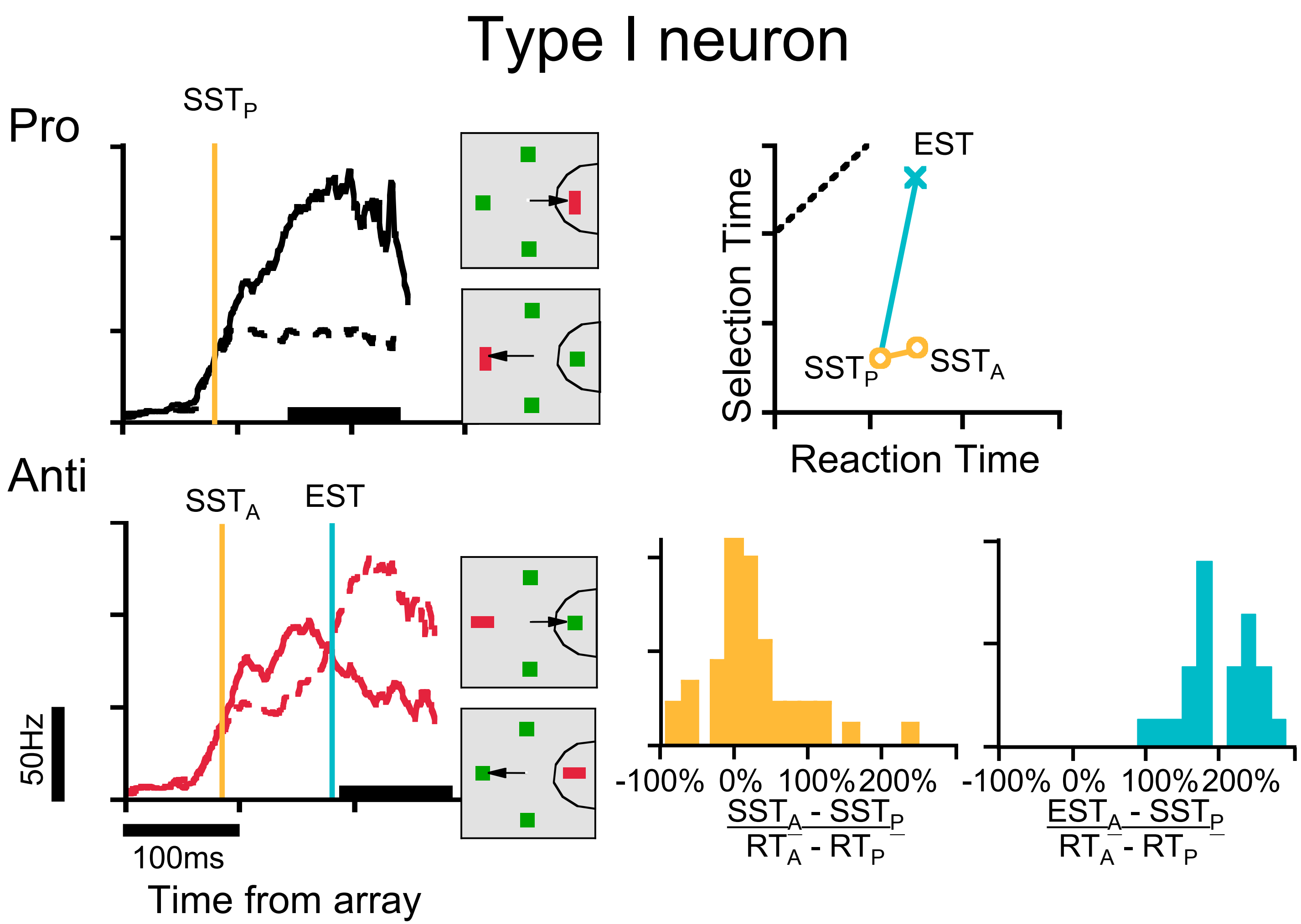
Singleton Selection Time (SST) - When activity representing the singleton exceeds activity representing the distractors.

Endpoint selection time (EST) - When activity representing the endpoint of the saccade exceeds activity representing the singleton.
EST measures the end of a transition.

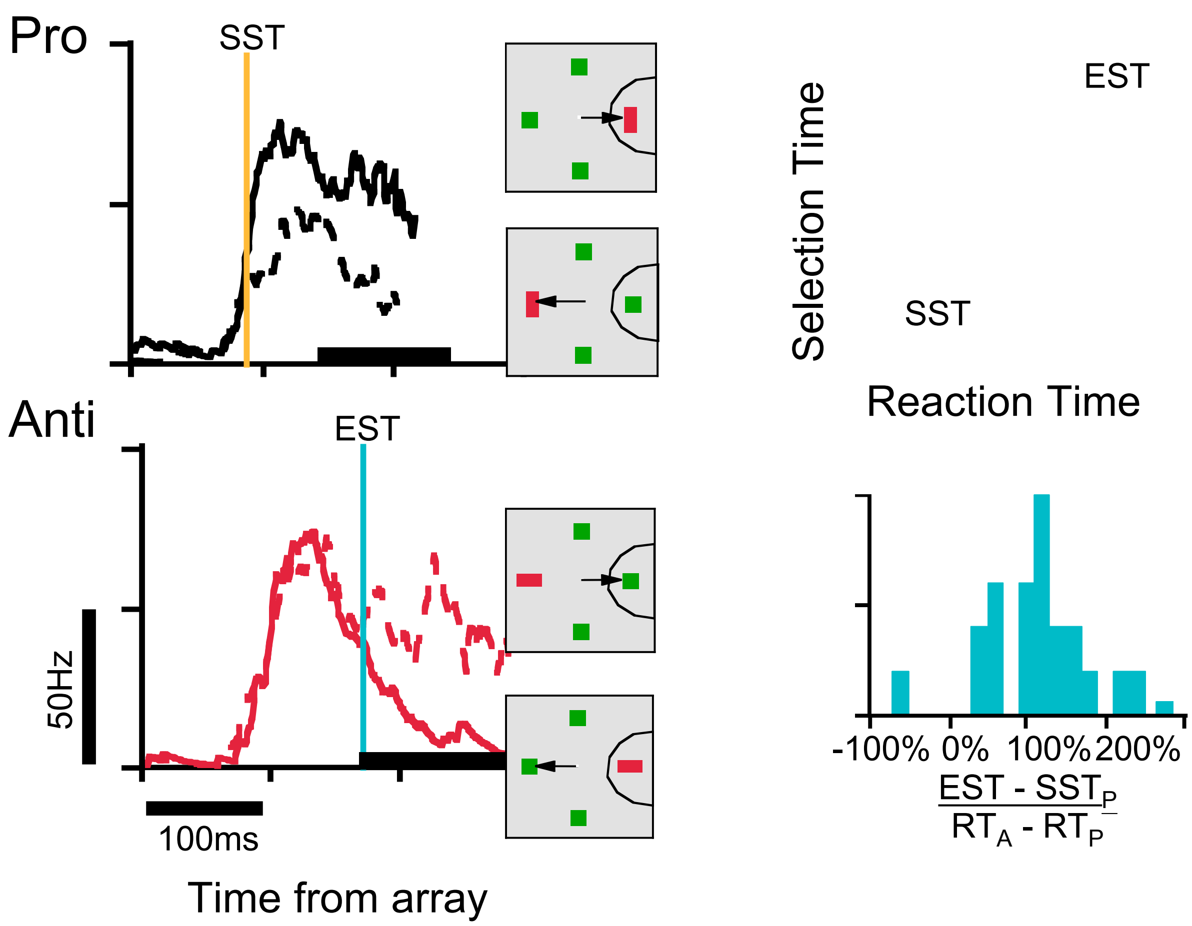
Stimulus response time (SRT) - When singleton shape is encoded and the mapping rule first influences activity.

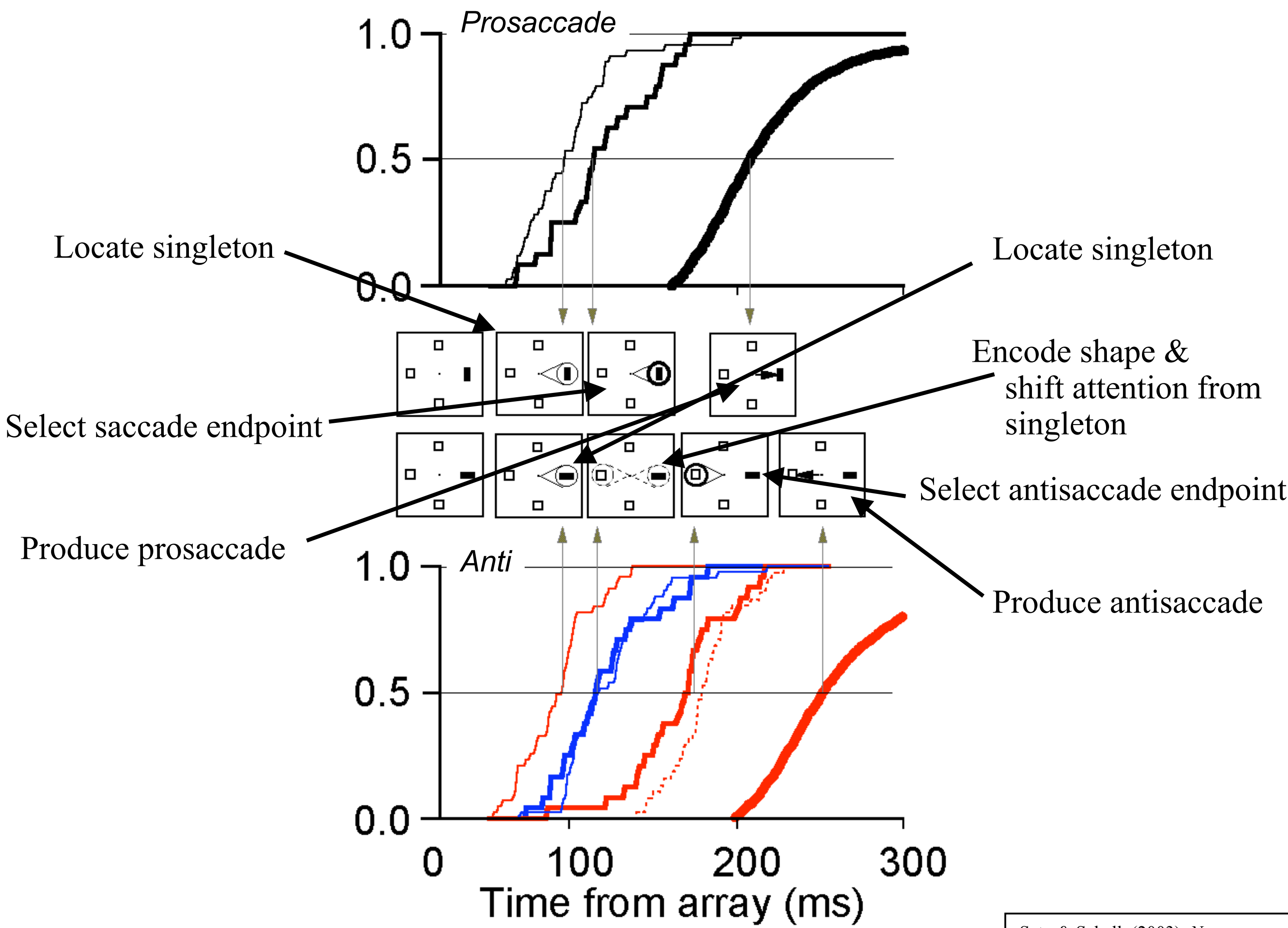
Measurement of SST, EST and SRT




Type I neuron
Pro
SST_P
Anti
SST_A
EST
50Hz
100ms
Time from array
Selection Time
Reaction Time
SST_P
SST_A
EST
-100% 0% 100% 200%
$\frac{SST_A - SST_P}{RT_A - RT_P}$
-100% 0% 100% 200%
$\frac{EST_A - SST_P}{RT_A - RT_P}$

Type II neuron



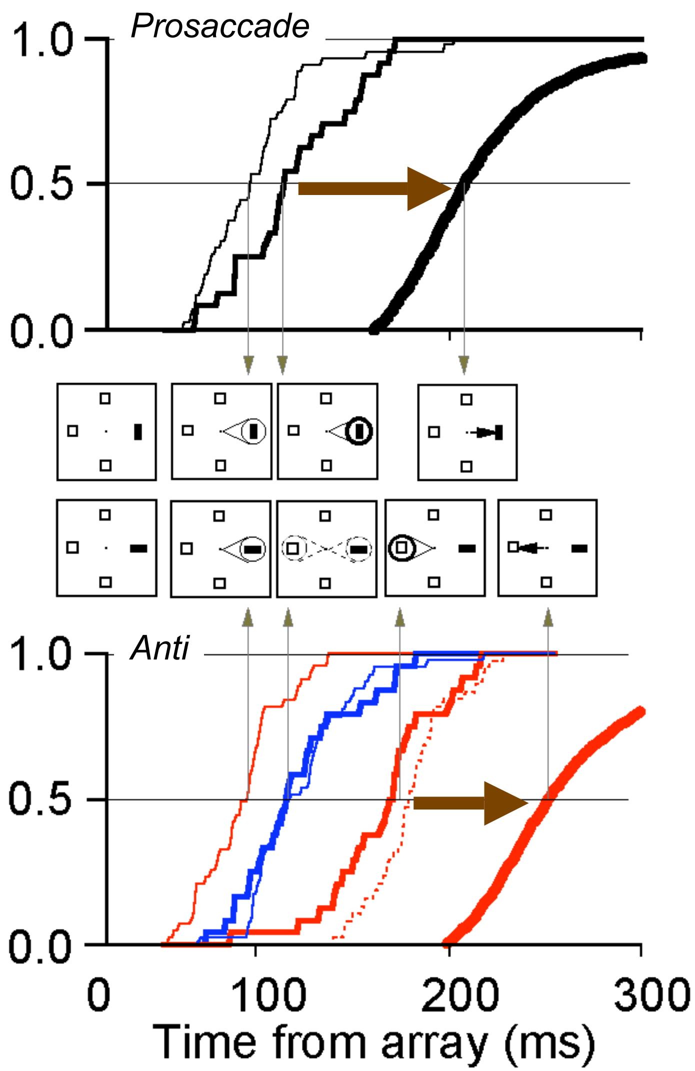


Sato & Schall, (2003). *Neuron* 38:637-648

How does selection of the singleton and of the endpoint relate to preparation of the saccade?

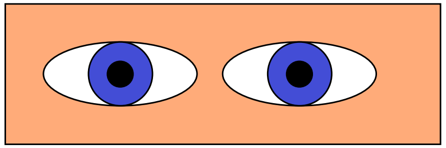
Once the endpoint is selected...

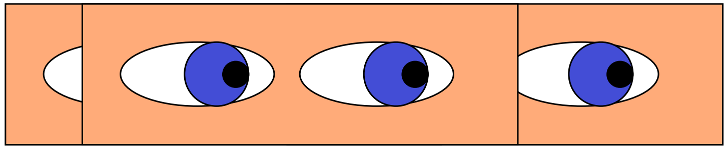
… why does it take so long to initiate the saccade?

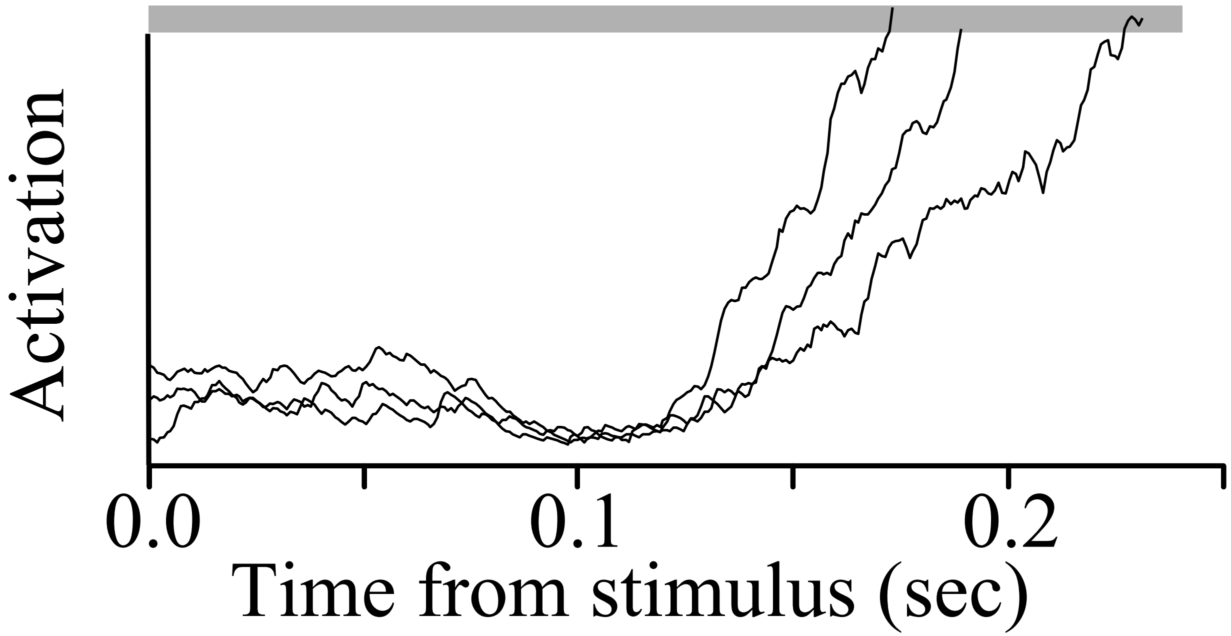


Frontal Eye Field (as part of a network!)

Controls when gaze shifts

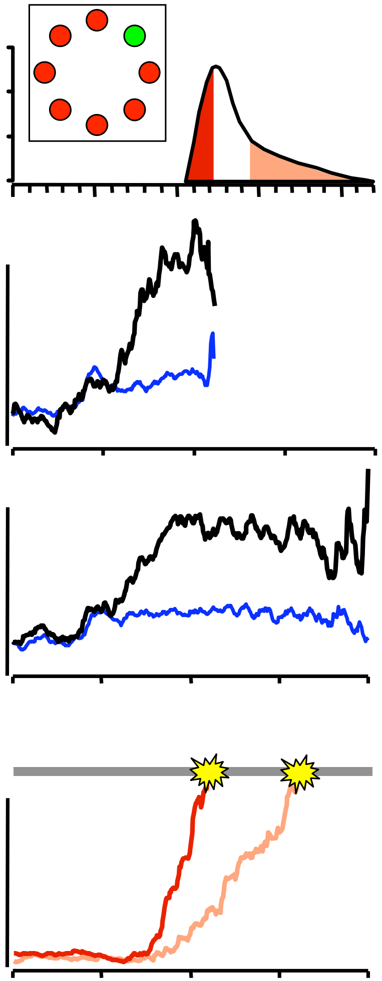






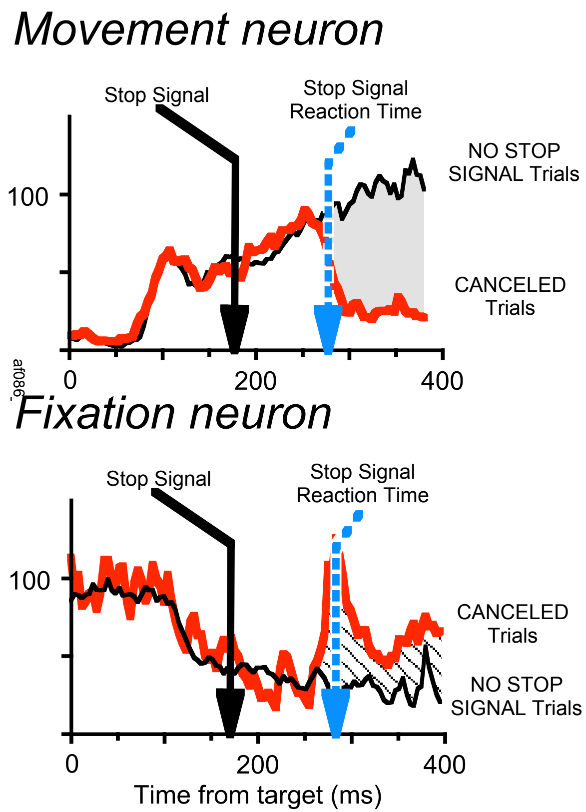
Hanes, D.P. and J.D. Schall (1996) Neural control of voluntary movement initiation. *Science* 274:427-430.

Variability in saccade preparation can account for some of the delay and variability of reaction times.



Frontal Eye Field (as part of a network!)

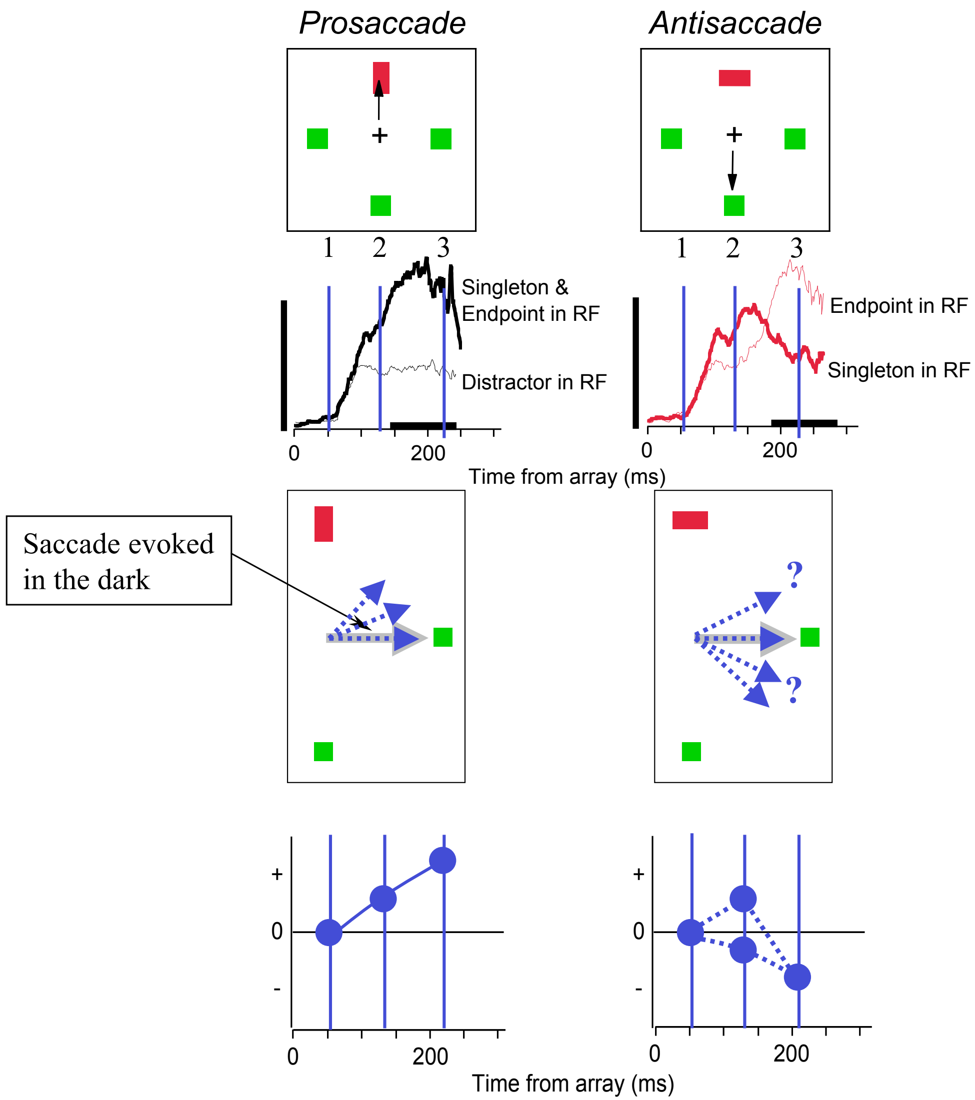
Also controls whether gaze shifts



Hanes, D.P., W.F. Patterson, J.D. Schall (1998) The role of frontal eye field in countermanding saccades: Visual, movement and fixation activity. *Journal of Neurophysiology* 79:817-834.

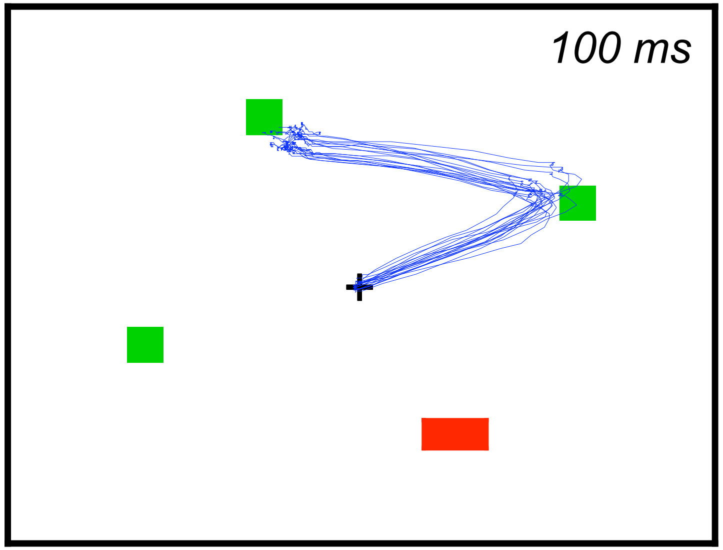
Does selection of the singleton correspond to preparation of a saccade?

Probe saccade preparation with intracortical microstimulation of FEF.

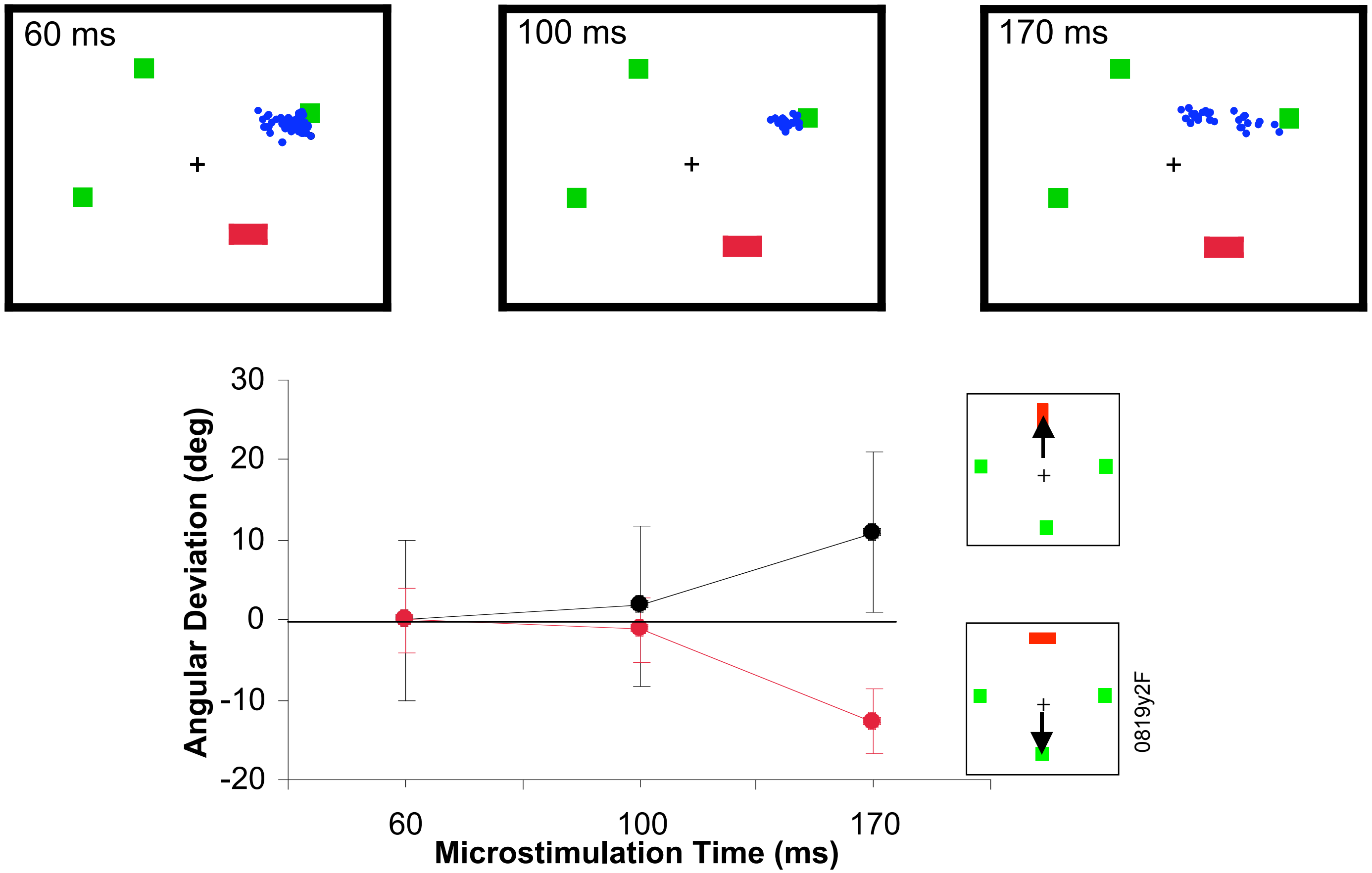


Prosaccade
Antisaccade
1 2 3
1 2 3
Singleton &
Endpoint in RF
Distractor in RF
Endpoint in RF
Singleton in RF
0
200
0
200
Time from array (ms)
Saccade evoked
in the dark
?
?
+
0
-
+
0
-
0
200
0
200
Time from array (ms)

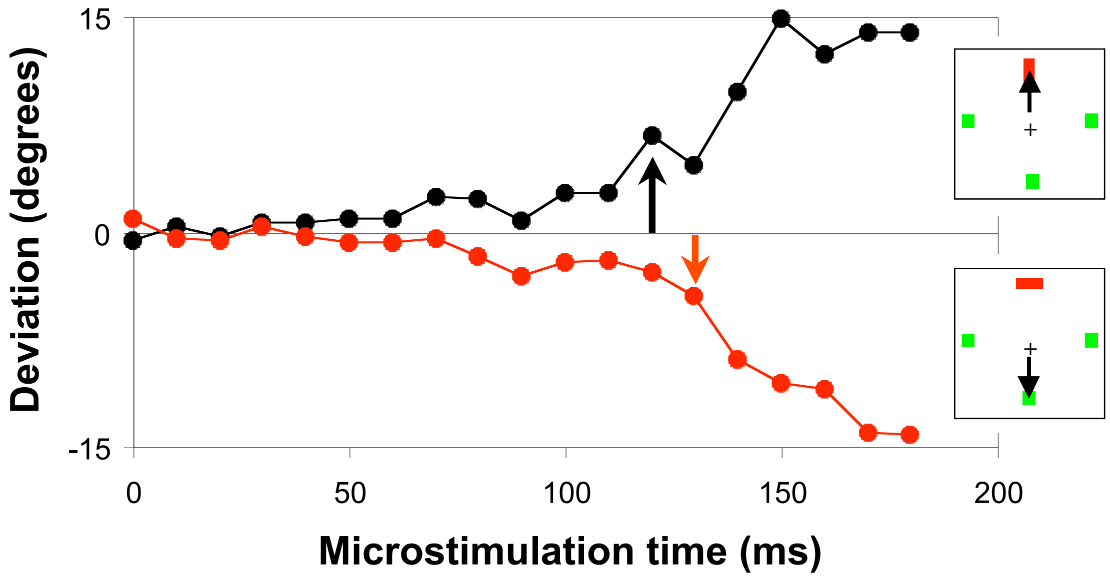
Electrical stimulation of FEF produces saccade that is followed by movement to the correct endpoint.



Later stimulation evokes saccades deviating toward the endpoint of the correct saccade.

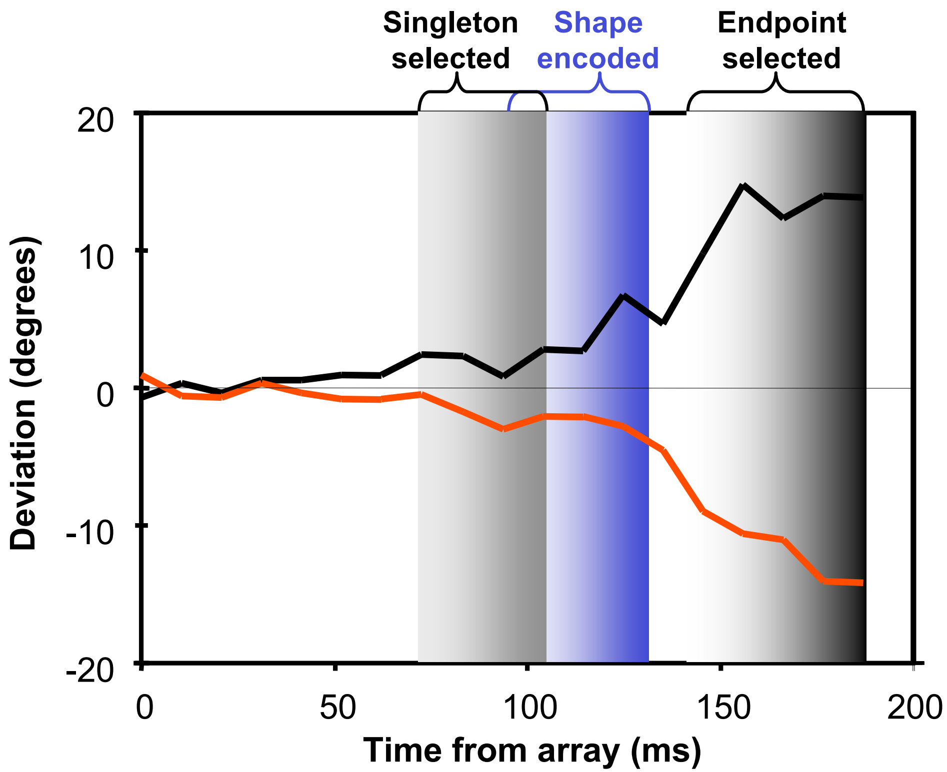


Microstimulation of 65 sites in 2 monkeys at a range of times



• During prosaccade trials evoked saccades deviated progressively toward the endpoint at the singleton.
• During antisaccade trials evoked saccades never deviated toward the singleton but only progressively toward the endpoint of the antisaccade.

How does timecourse of saccade preparation (measured through deviations) relate to timecourse of neural selection?



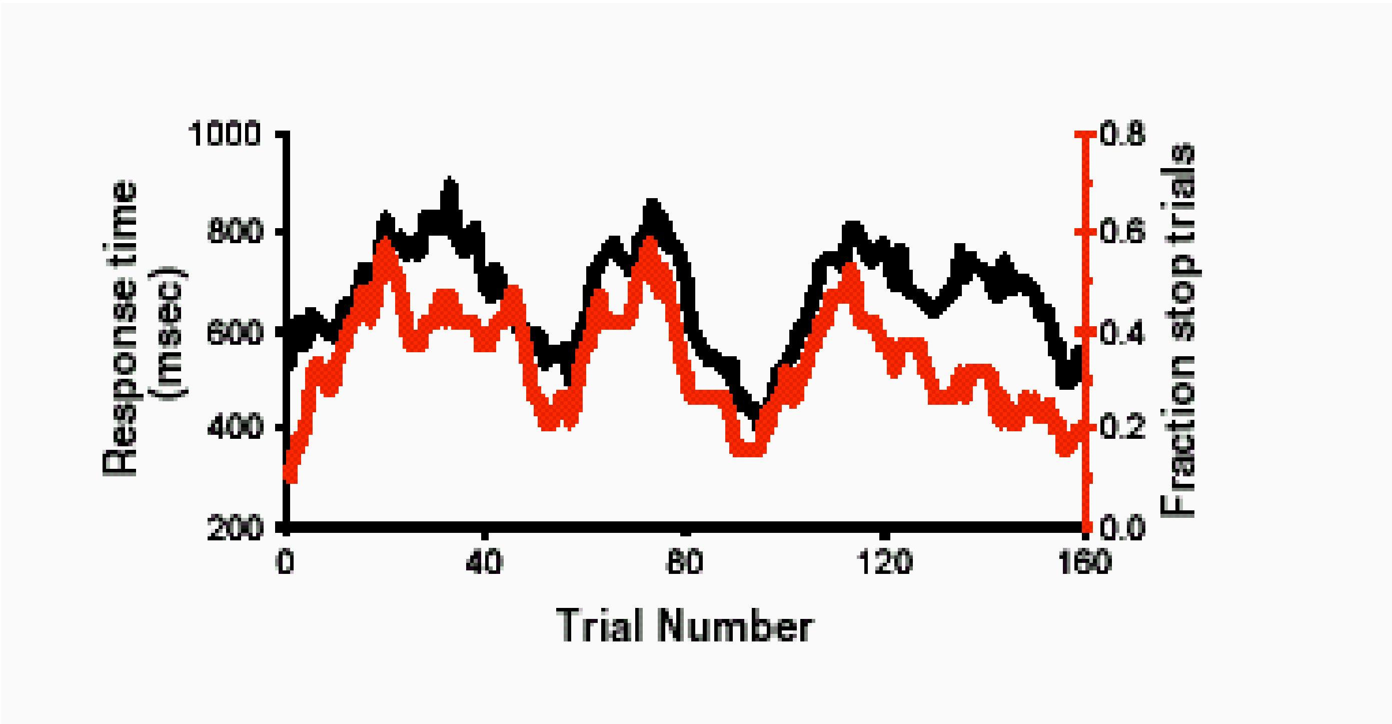
Conclusions

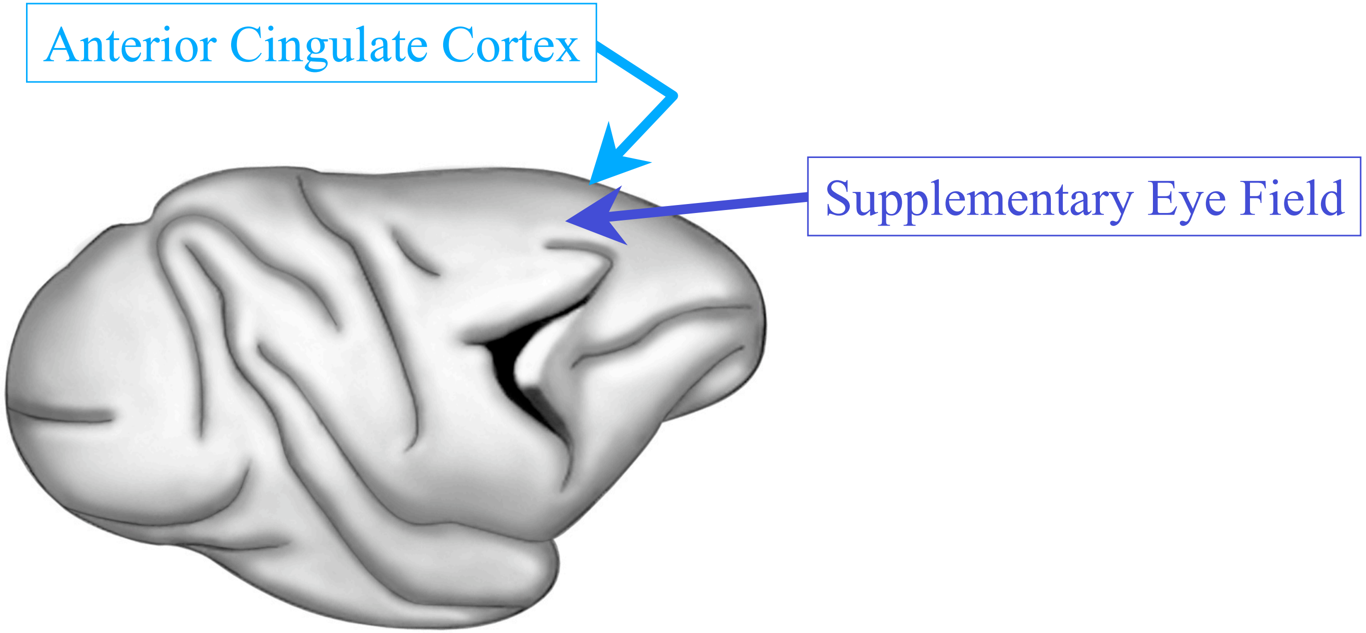
- Frontal eye field (as part of network) is critical for overt orienting
  - Saccades are initiated if and only if the activity of particular neurons reaches a threshold
  - The time taken to reach the threshold is stochastic

- Frontal eye field (as part of network) is involved in covert orienting
  - Visually responsive neurons do not control saccade initiation...
  - … but they do select the location of objects
  - … at a time and to a degree proportional to target-distractor similarity
  - … and relevance
  - Attention is allocated when and to the extent that the activity of these neurons represents one as opposed to another location.

What about errors?

Behavior is adaptive.

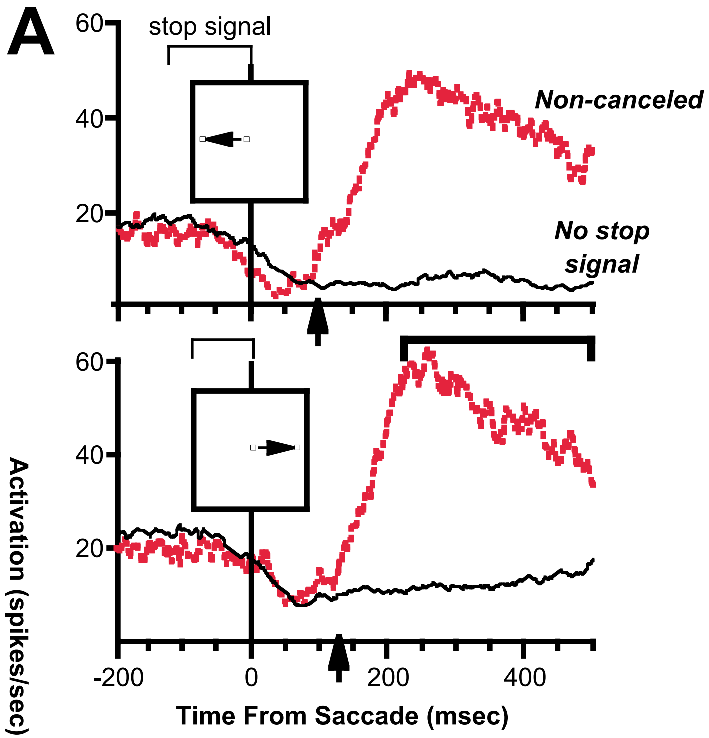



Anterior Cingulate Cortex
Supplementary Eye Field

Supplementary Eye Field
& Anterior Cingulate Cortex

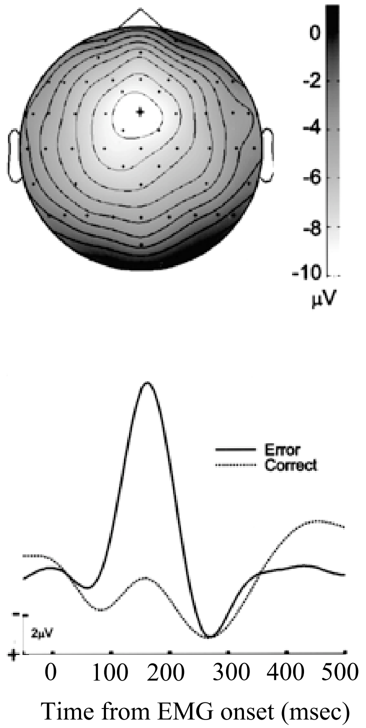
Monitor behavior by signaling errors...

Error-related unit activity



Stuphorn V, Taylor TL, Schall JD (2000) Performance monitoring by supplementary eye field. *Nature* 408:857-860.

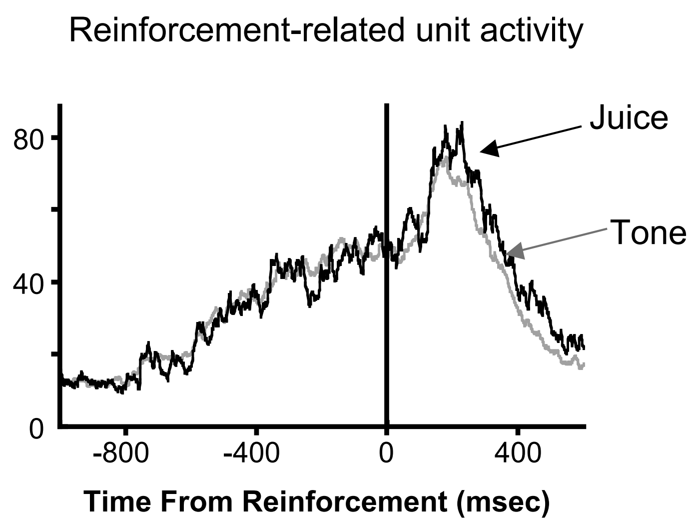
Error-related negativity



from Gehring and Fencsik, The Journal of Neuroscience 21(23):9430-9437

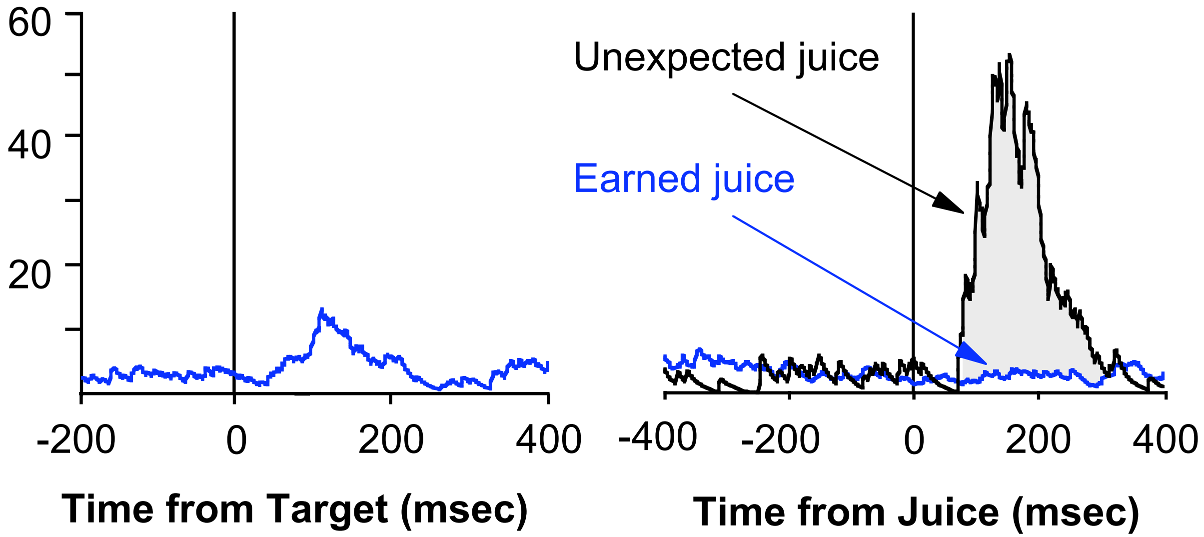
Supplementary Eye Field

Monitor behavior by signaling success



Stuphorn V, Taylor TL, Schall JD (2000) Performance monitoring by supplementary eye field. *Nature* 408:857-860.

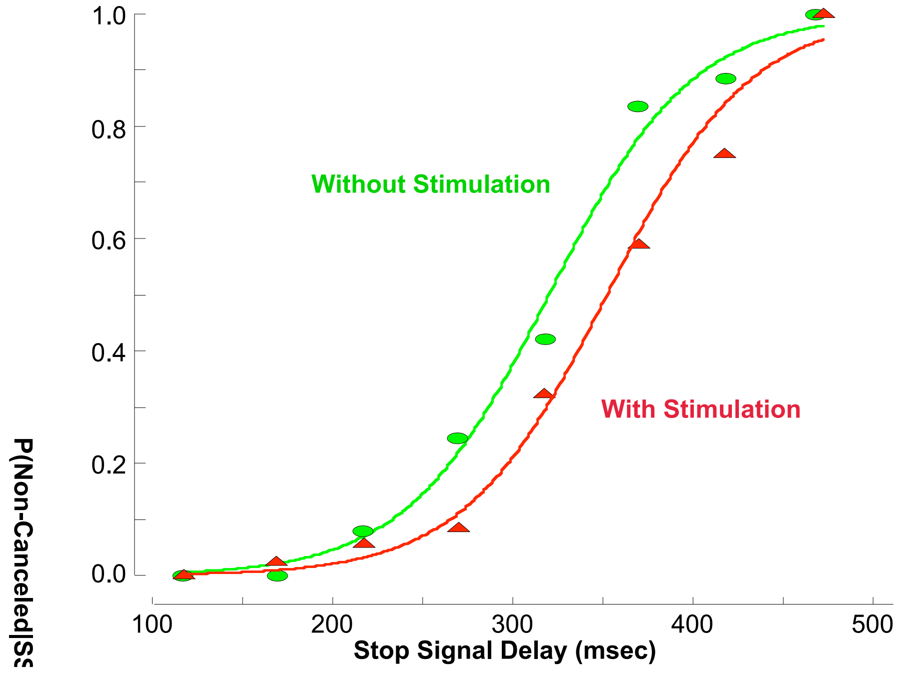
Anterior Cingulate Cortex



Supplementary Eye Field

Can monitoring signals have any influence?

Microstimulation of sites in SEF reduced probability of producing saccade



Monitoring and control brain subsystems?