Dynamic Field Theory

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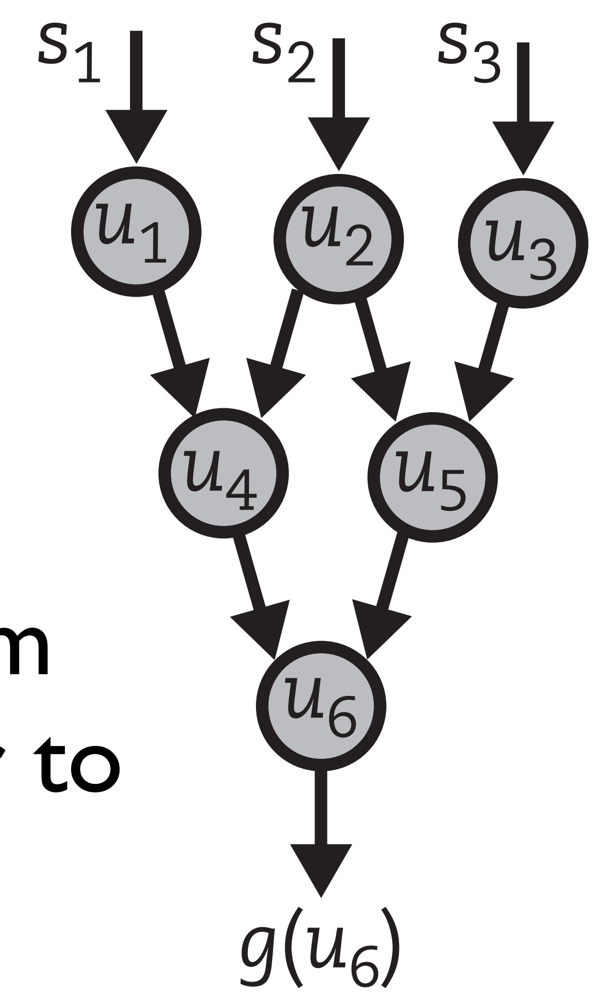
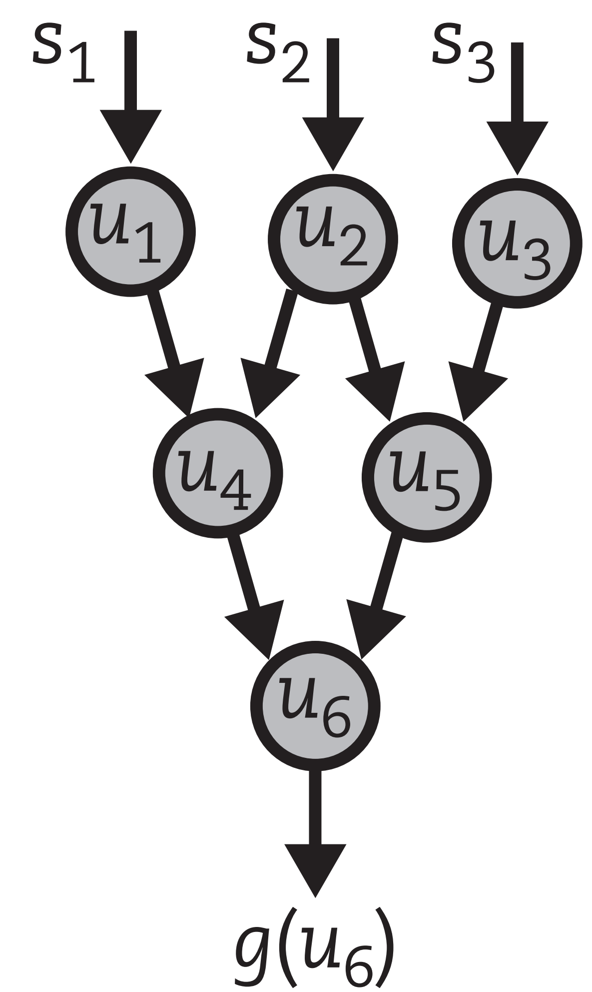
… toward fields

- where do "inputs" come from…?
  - from sensory systems
  - from other neurons
- => activation variables gain their meaning from the connections from the sensory surfaces or to the motor surfaces



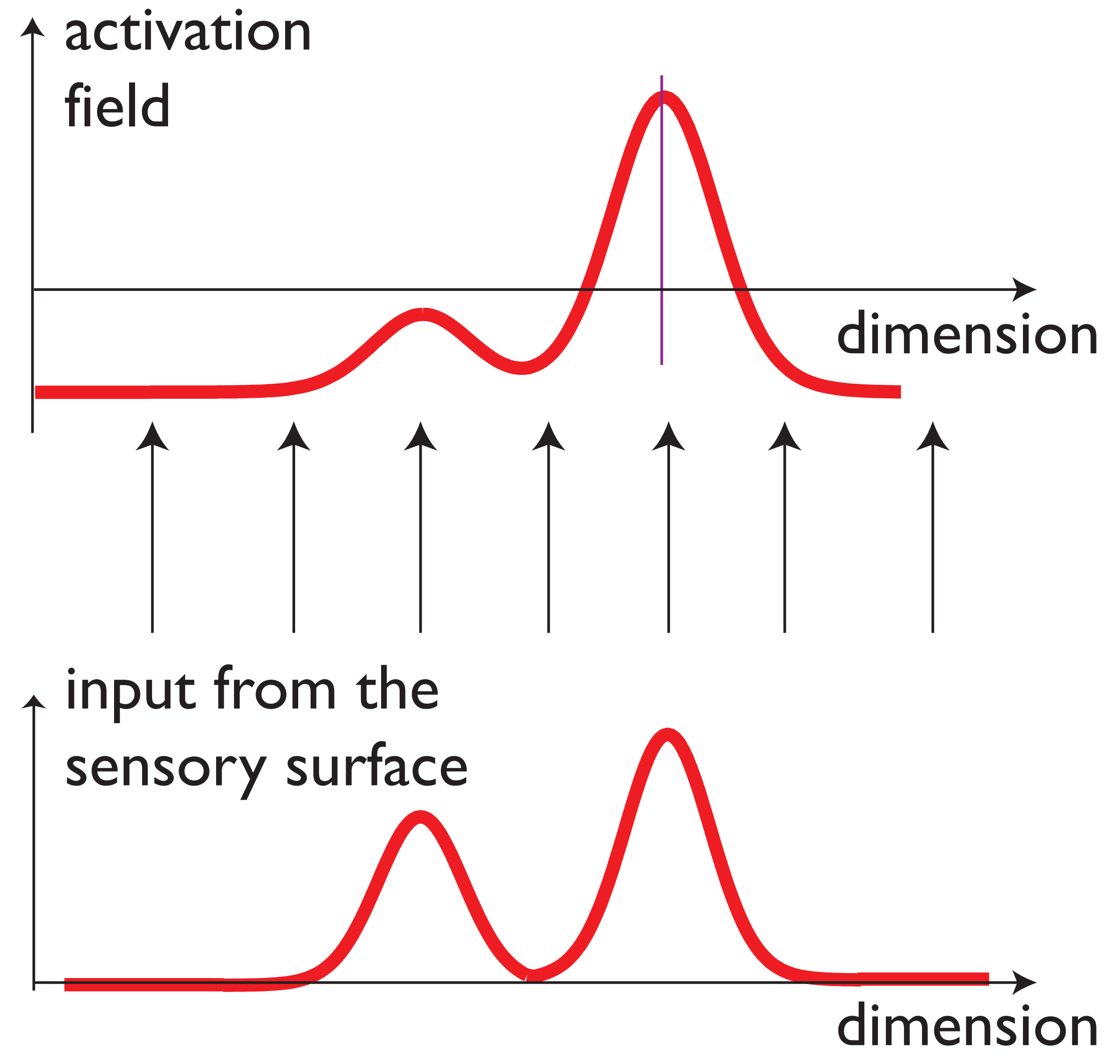
… toward fields

- there is no behavioral evidence for discrete sampling…
- => abstract from discrete sampling…

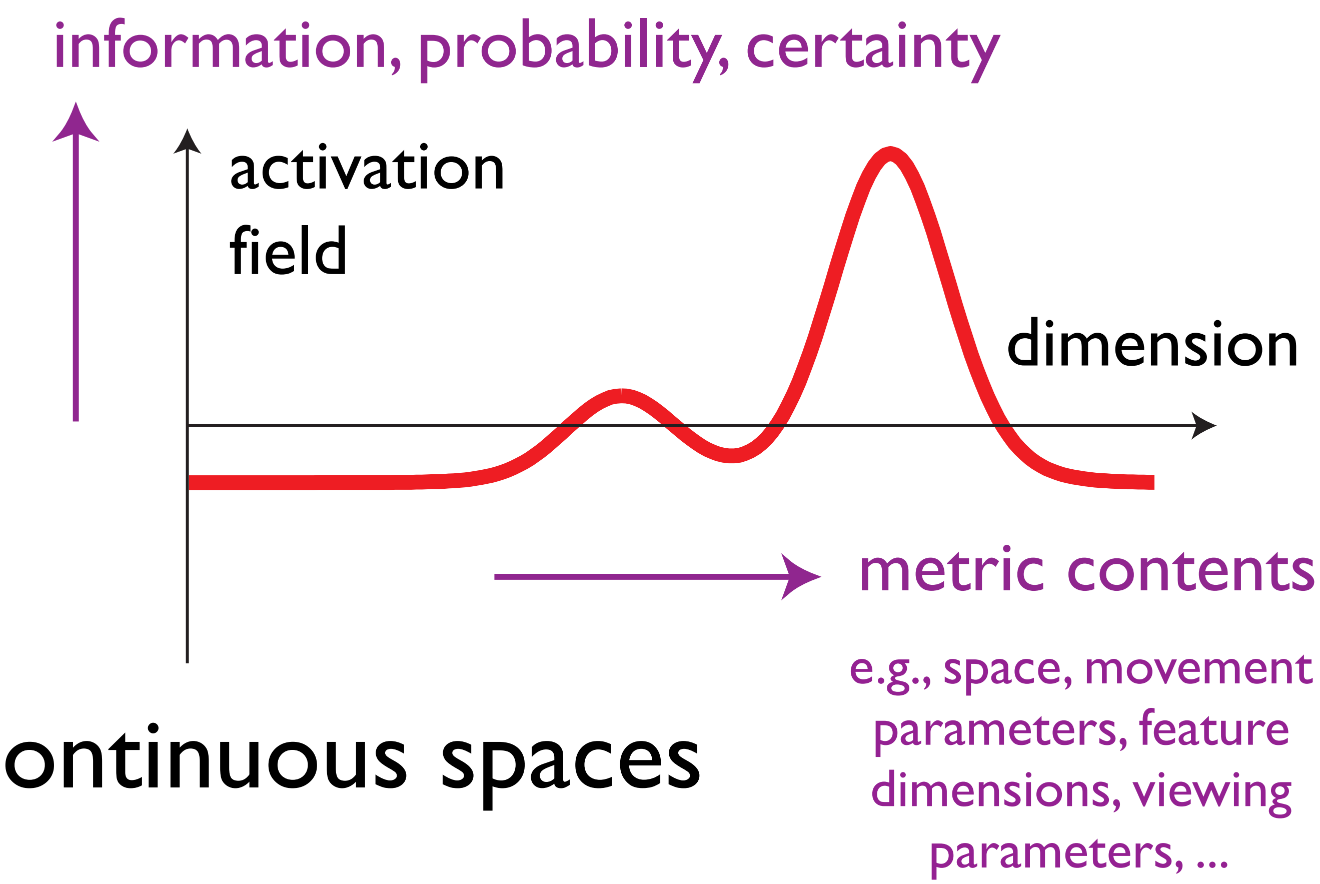


… toward fields

- define field is over the continuous stimulus dimension
- … as dictated by input/output connectivity…

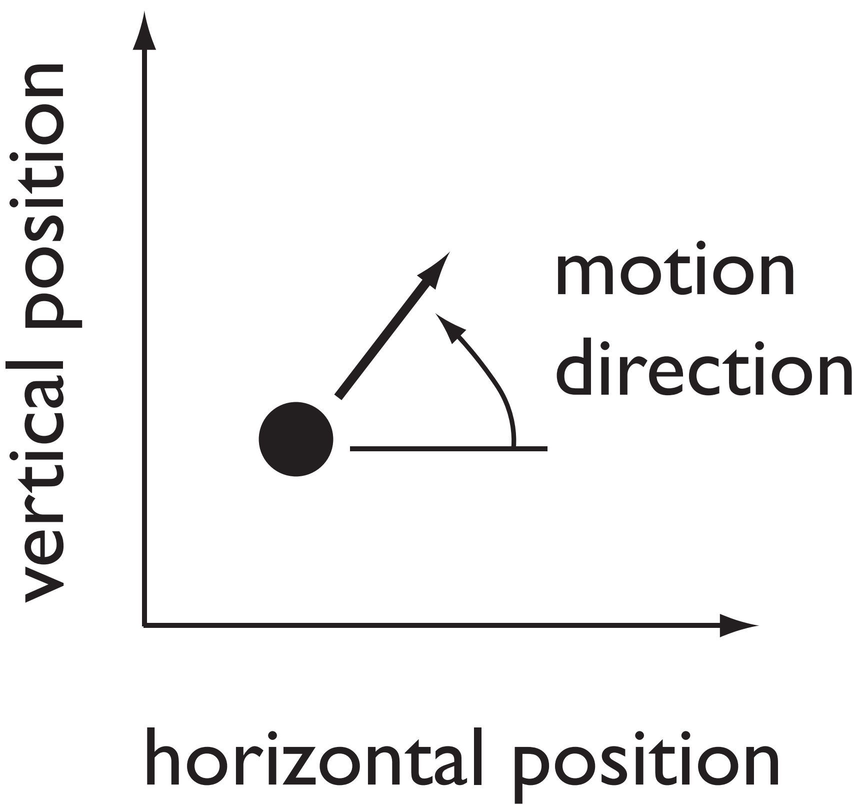


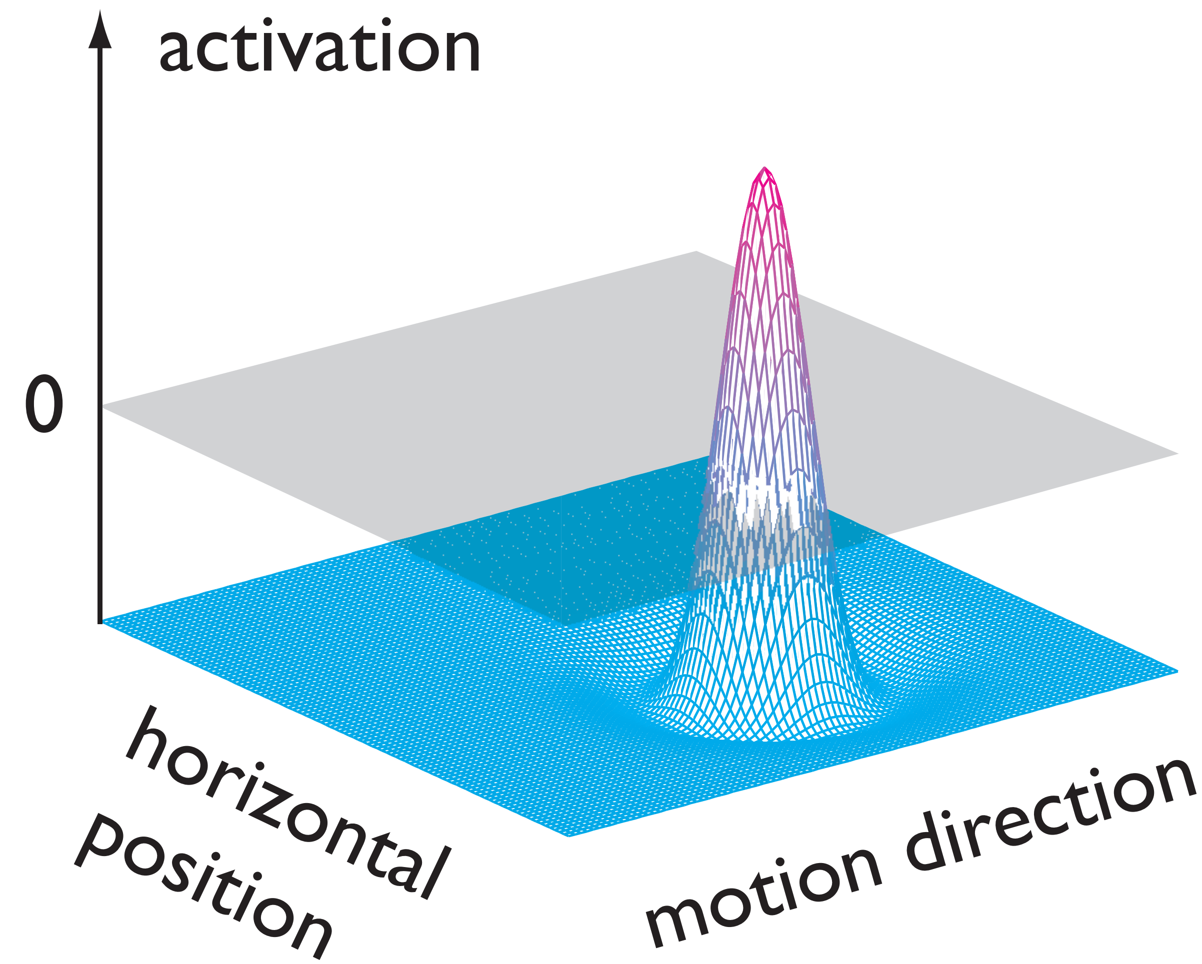
activation fields



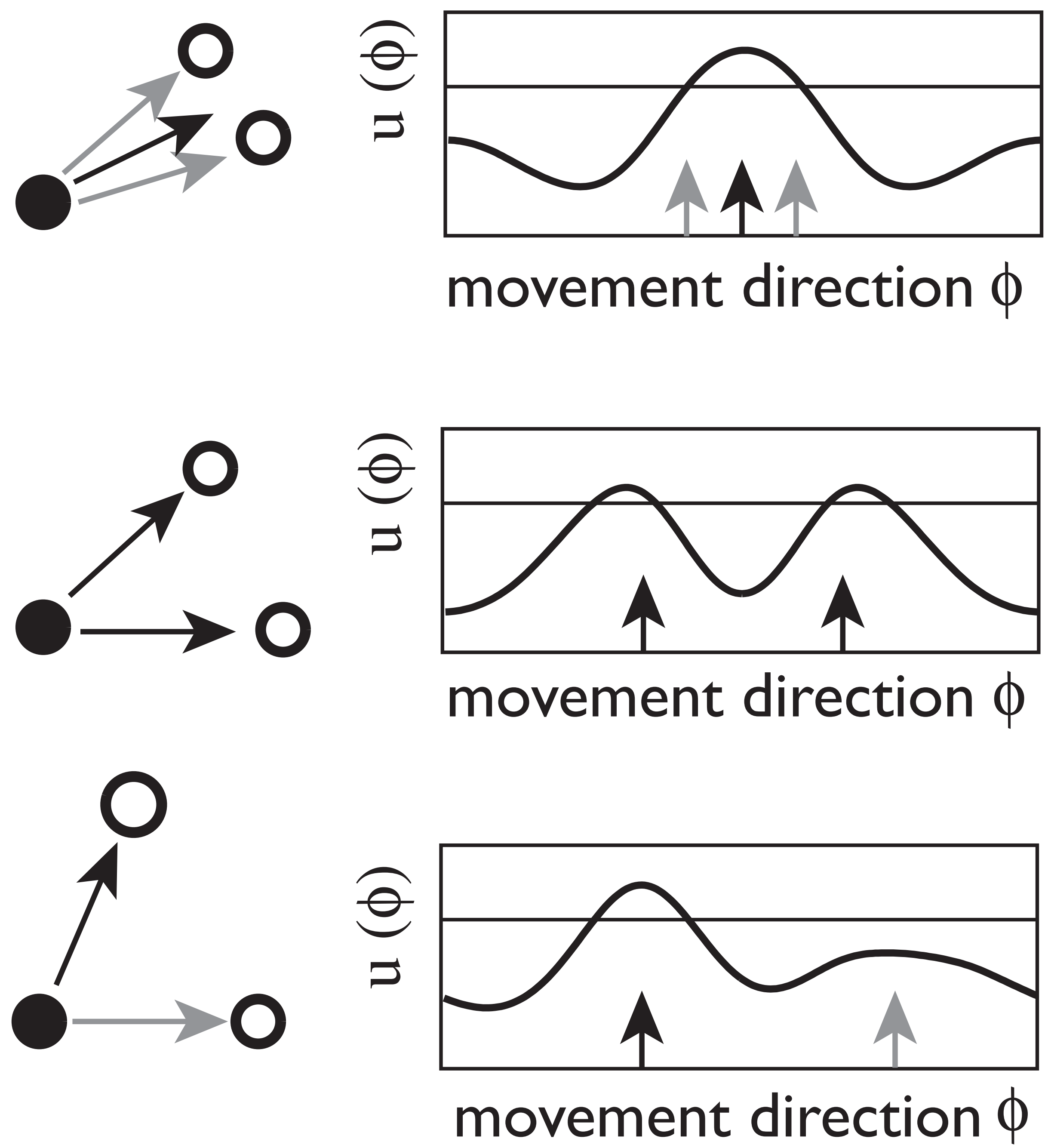
- define activation fields over continuous spaces
  - homologous to sensory surfaces, e.g., visual or auditory space (retinal, allocentric, ...)
  - homologous to motor surfaces, e.g., saccadic end-points or direction of movement of the end-effector in outer space
  - feature spaces, e.g., localized visual orientations, color, impedance, ...
  - abstract spaces, e.g., ordinal space, along which serial order is represented

Example motion perception: space of possible percepts

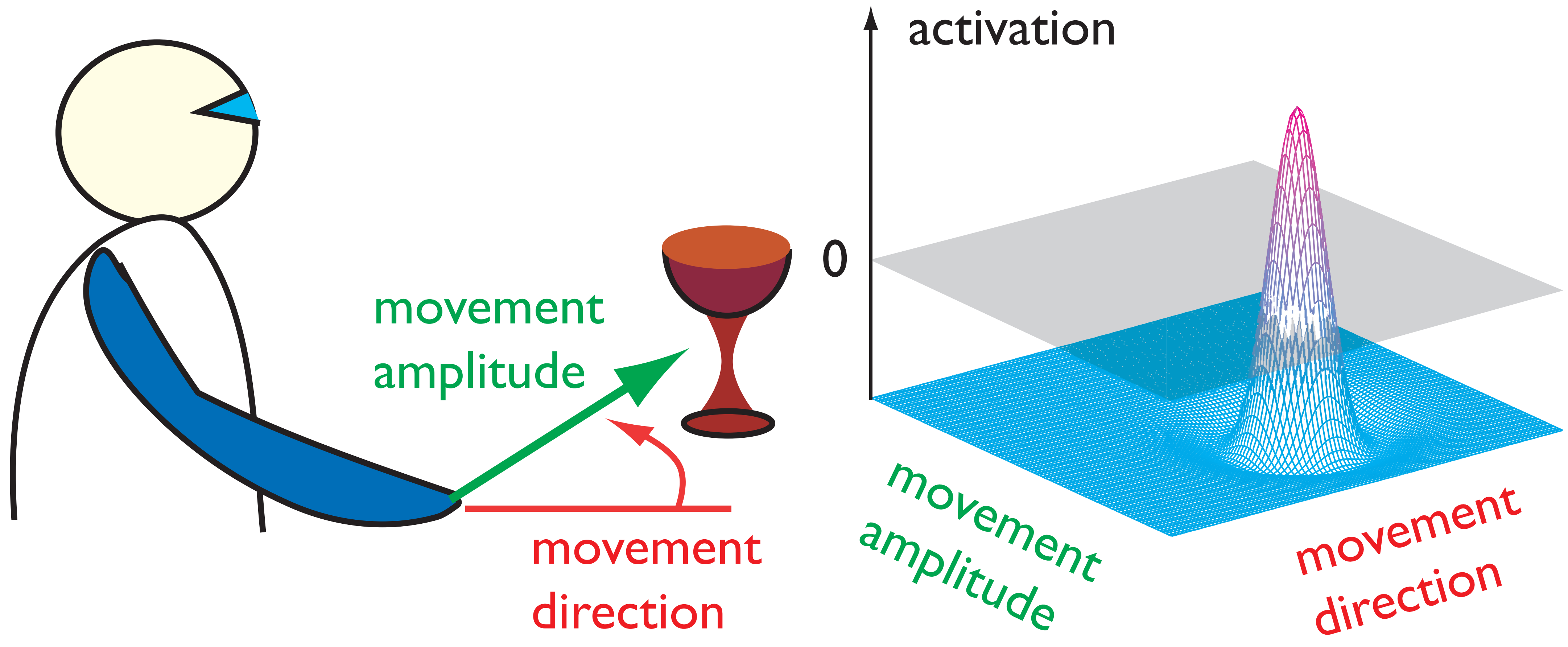




Activation patterns representing different percepts



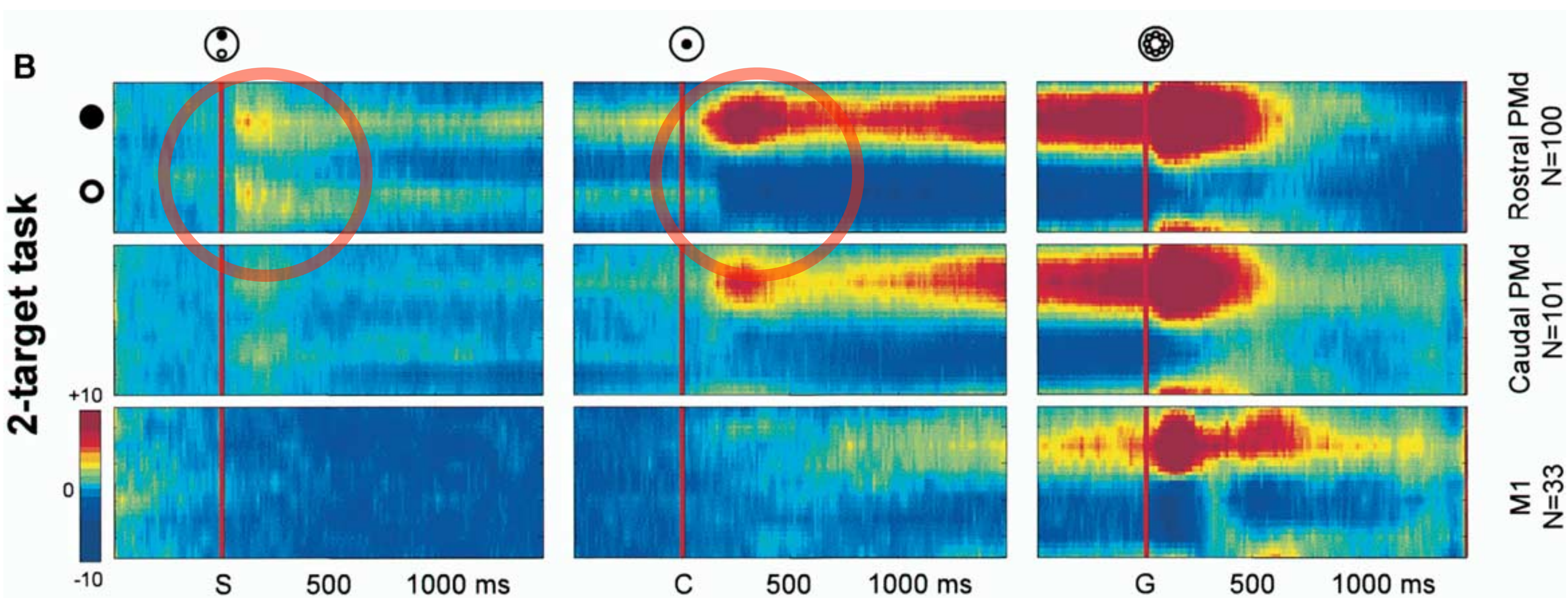
Example: movement planning: space of possible actions



Activation patterns representing states of motor decision making

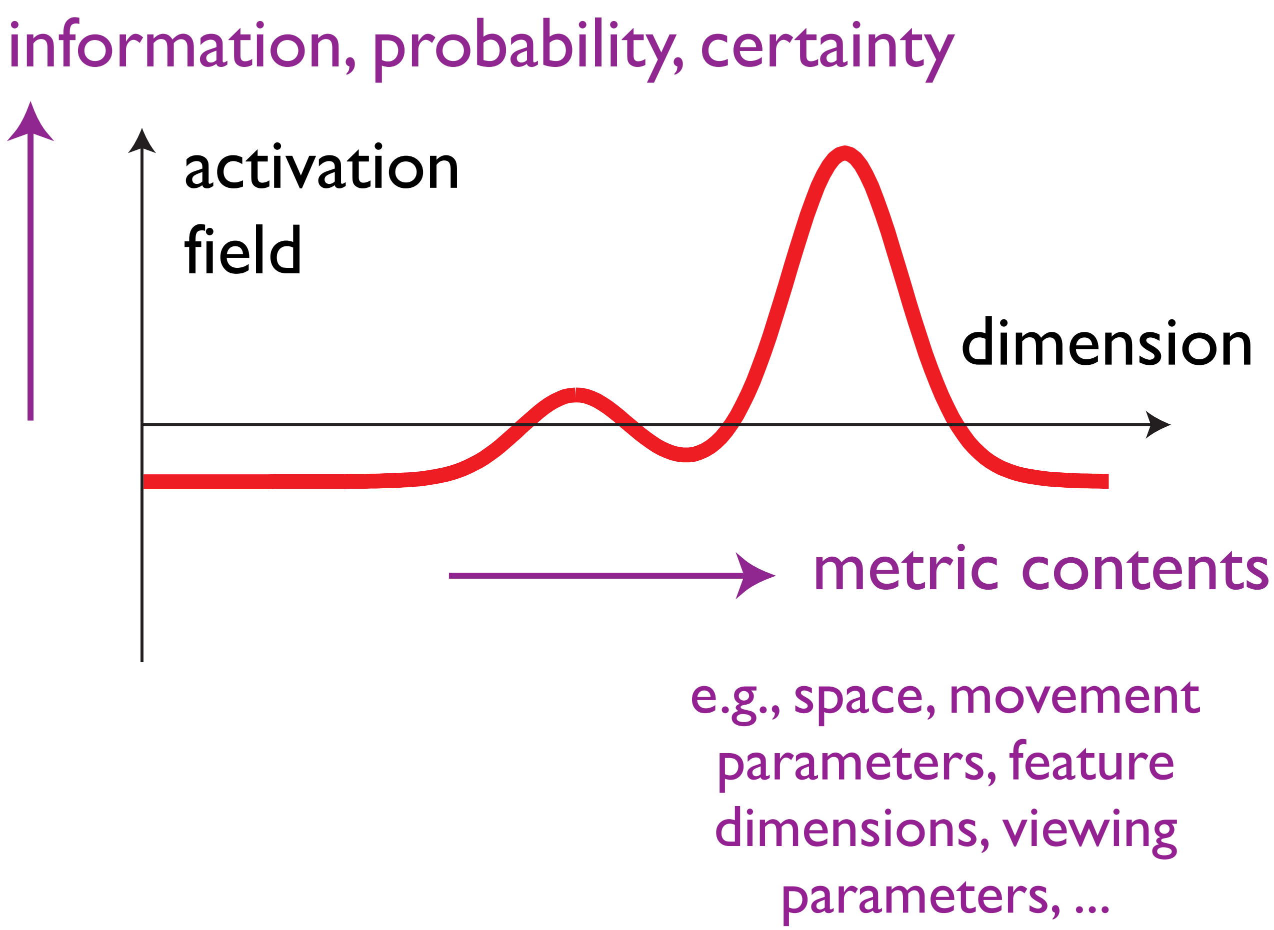
- bi-modal distribution of activation over movement direction in pre-motor cortex before a selection decision is made

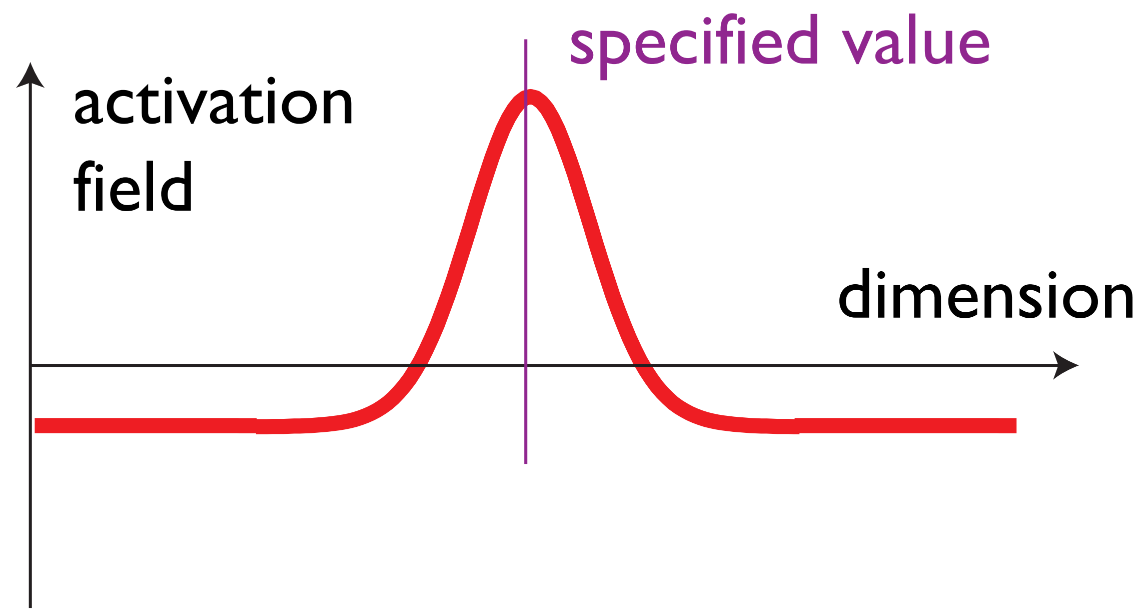
- mono-modal distribution once the decision is made

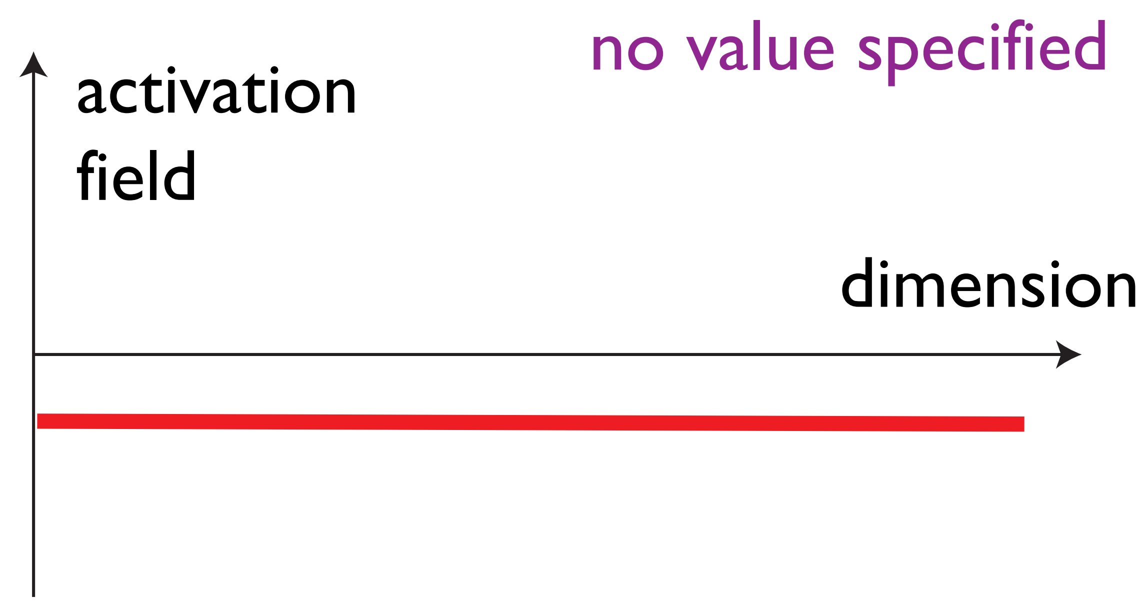


[Cisek, Kalaska: Neuron 2005]

Summary: activation fields

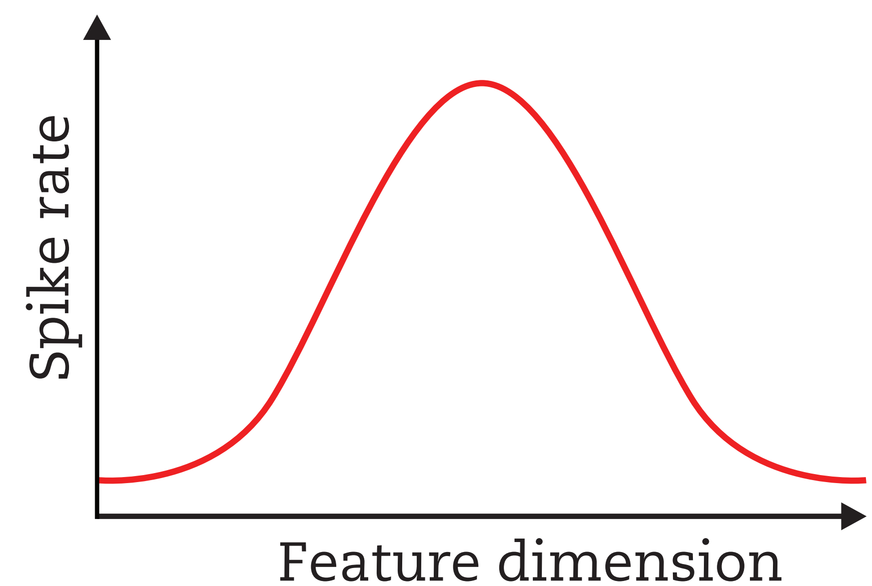




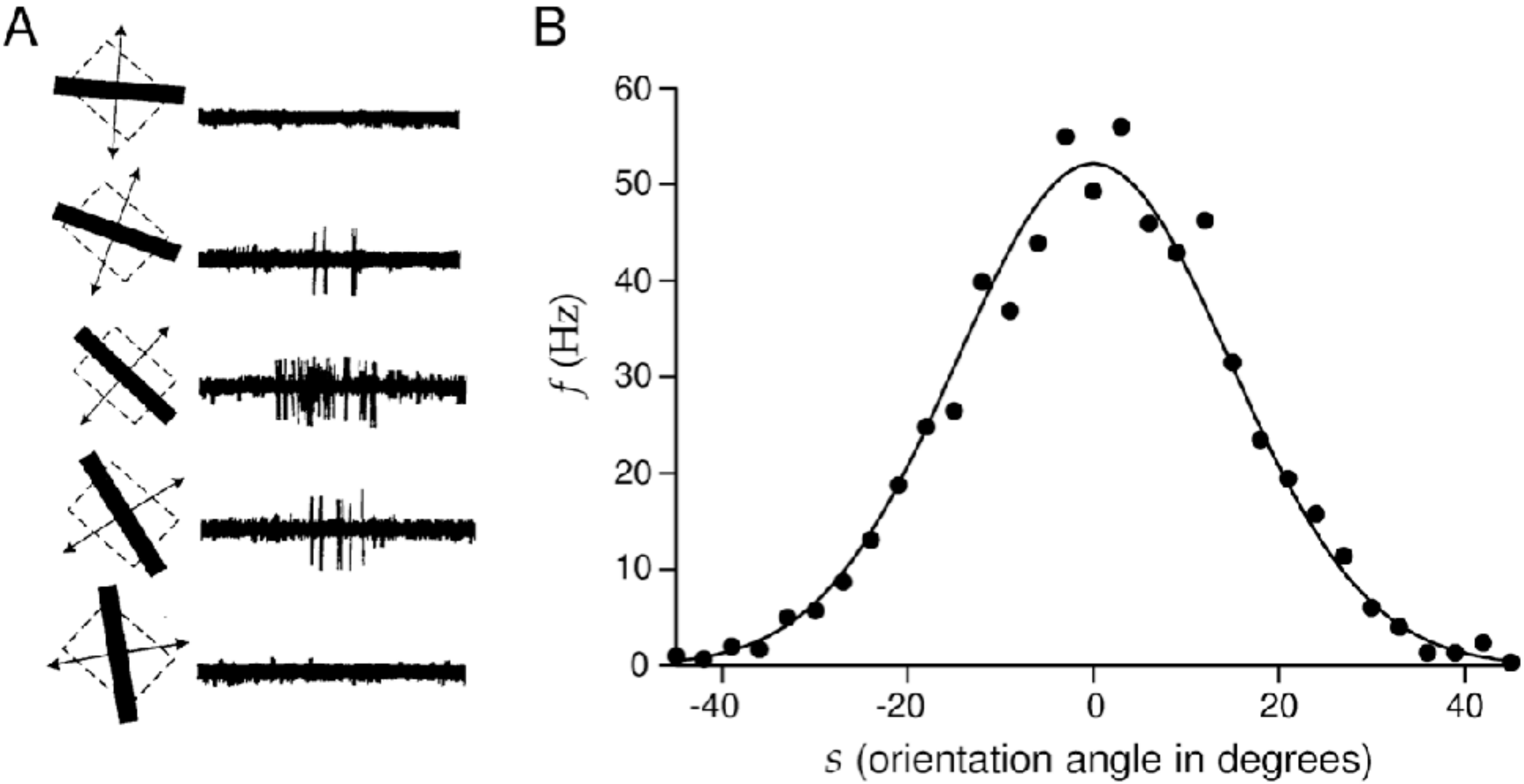


On the link between DFT and neurophysiology

- What do neurons represent?
  - notion of a tuning curve that links something outside the nervous system to the state of a neuron (e.g. through firing rate)
  - based on the forward picture in which
    - the connectivity from the sensory surface
    - or the connectivity from the neuron to the motor surface
  - determine the activity of the neuron

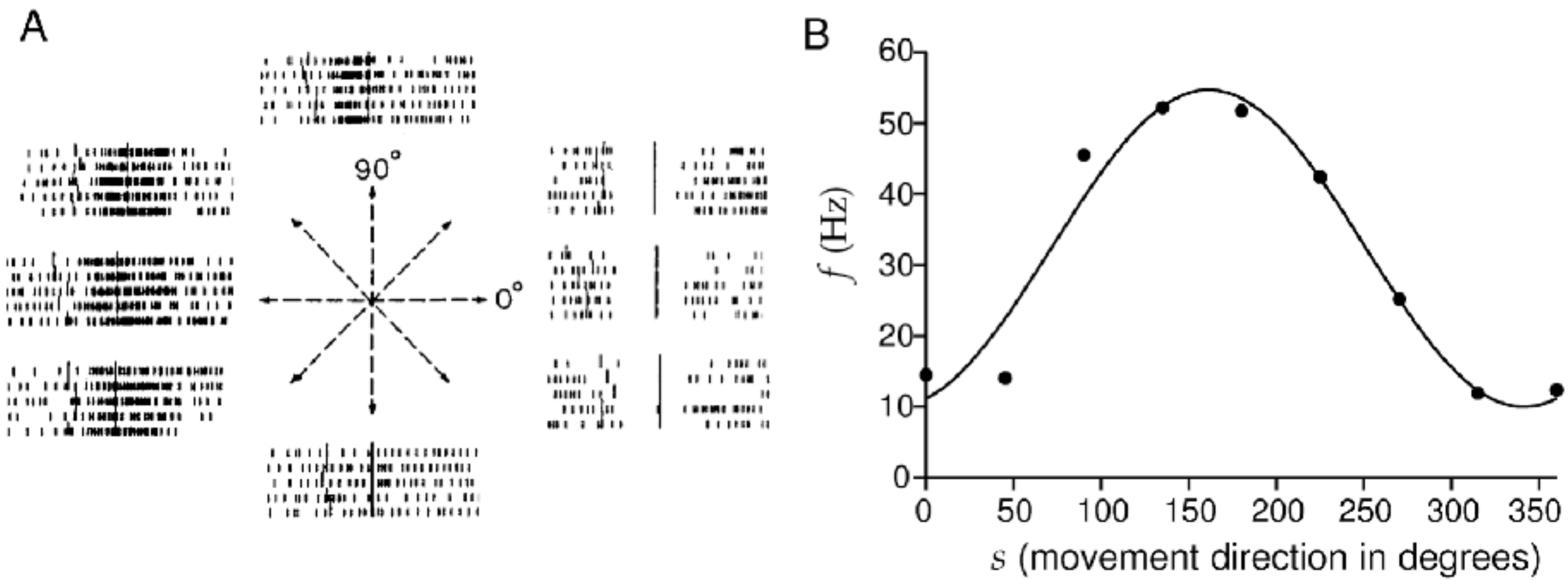


Example tuning curve in primary visual cortex (monkey)



[Hubel, Wiesel, 1962]

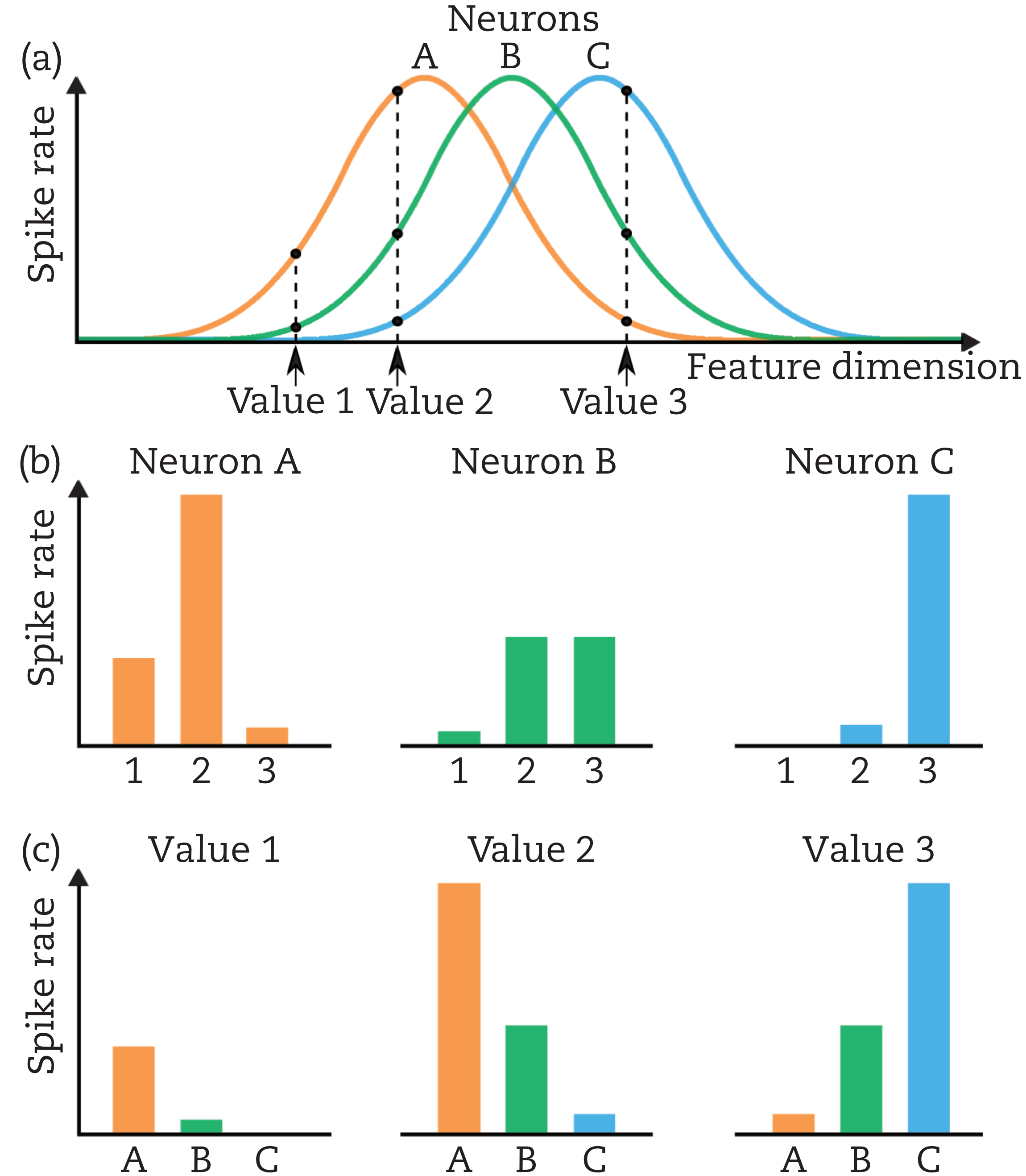
Example: tuning curve in primary motor cortex (monkey)



[Georgopoulos, Schwartz, Kalaska, 1986]

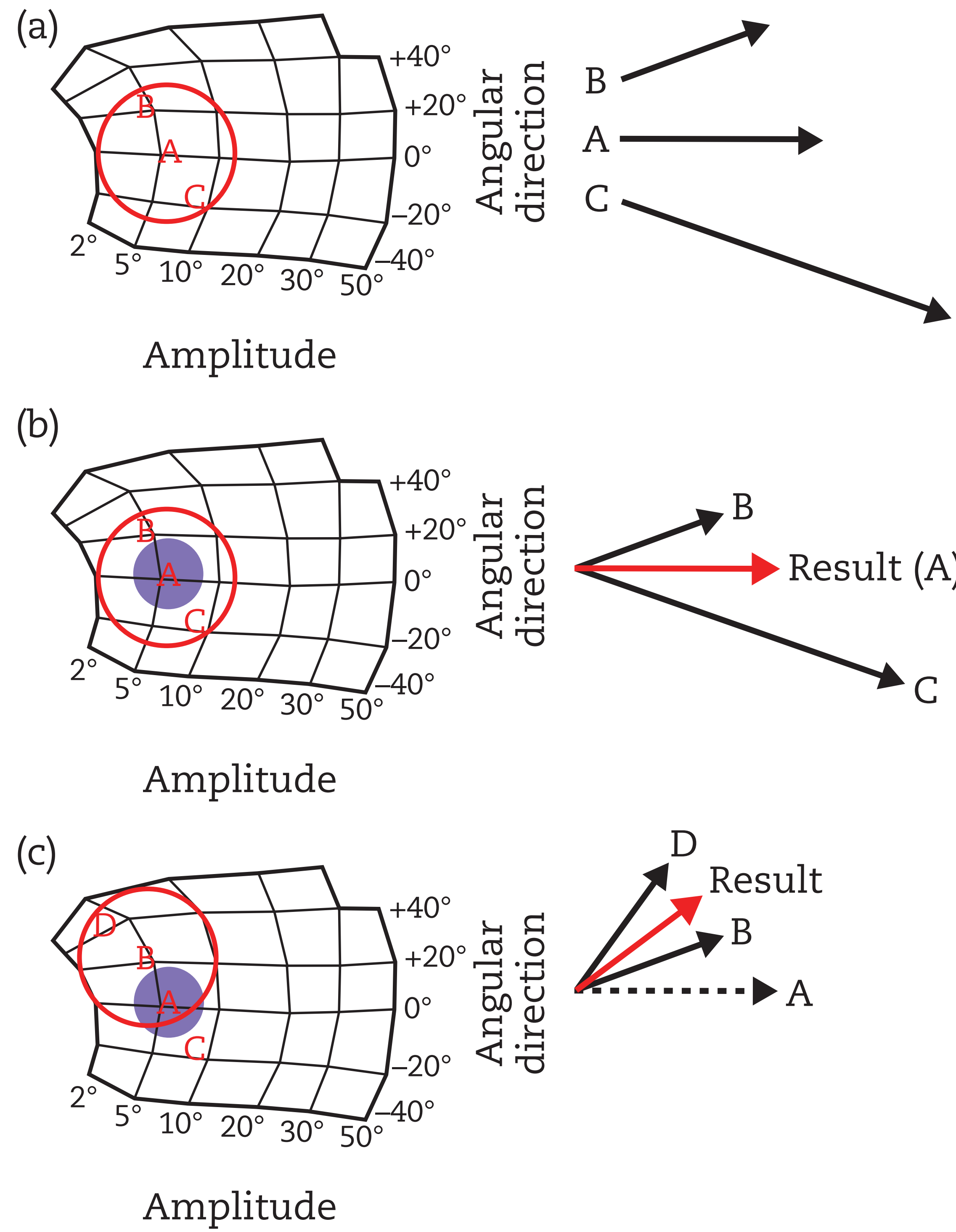
What do ensembles of neurons represent?

- the pattern of neural activity across multiple neurons represents a feature value much more precisely than individual neurons do



Do all activated neurons contribute?

- superior colliculus: topographic map of saccadic endpoint
- deactivate portions of the population: observe predicted deviations of saccadic endpoint



[after Lee, Rohrer, Sparks: Nature (1988) in Chapter 3 of the book]

Population code

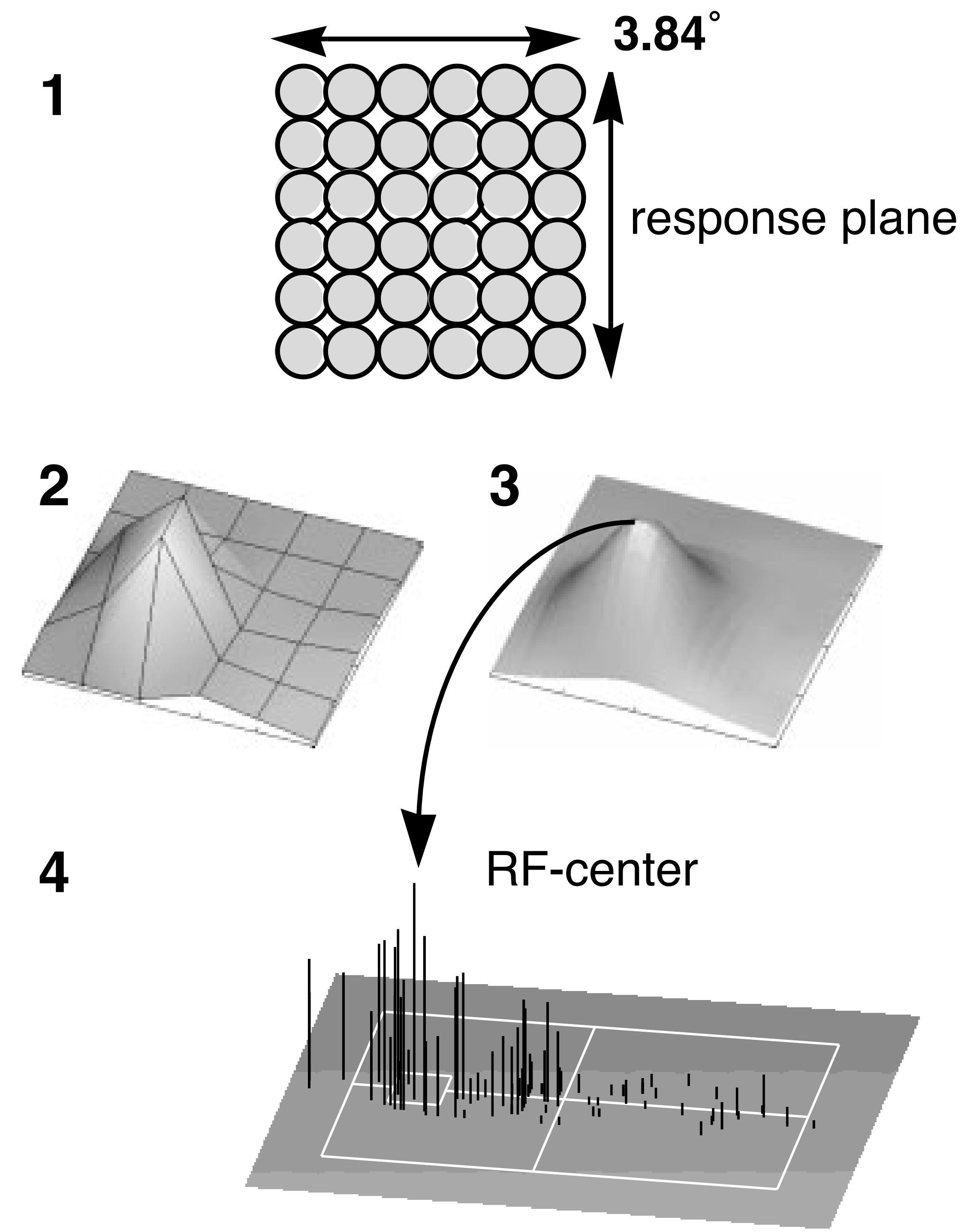
- similar work in MT
  - Purushothaman, G., & Bradley, Da. C. (2005). Neural population code for fine perceptual decisions in area MT. Nature Neuroscience, 8(1), 99–106.
- consensus, that localized populations of neurons best correlated with behavior
  - there are subtle issues of noise and correlation in populations
  - e.g., Cohen, Newsome J Neurosci 2009: about 1000 neurons needed to match behavioral performance
  - review: Shamir, M. (2014). Emerging principles of population coding: In search for the neural code. *Current Opinion in Neurobiology*, *25*, 140–148.

Neurophysiological grounding of DFT

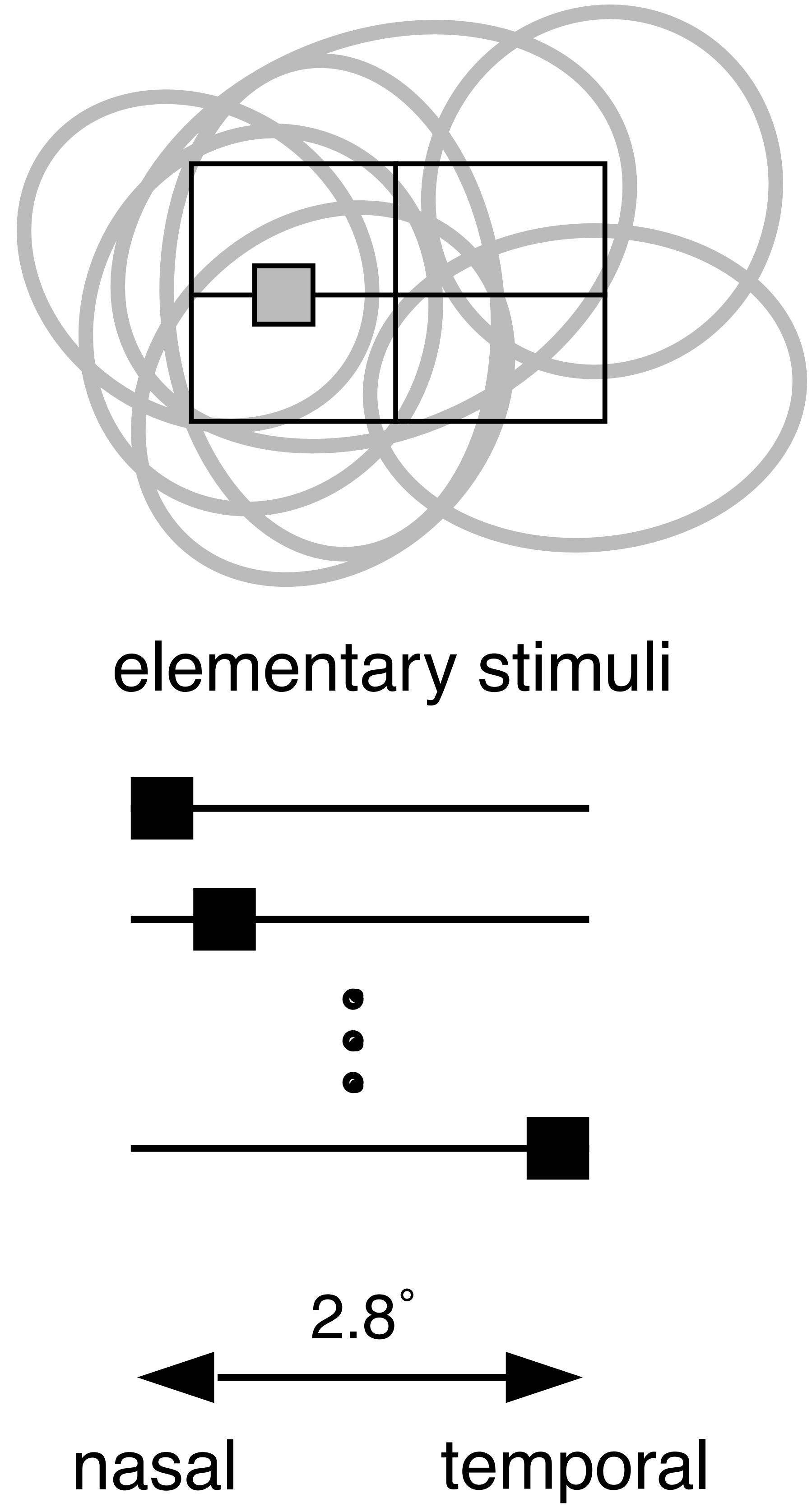
- Example 1: primary visual cortex A17 in the cat, population representation of retinal location

Jancke, Erlhagen, Dinse, Akhavan, Giese, Steinhage, Schöner JNsci 19:9016 (99)

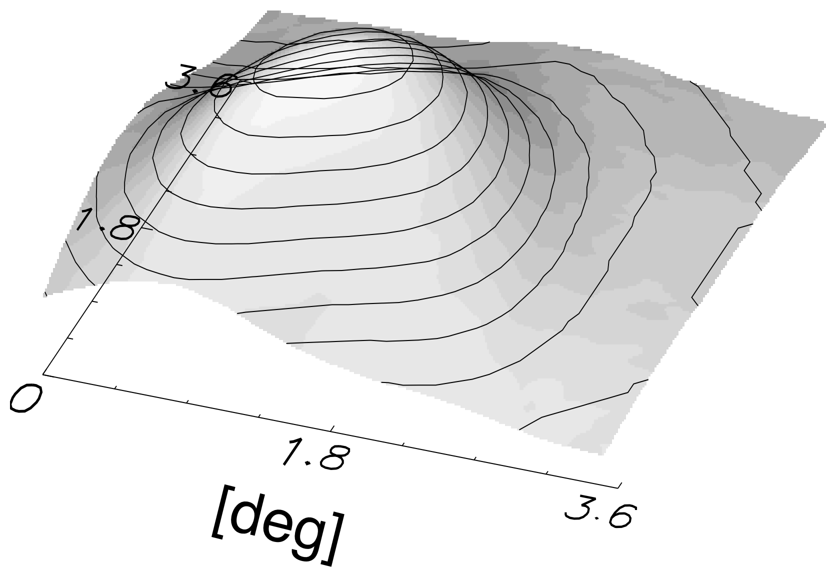
- determine RF profile for each cell
- it's center determines what that neuron codes for
- compute a distribution of population activation by superposing RF profiles weighted with current neural firing rate

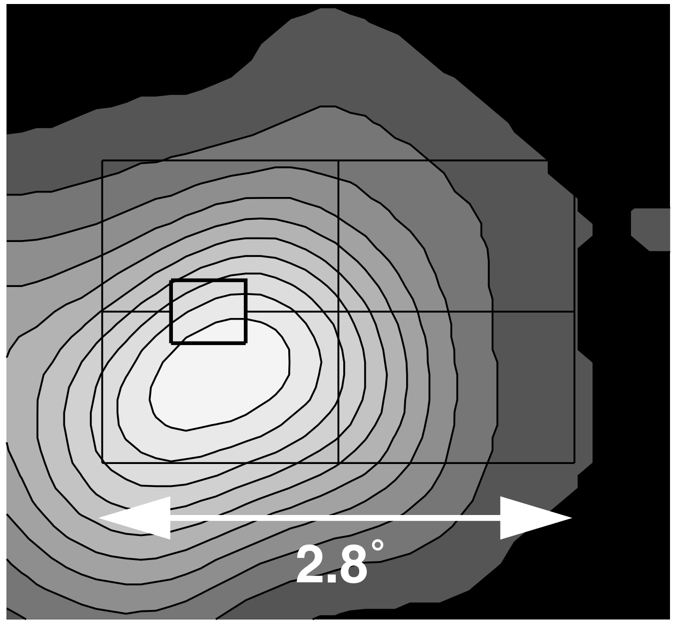


- The current response refers to a stimulus experienced by all neurons
- Reference condition: localized points of light

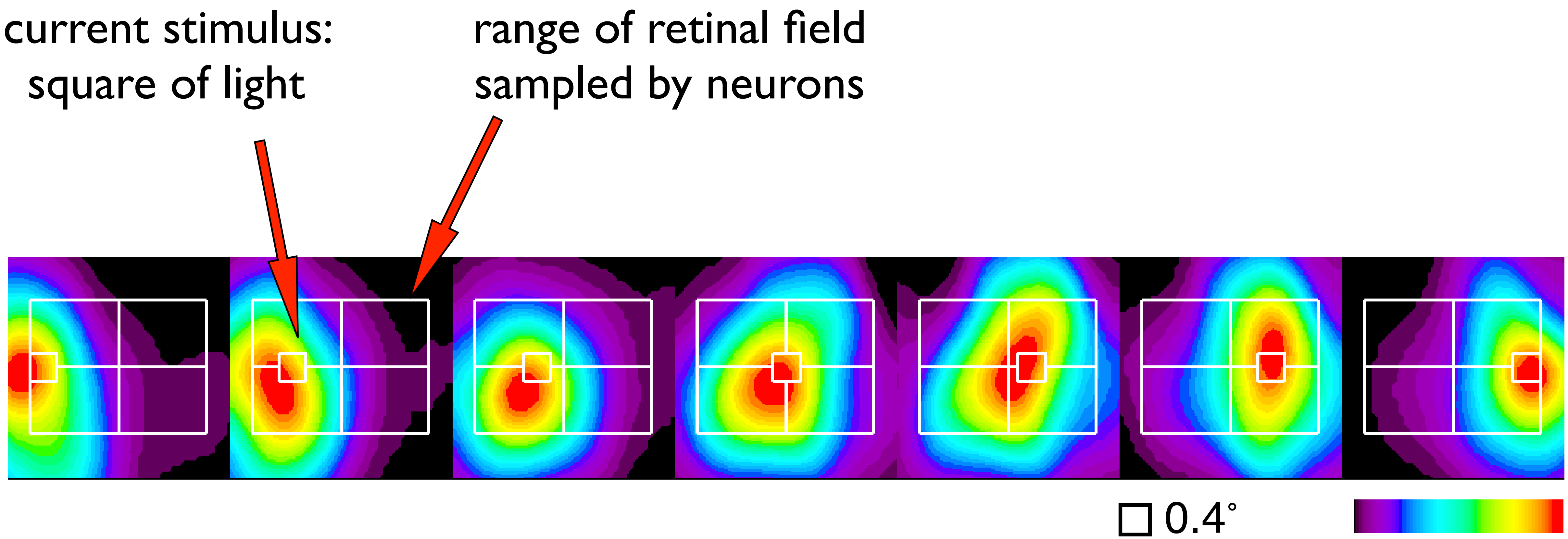


- result: population distribution of activation defined over retinal space = representation of visual location

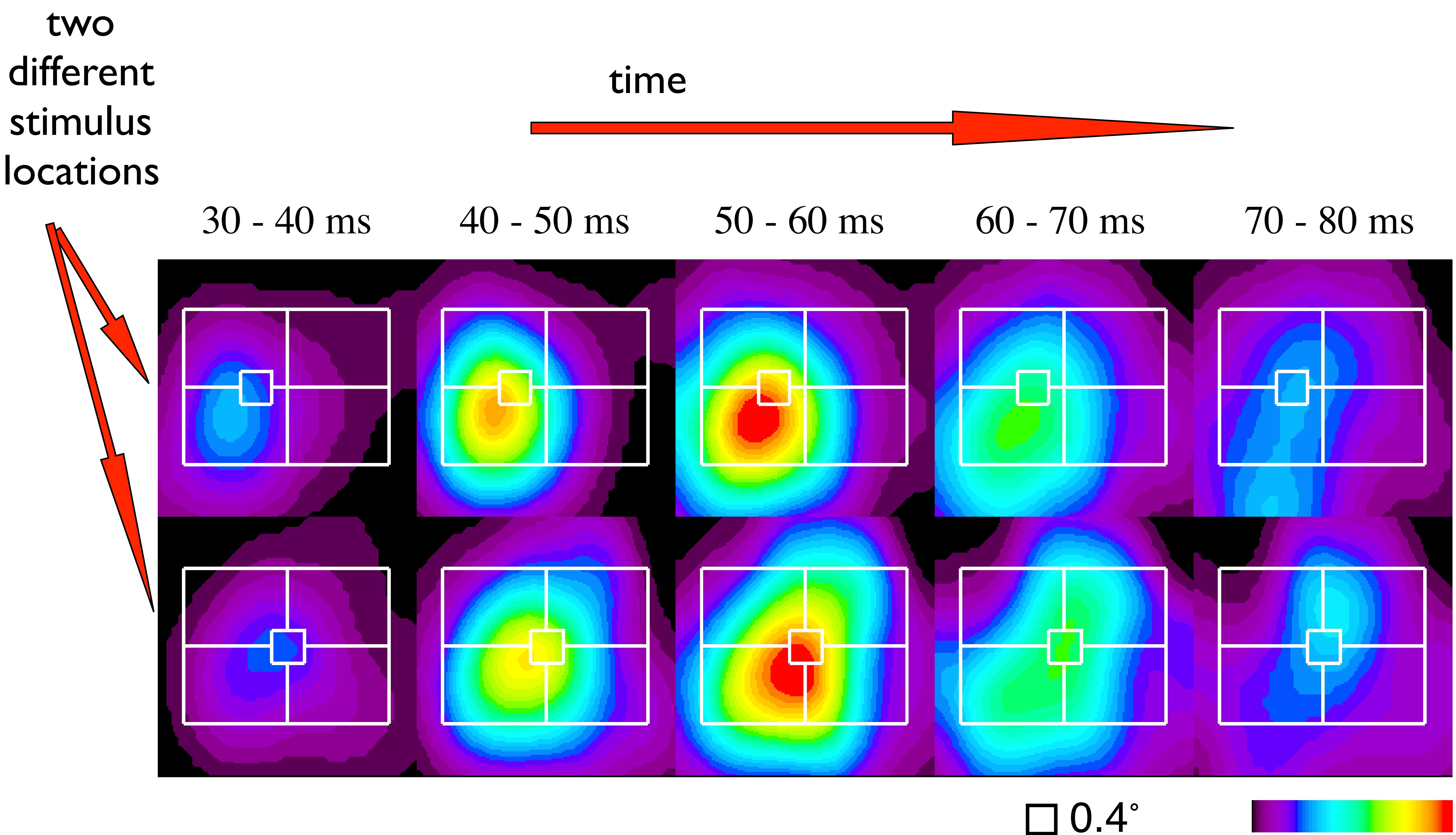




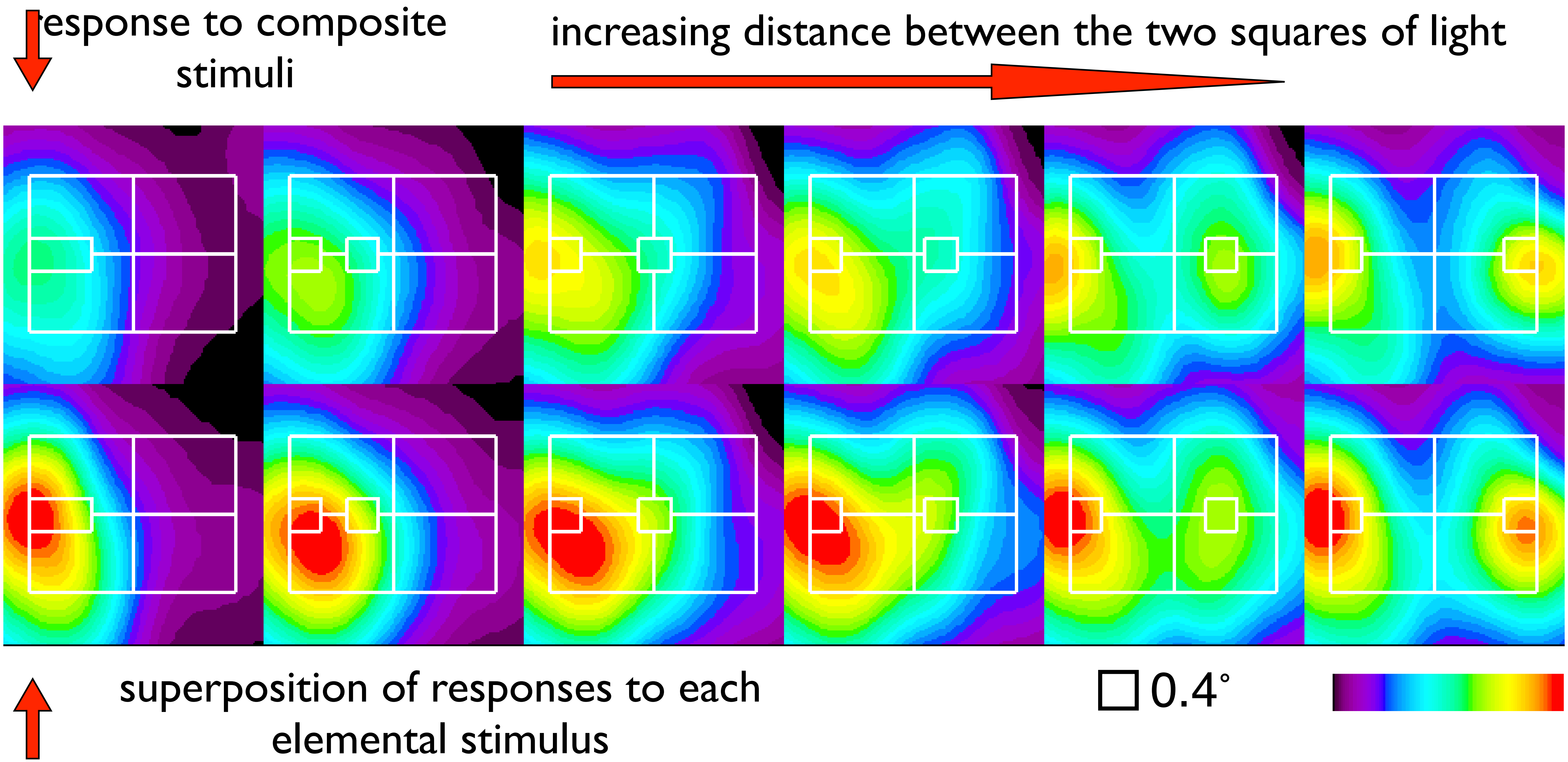
=> does a decent job estimating retinal position



- Extrapolate measurement device to new conditions
- e.g., time resolved

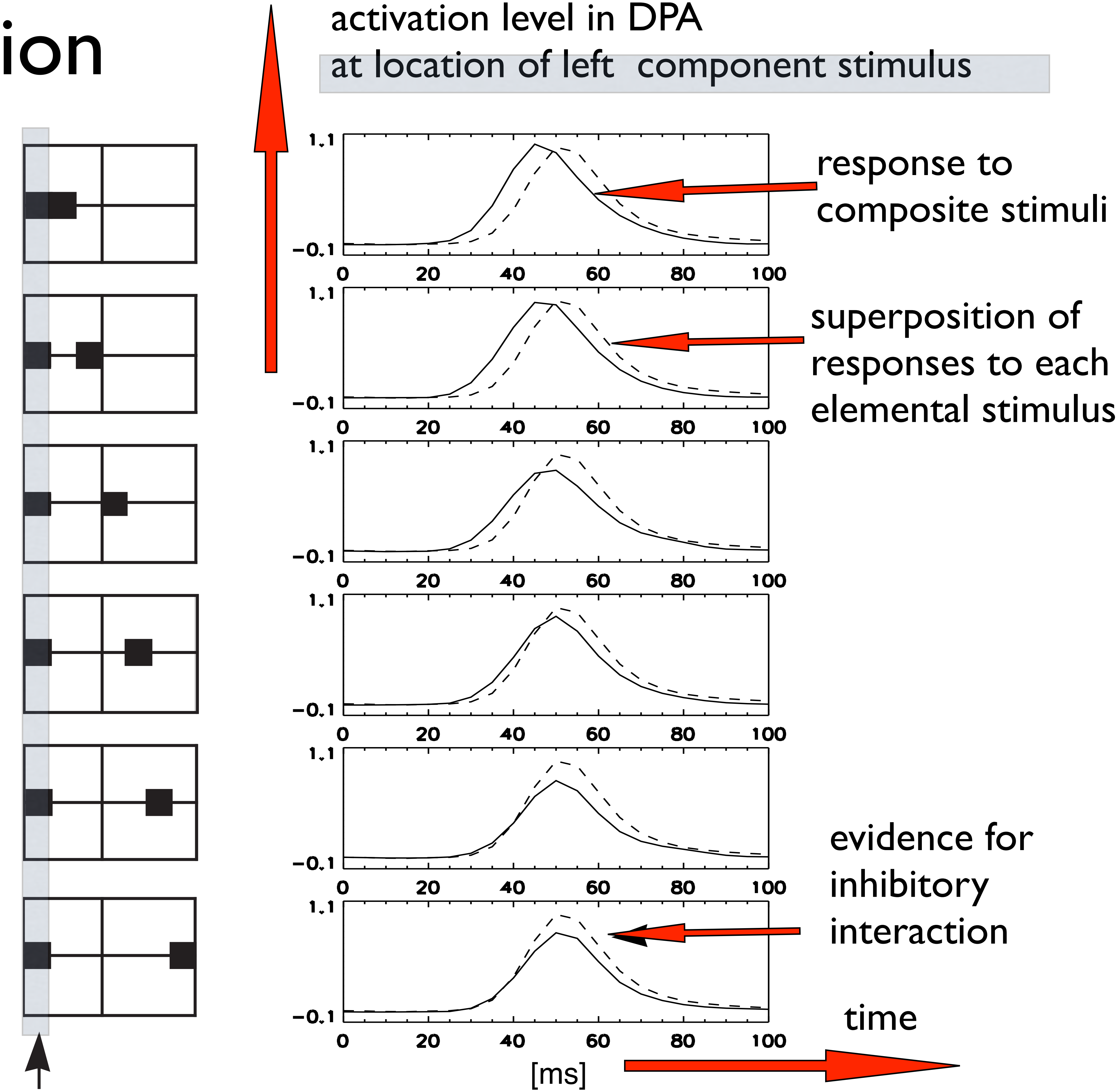


- or when complex stimuli are presented (here: two spots of light)

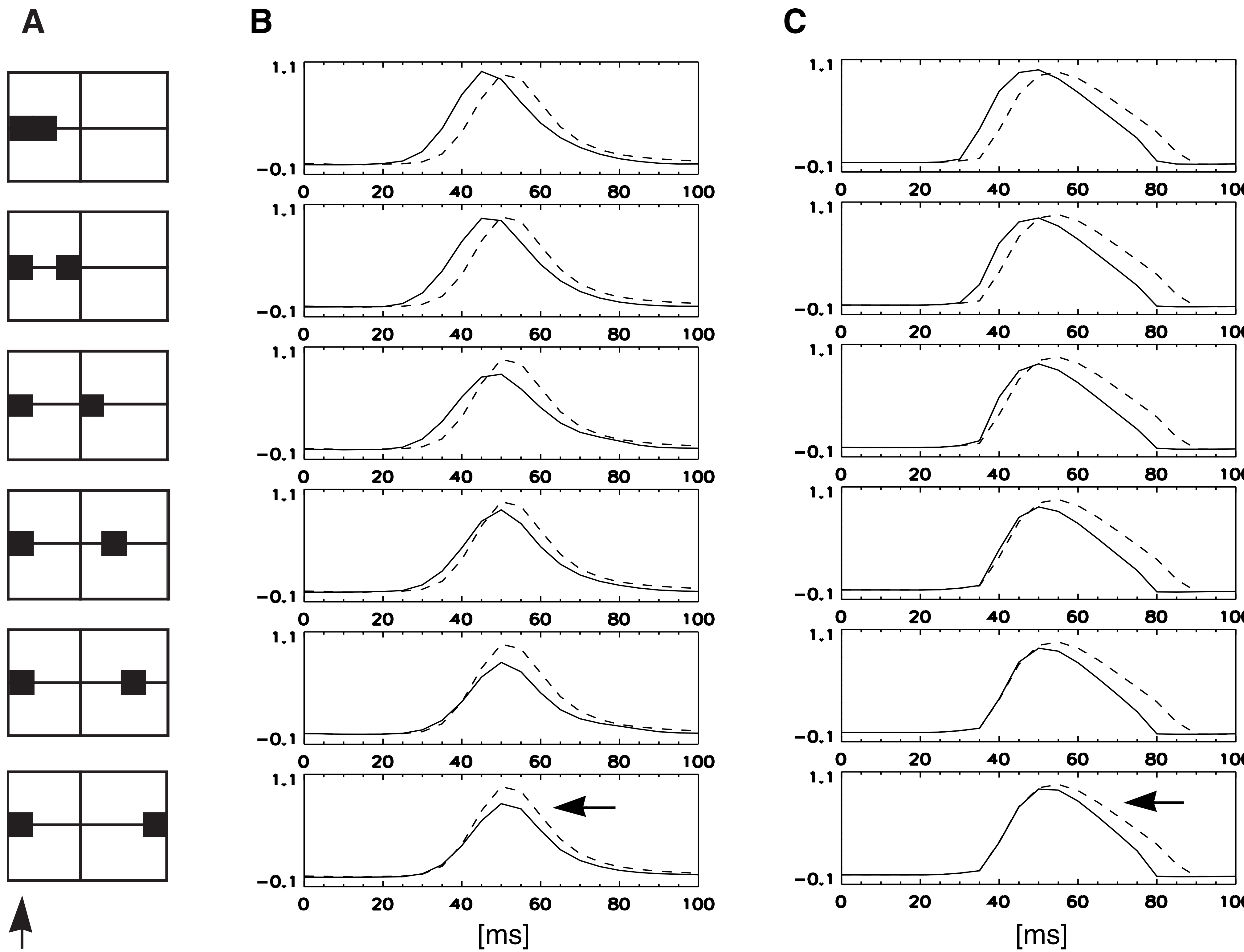


- by comparing DPA of composite stimuli to superposition of DPAs of the two elementary stimuil obtain evidence for interaction
  - early excitation
  - late inhibition

interaction



model by dynamic field:



stimulus experiment DFT model

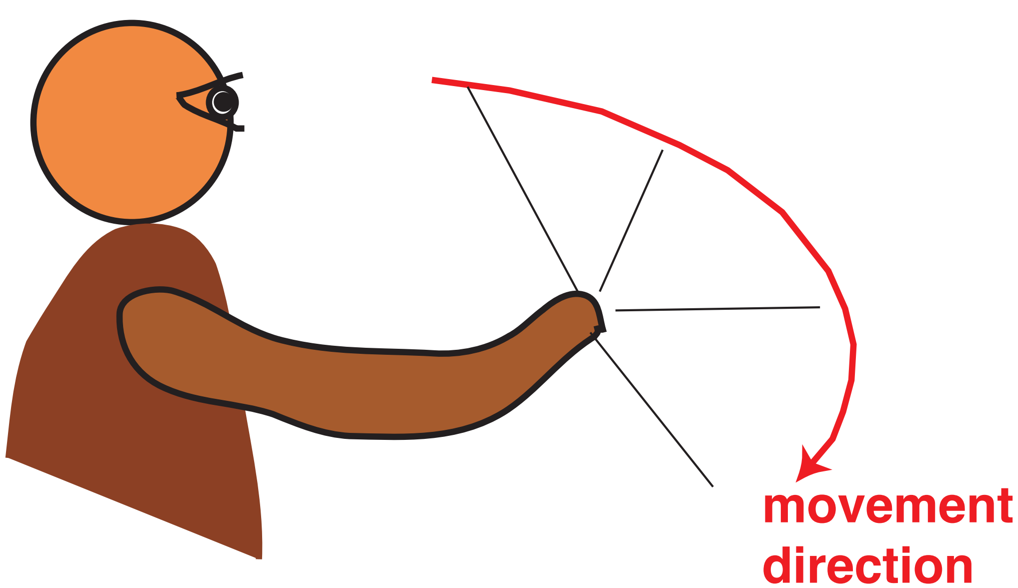
Neurophysiological grounding of DFT

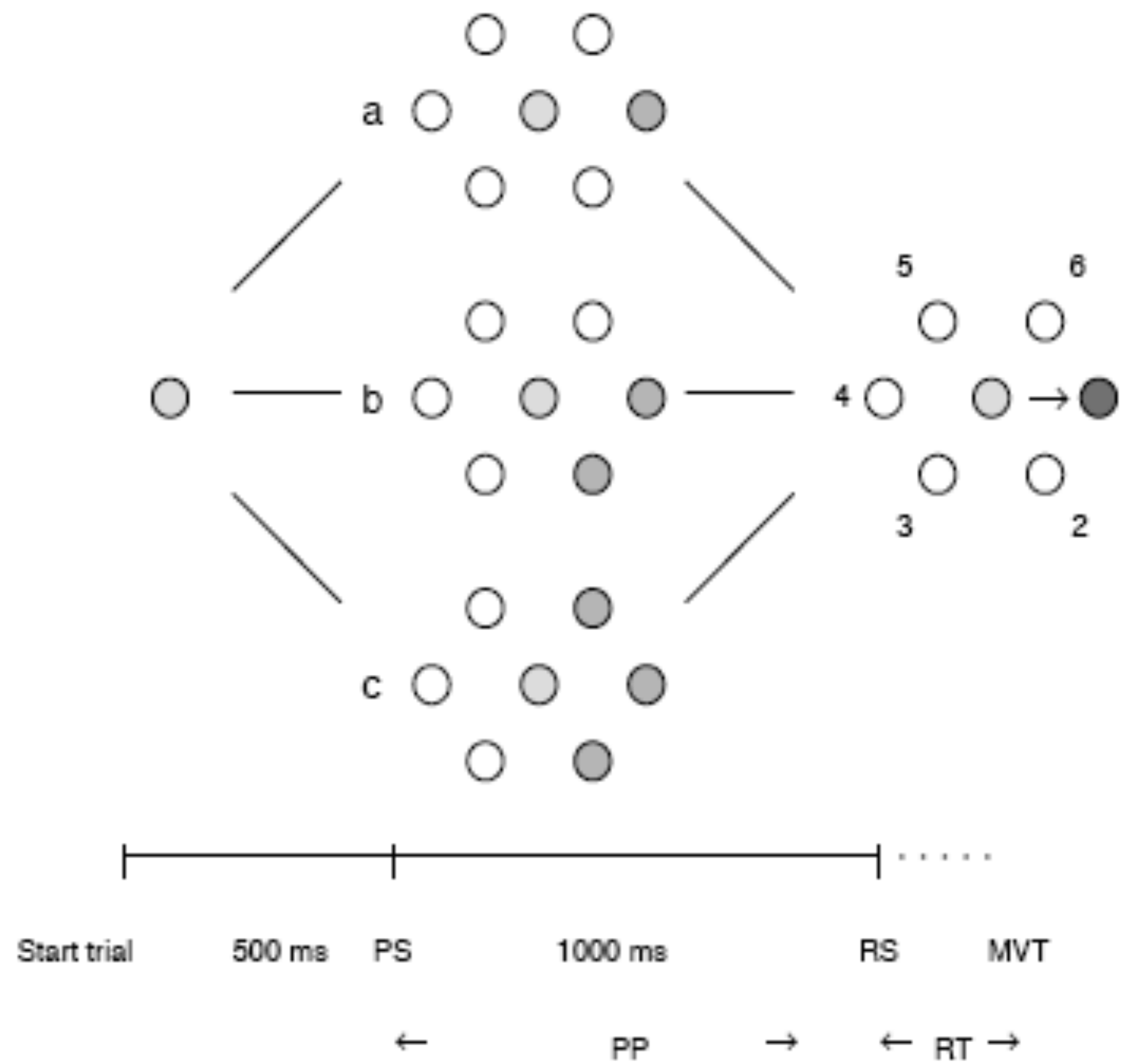
- Example 2: primary motor cortex (M1), population representation of movement direction of the hand

Bastian, Riehle, Schöner, 2003

Task

- center-out movement task for macaque
- with varying amounts of prior information

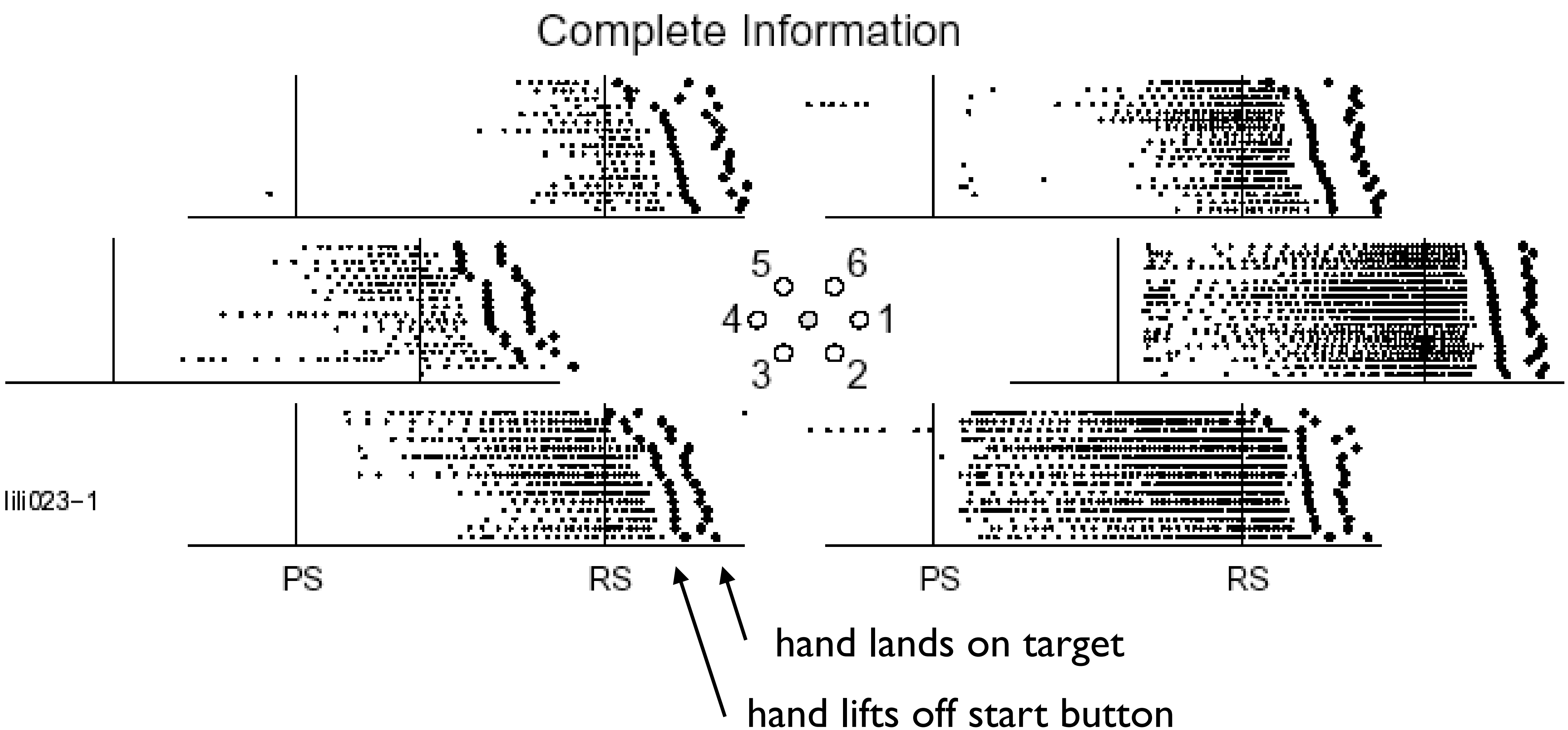




Bastian, Riehle, Schöner, 2003

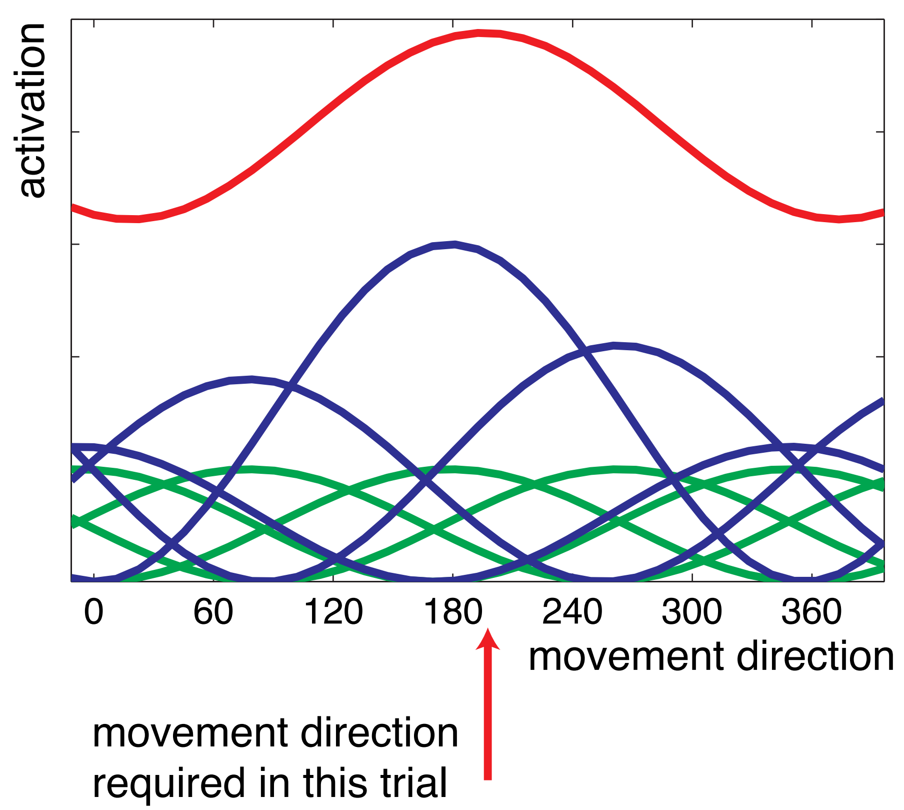
Tuning of neurons in MI to movement direction

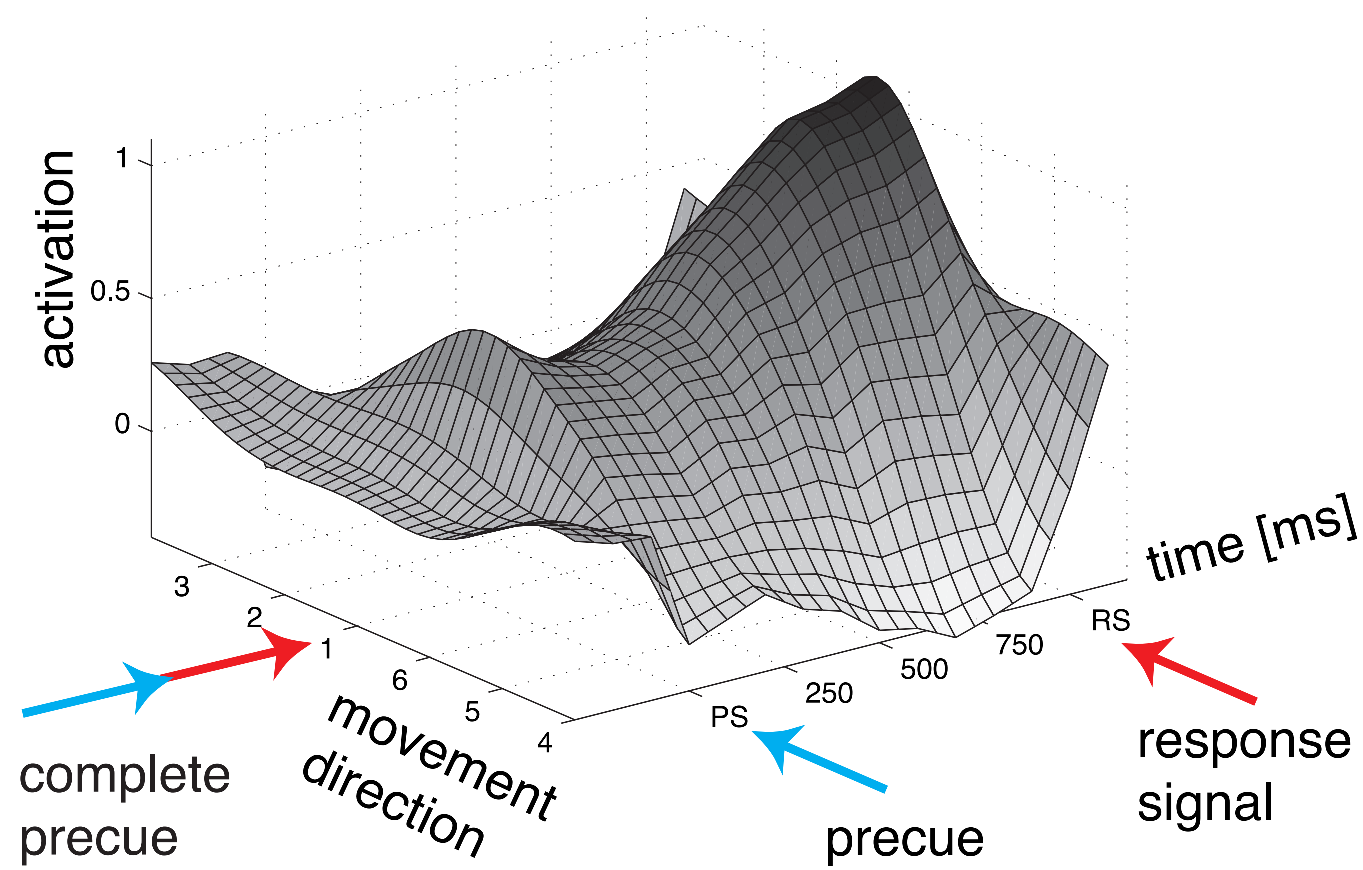
- trials aligned by go signals, ordered by reaction time



Distribution of Population Activation (DPA)

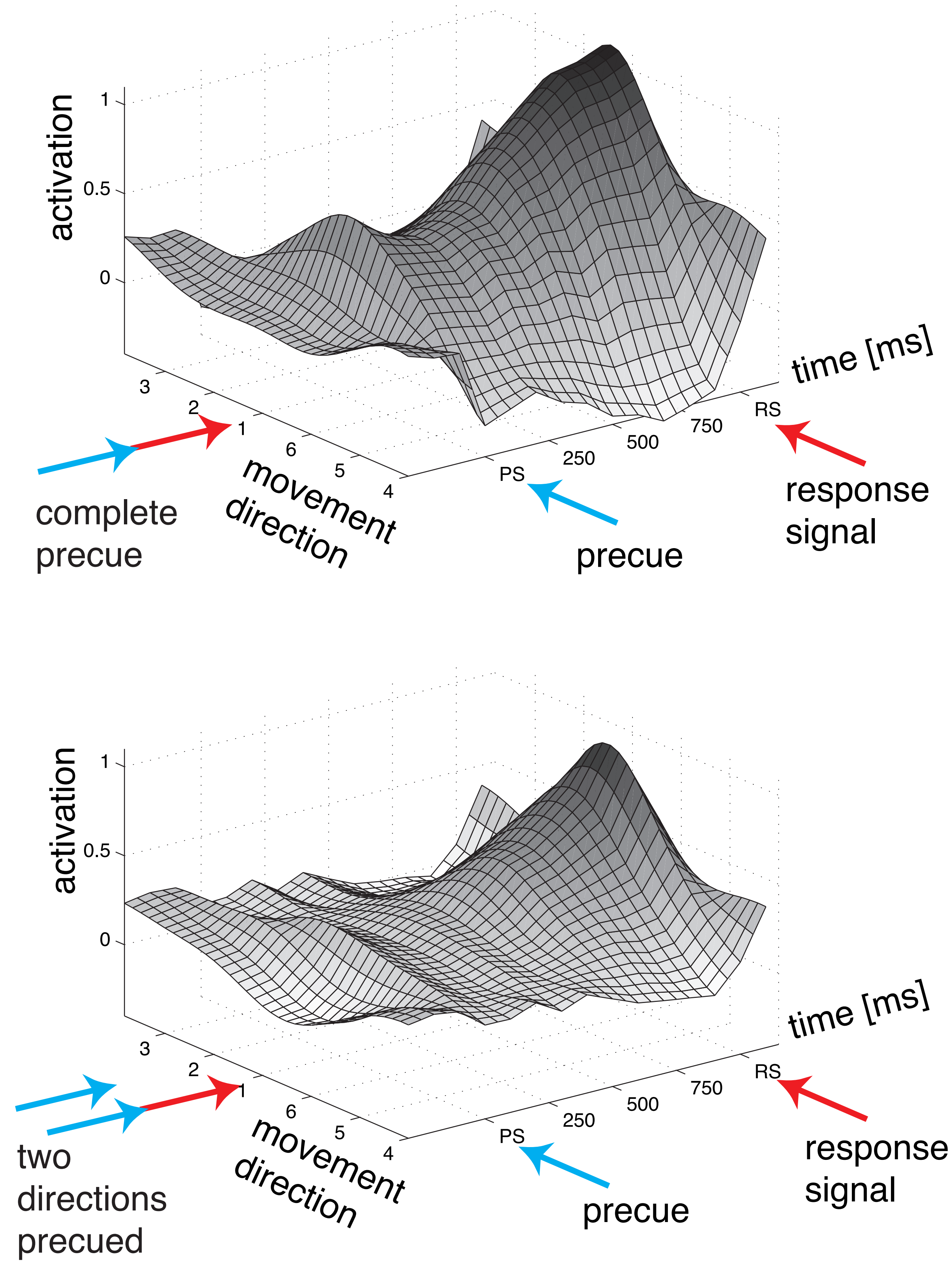
Distribution of population activation =
$\sum_{\text{neurons}}$ tuning curve * current firing rate



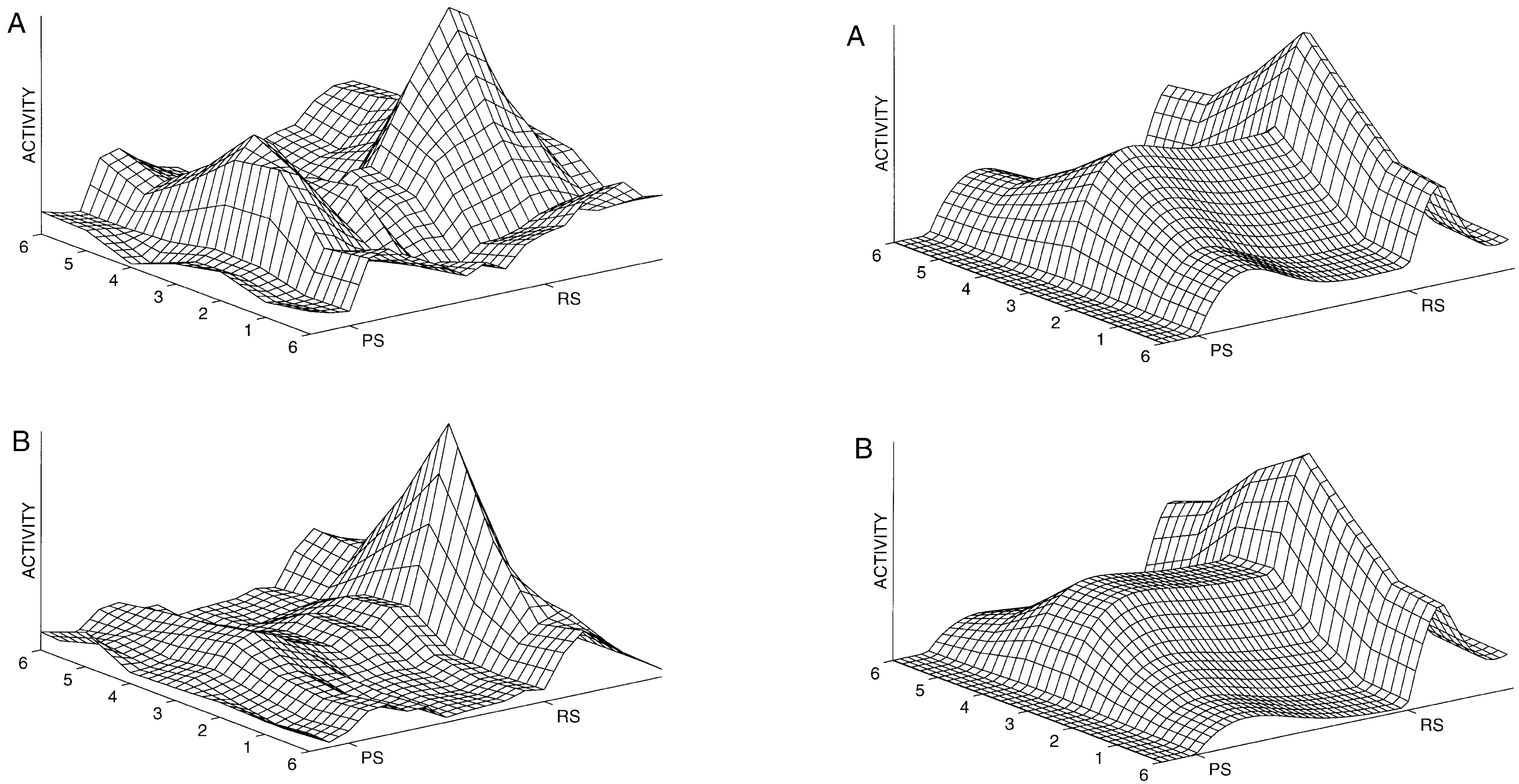


[Bastian, Riehle, Schöner, 2003]

- look at temporal evolution of DPA
- or DPAs in new conditions, here: DPA reflects prior information



Theory-Experiment



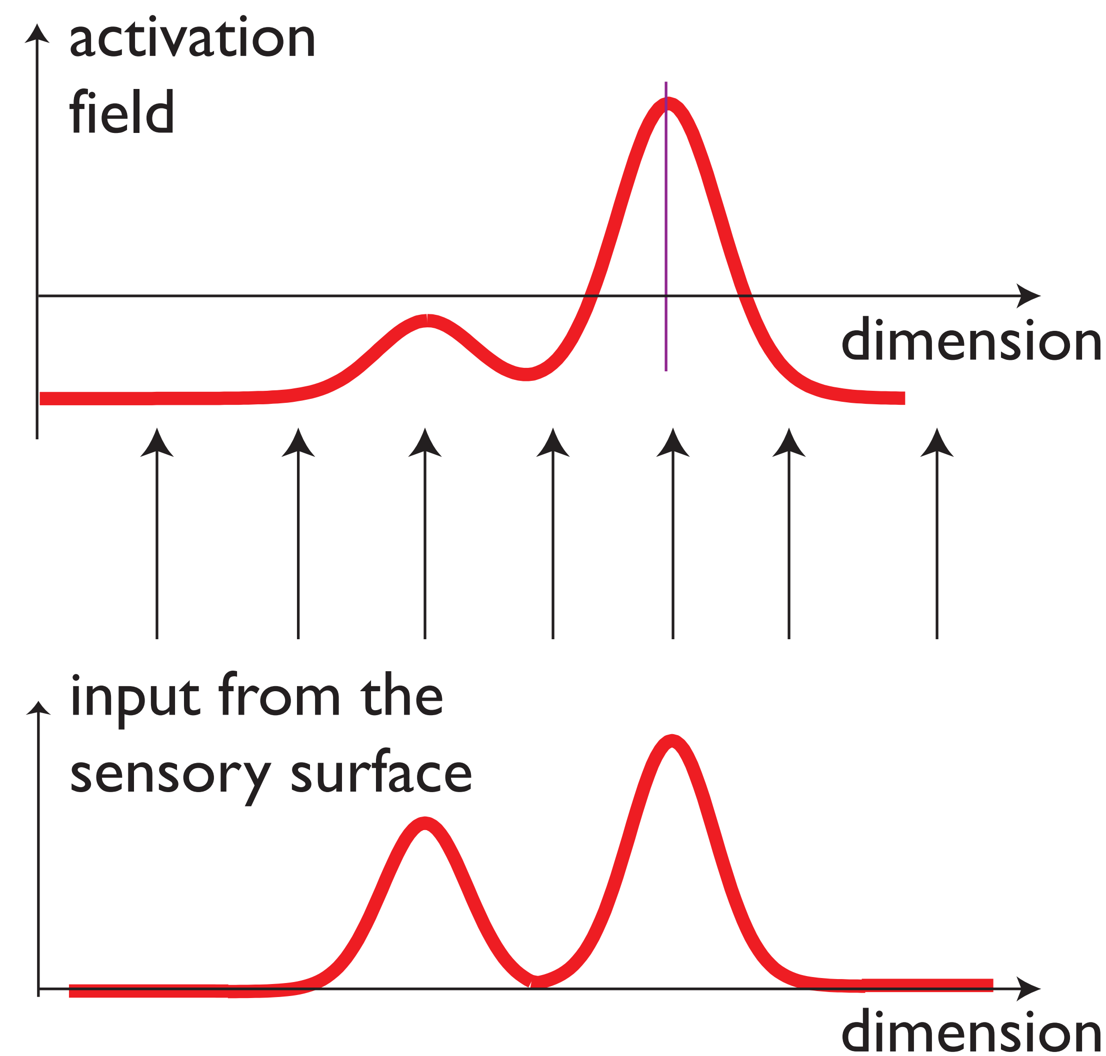
[Bastian, Riehle, Erlhagen, Schöner, 98]

Distributions of Population Activation are abstract

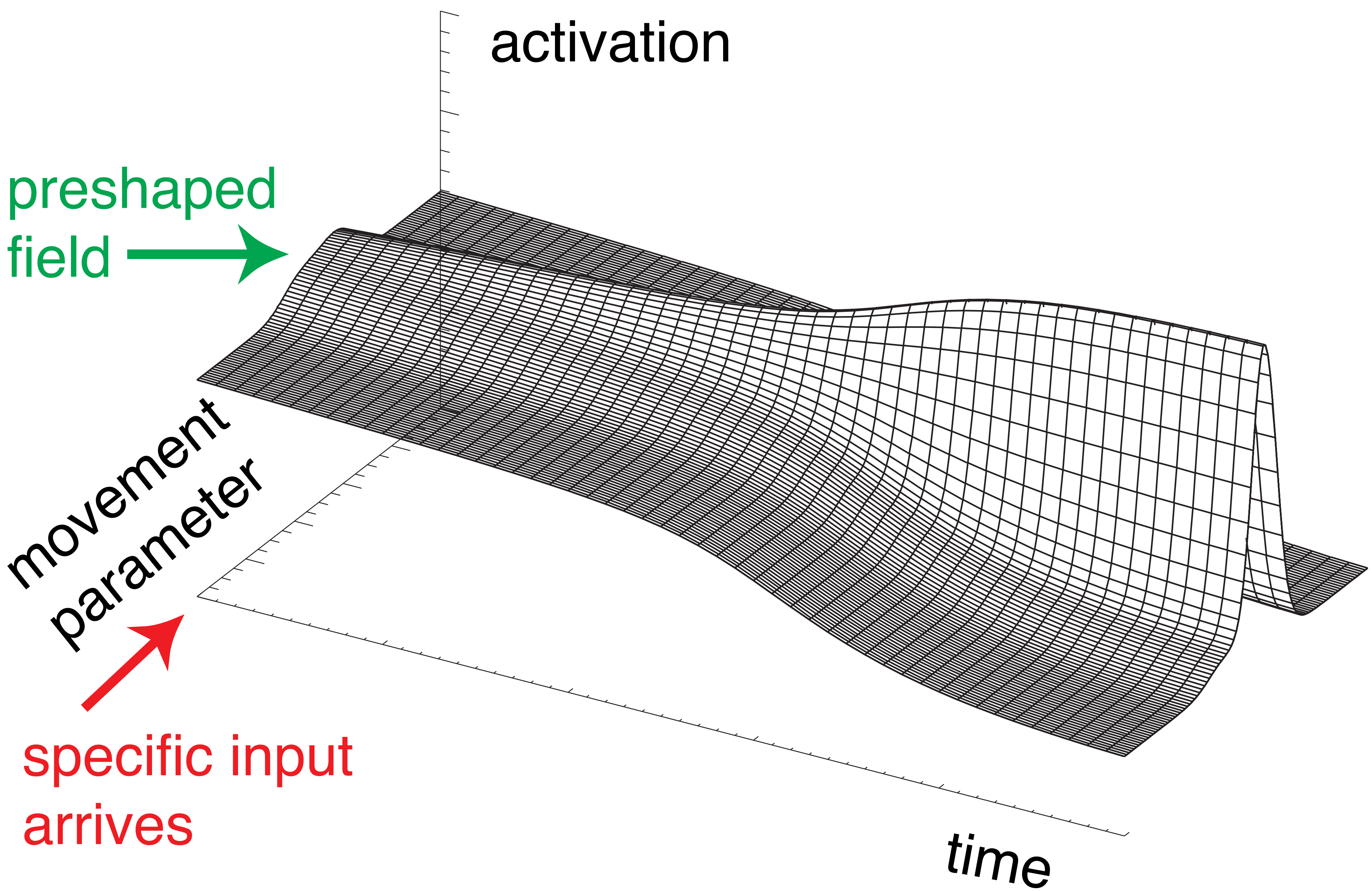
- neurons are not localized within DPA!
- cortical neurons really are sensitive to many dimensions
  - motor: arm configuration, force direction
  - visual: many feature dimensions such as spatial frequency, orientation, direction...
- => DPA is a projection from that high-dimensional space onto a single dimension

… back to the activation fields

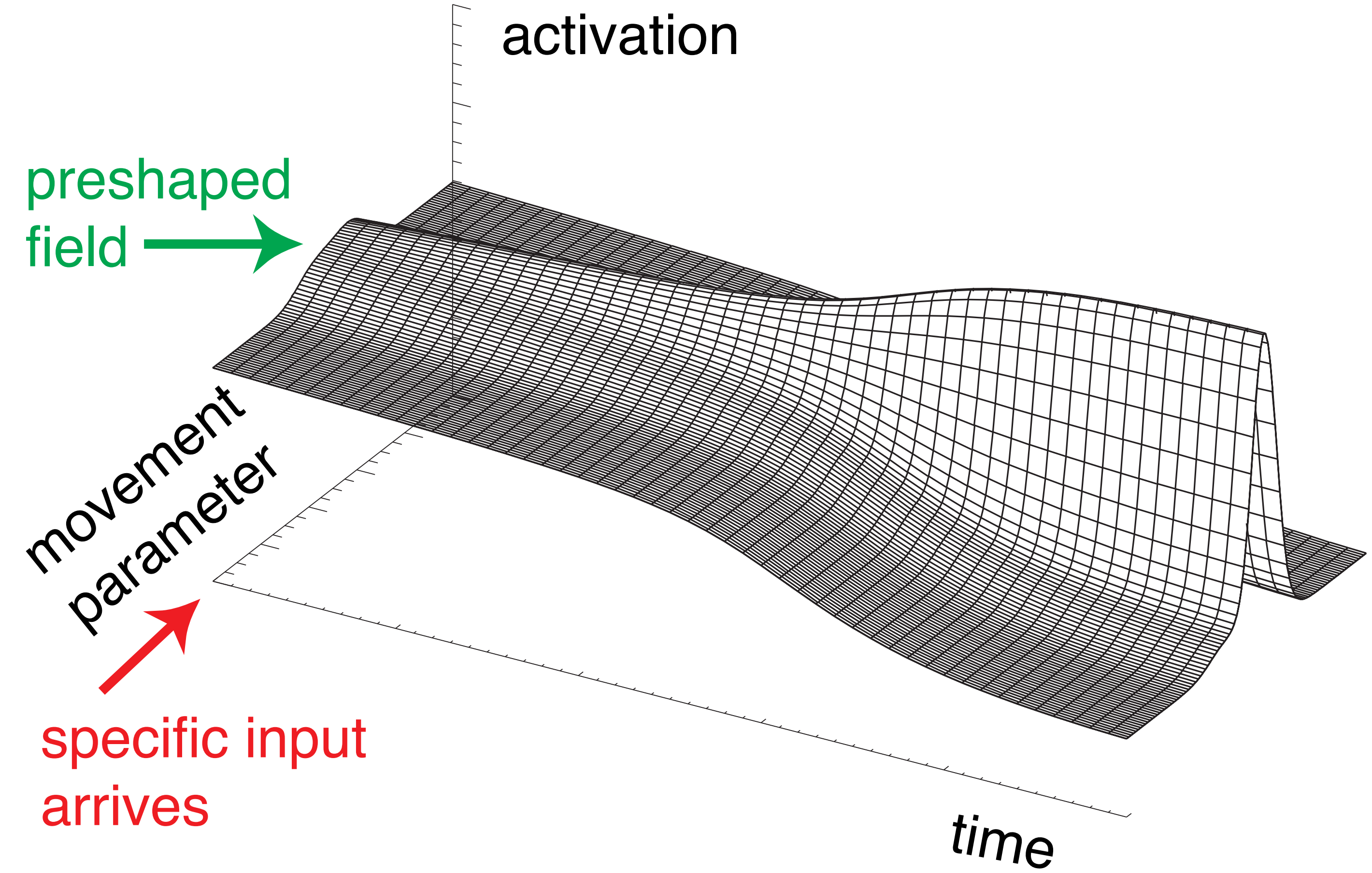
- that are "defined" over the appropriate dimension just as population code is…
- in building DFT models, we must ensure that this is actually true by setting up the appropriate input/output connectivity

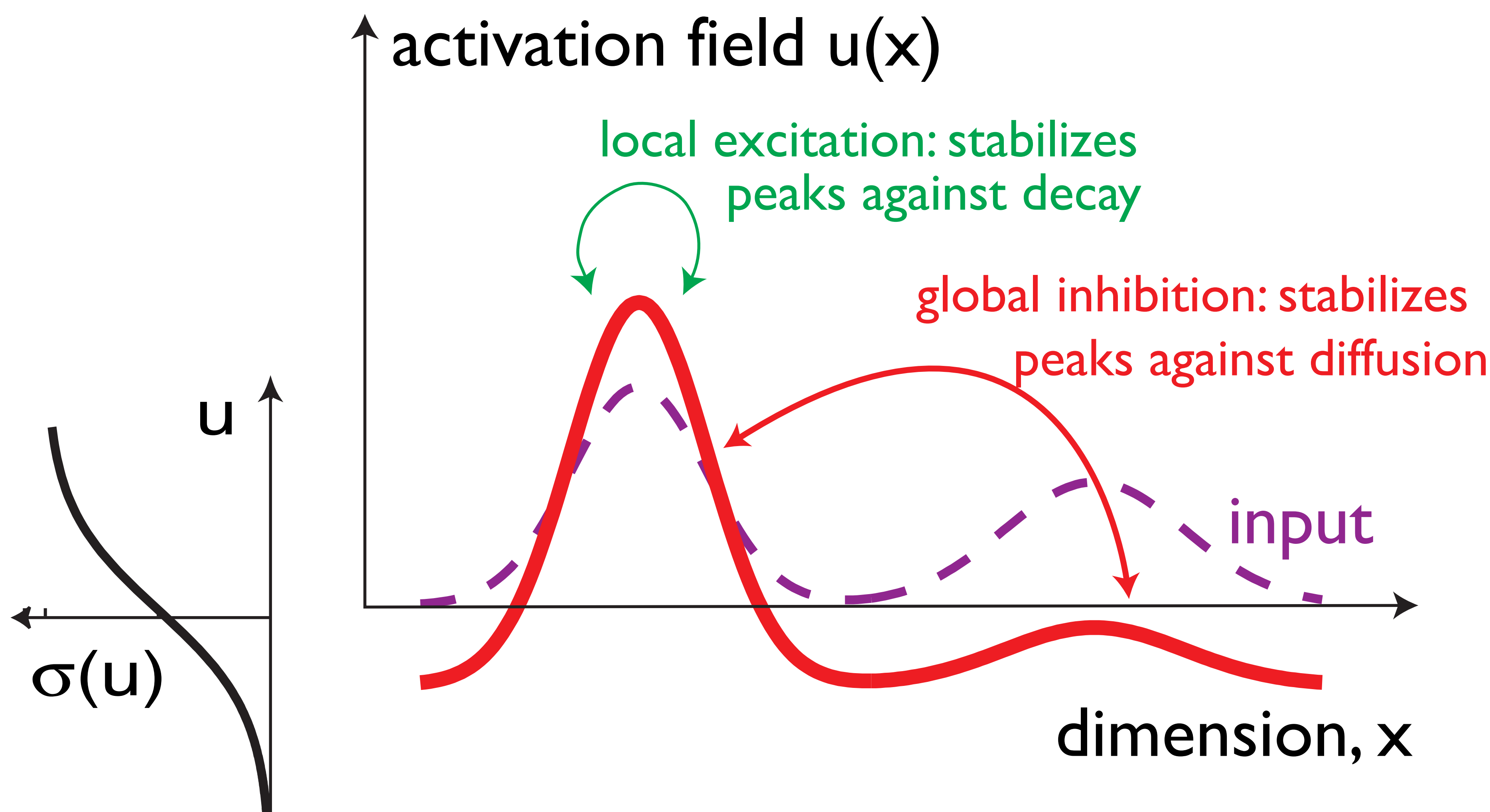


Neural dynamics of activation fields



The neural dynamics a activation fields is structured so that localized peaks are attractors





mathematical formalization

Amari equation

$$\tau\dot{u}(x,t) = -u(x,t) + h + S(x,t) + \int w(x-x')\sigma(u(x',t))\ dx'$$

where

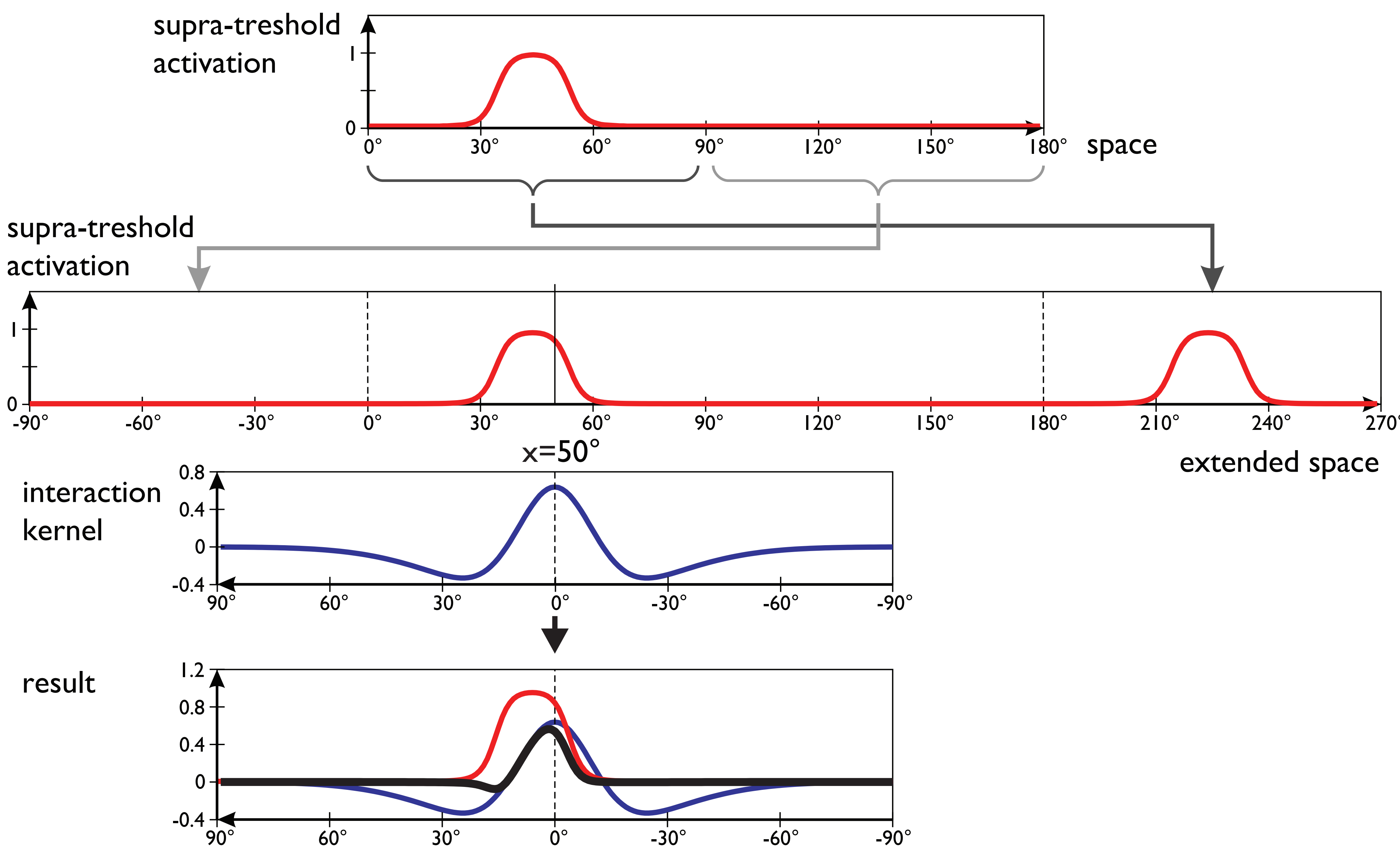
- time scale is τ
- resting level is $h < 0$
- input is $S(x,t)$
- interaction kernel is

$$w(x-x') = w_i + w_e \exp\left[-\frac{(x-x')^2}{2\sigma_i^2}\right]$$

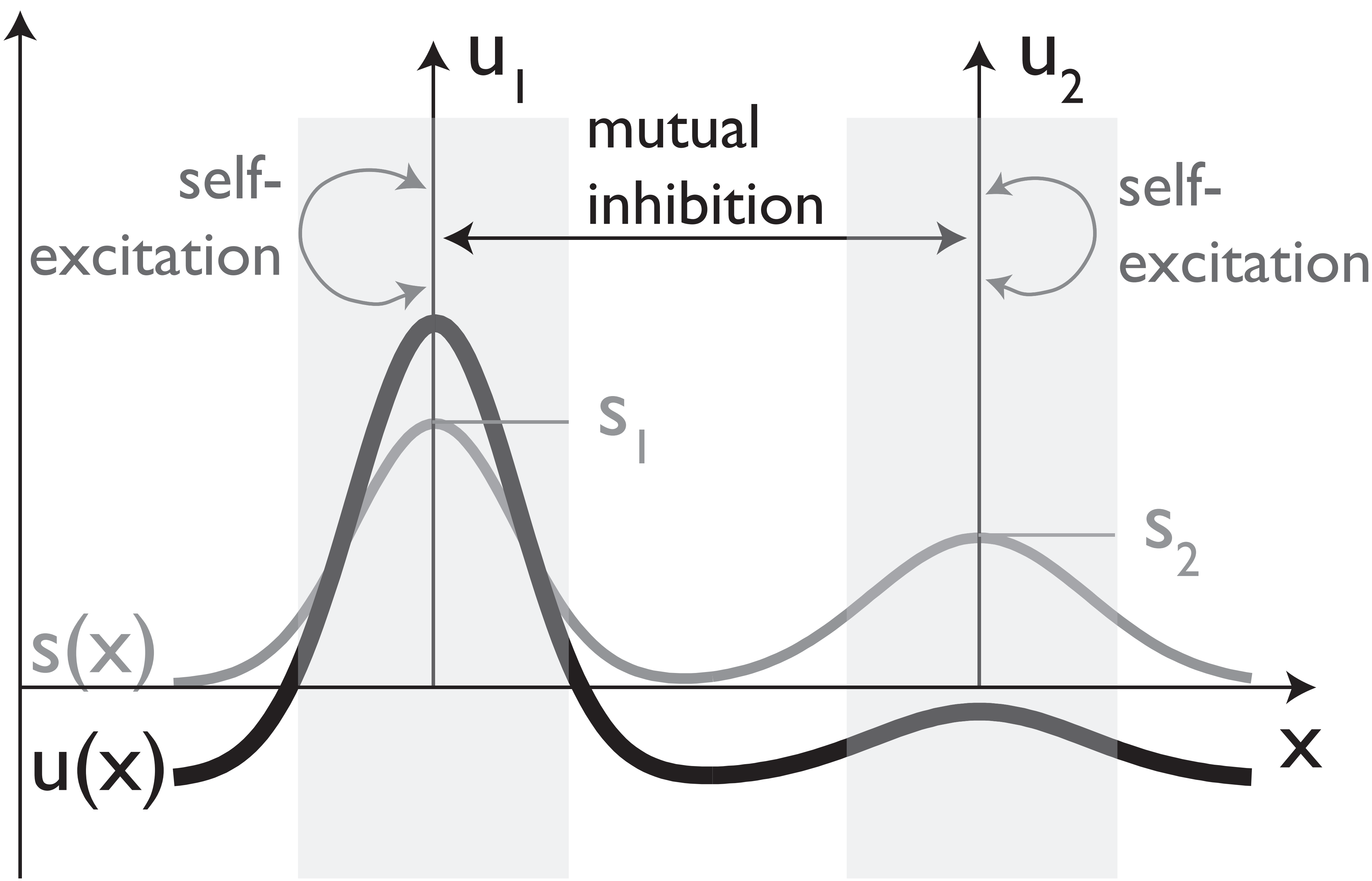
- sigmoidal nonlinearity is

$$\sigma(u) = \frac{1}{1+\exp[-\beta(u-u_0)]}$$

Interaction: convolution



Relationship to the dynamics of discrete activation variables

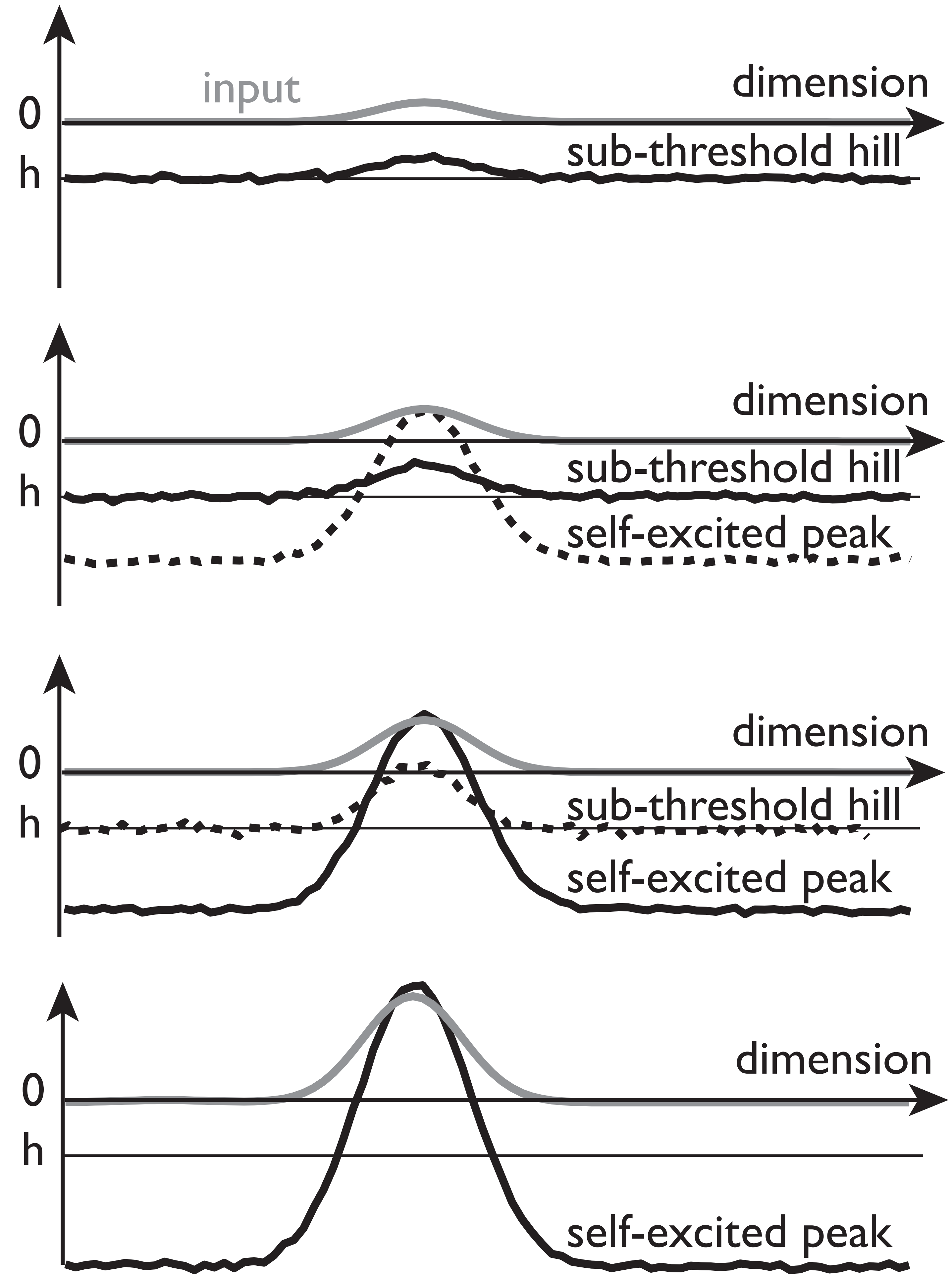


=> simulations

Solutions and instabilities

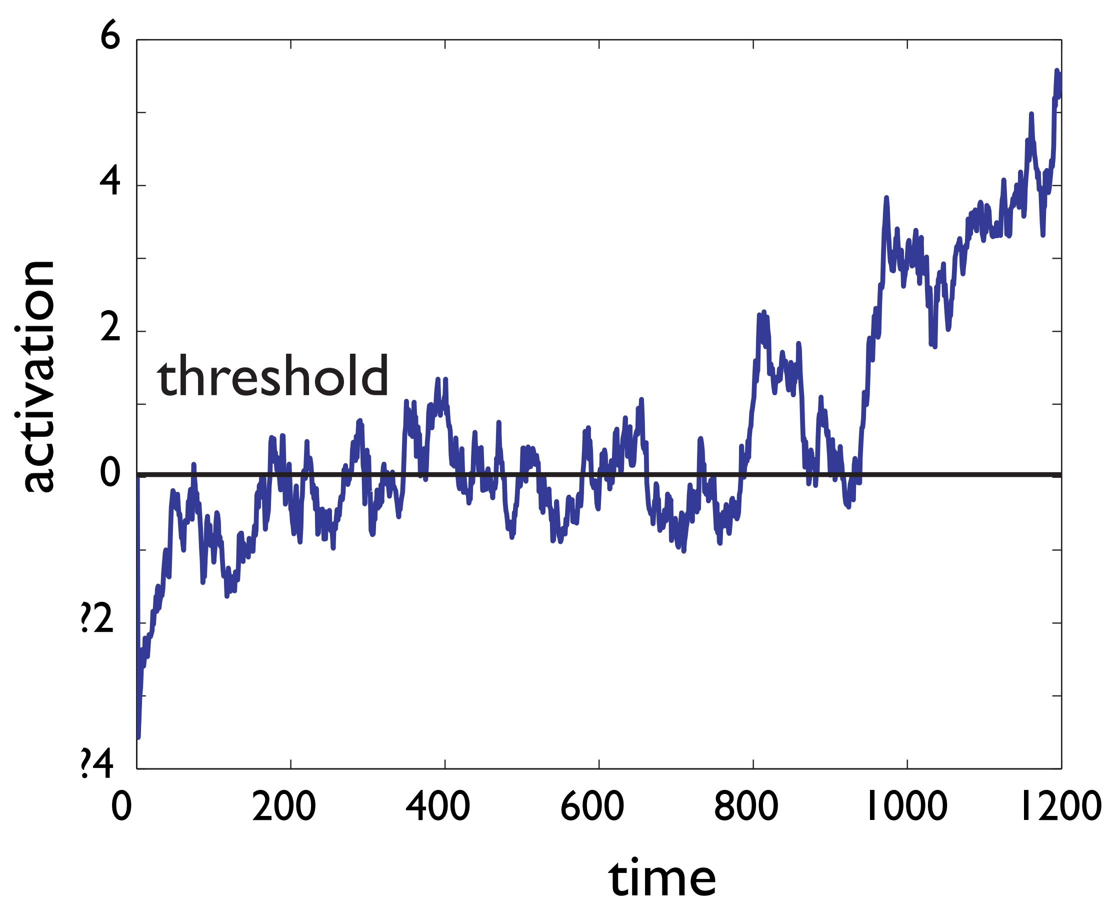
- input driven solution (sub-threshold) vs. self-stabilized solution (peak, supra-threshold)
- detection instability
- reverse detection instability
- selection
- selection instability
- memory instability
- detection instability from boost

Detection instability

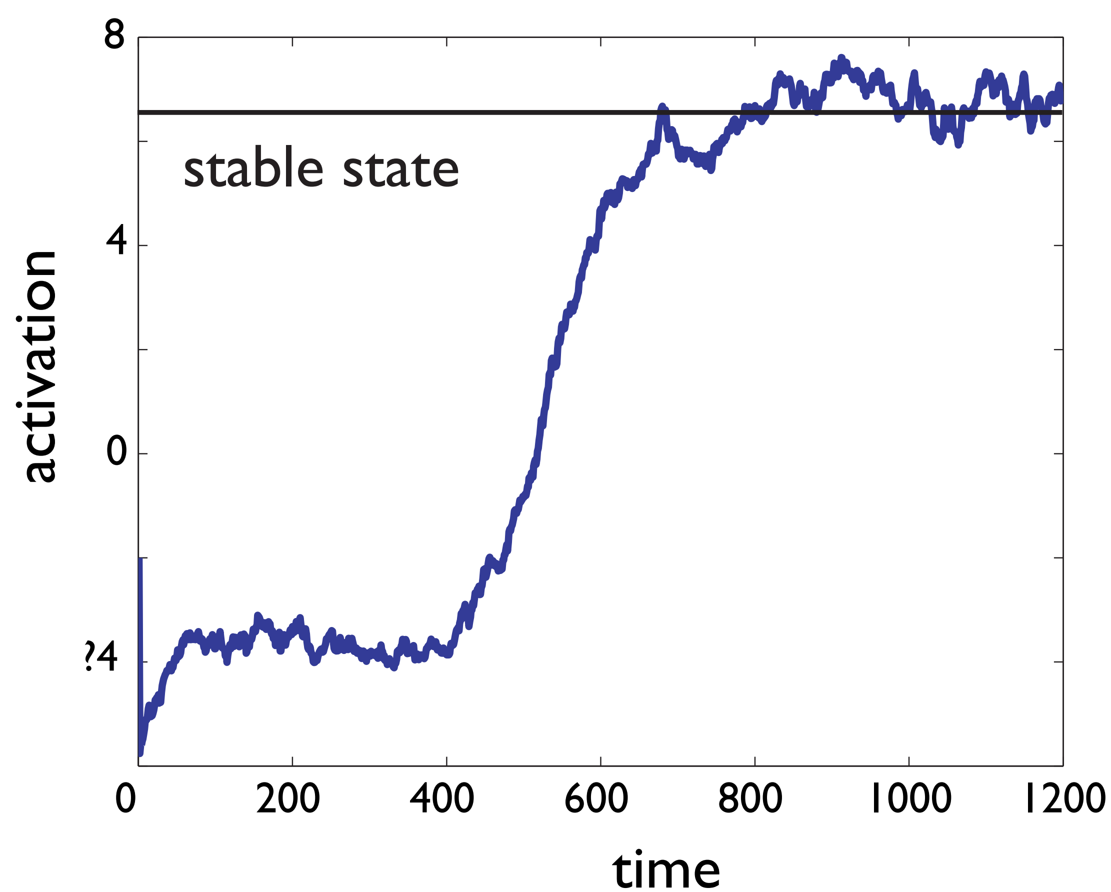


the detection instability helps stabilize decisions

threshold piercing



detection instability



the detection instability helps stabilize decisions

- self-stabilized peaks are macroscopic neuronal states, capable of impacting on down-stream neuronal systems
- (unlike the microscopic neuronal activation that just exceeds a threshold)

emergence of time-discrete events

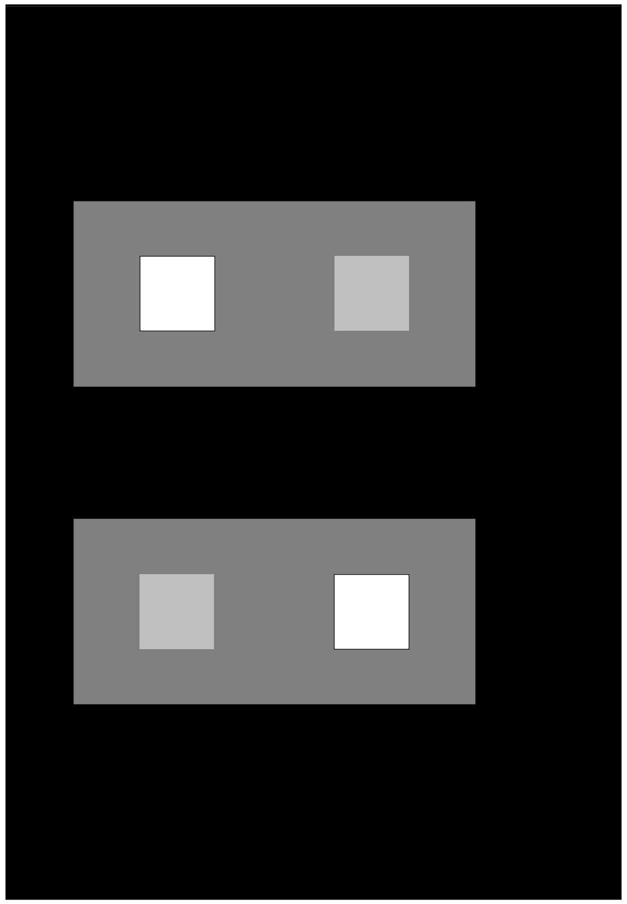
- the detection instability also explains how a time-continuous neuronal dynamics may create macroscopic, time-discrete events

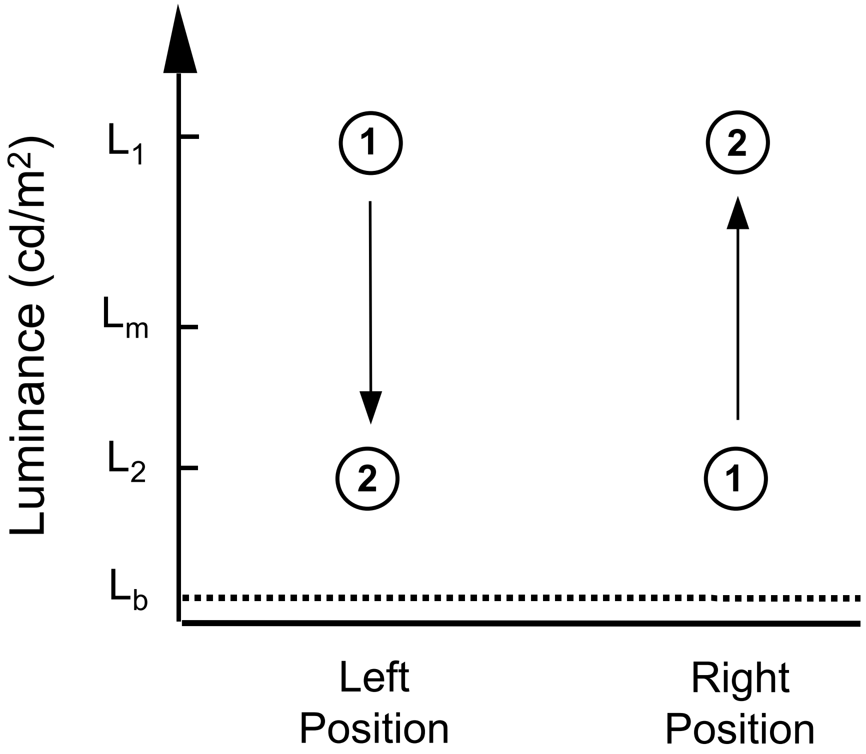
behavioral signatures of detection decisions

- detection in psychophysical paradigms is rife with hysteresis
- but: minimize response bias

Detection instability

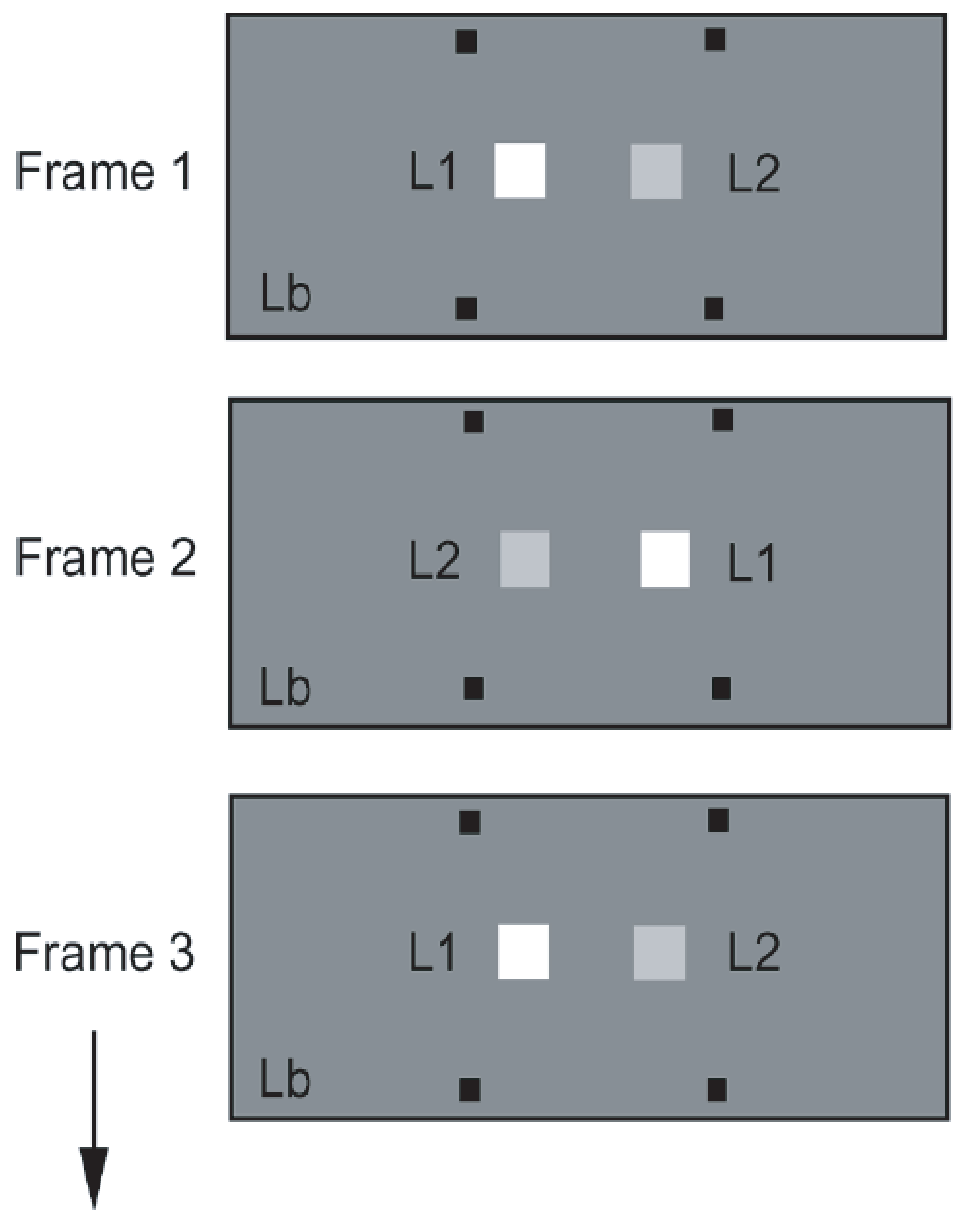
- in the detection of Generalized Apparent Motion





Detection instability

- varying BRLC



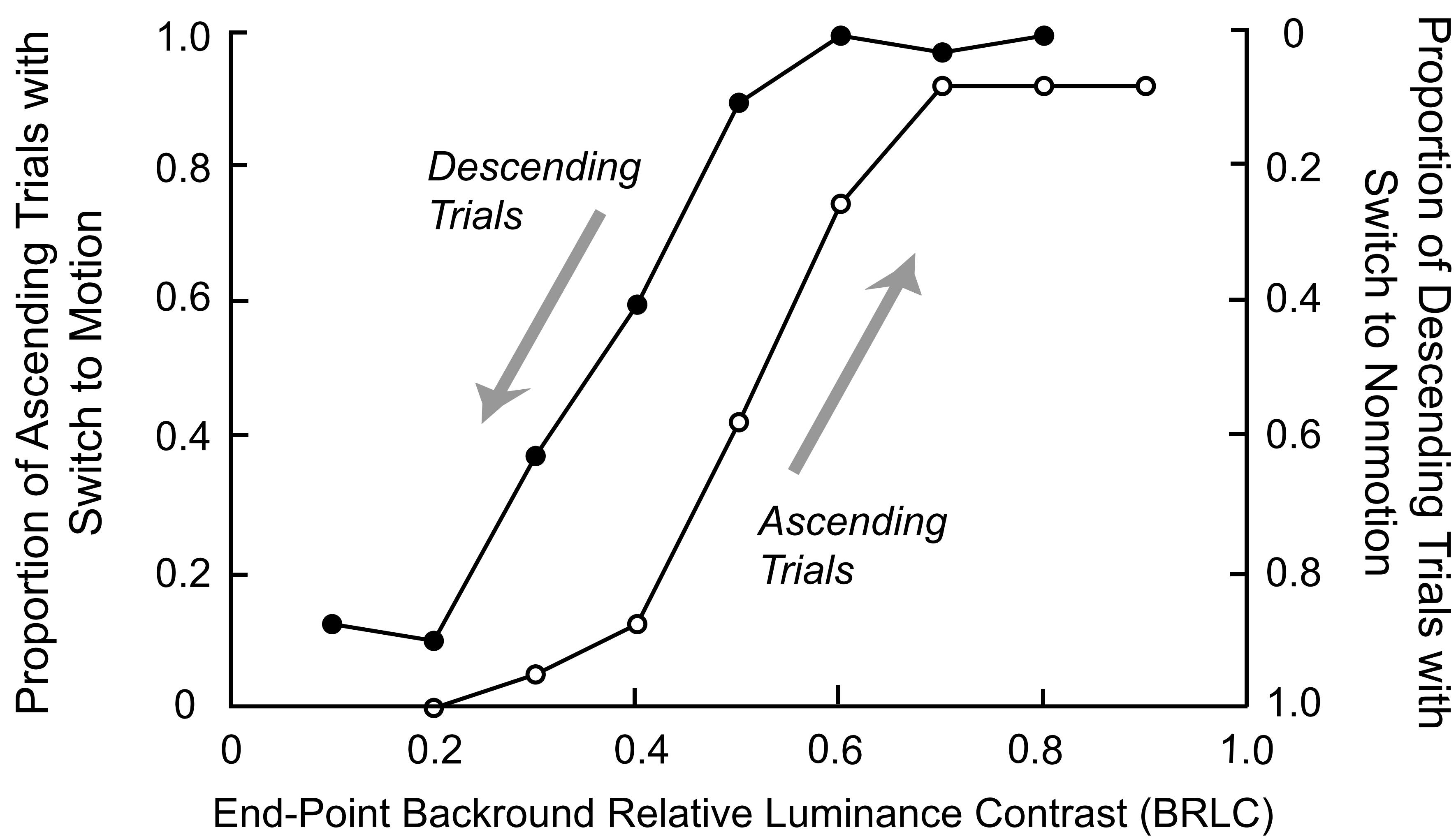
$$Lm = \frac{L1 + L2}{2}$$

$$\text{Background-Relative Luminance Change (BRLC)} = \frac{L1 - L2}{Lm - Lb}$$

Detection instability

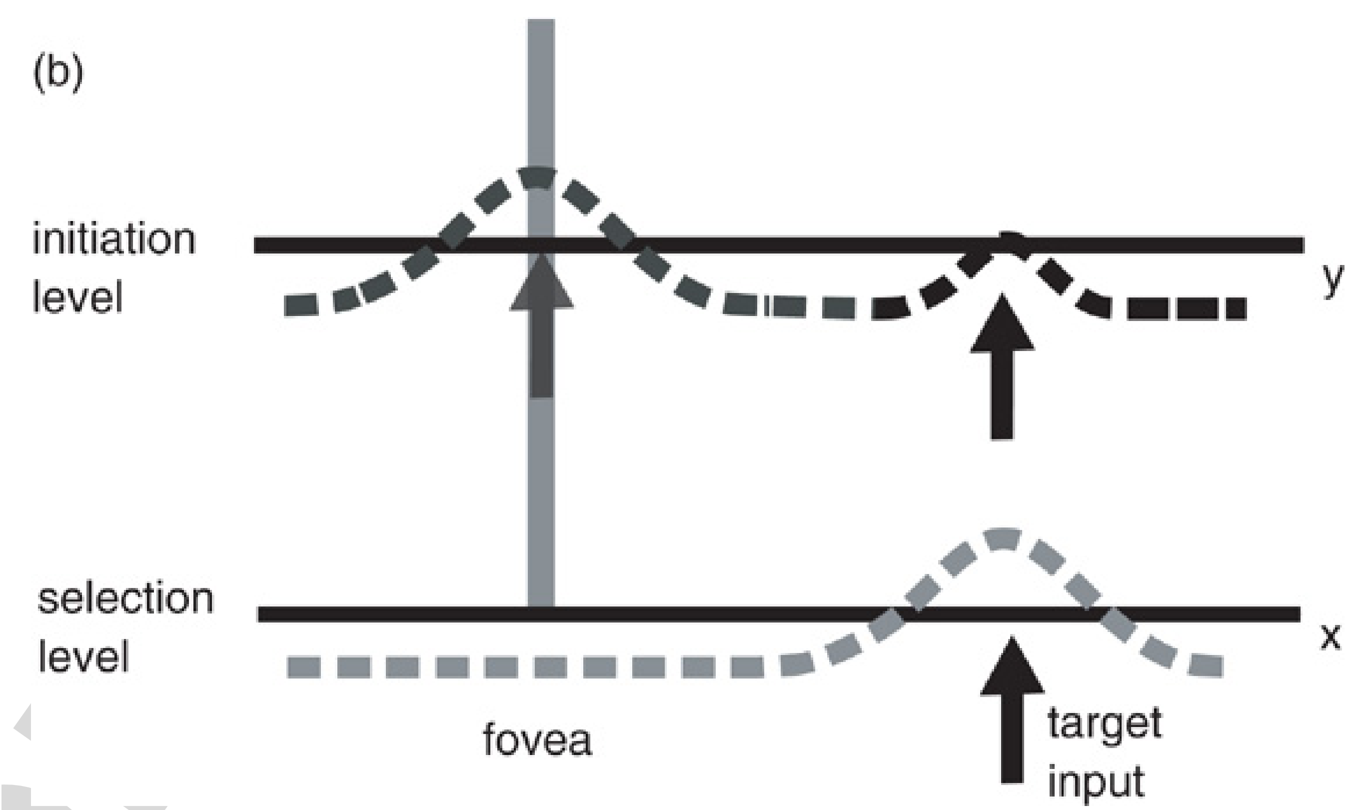
- hysteresis of motion detection as BRLC is varied
- (while response bias is minimized)

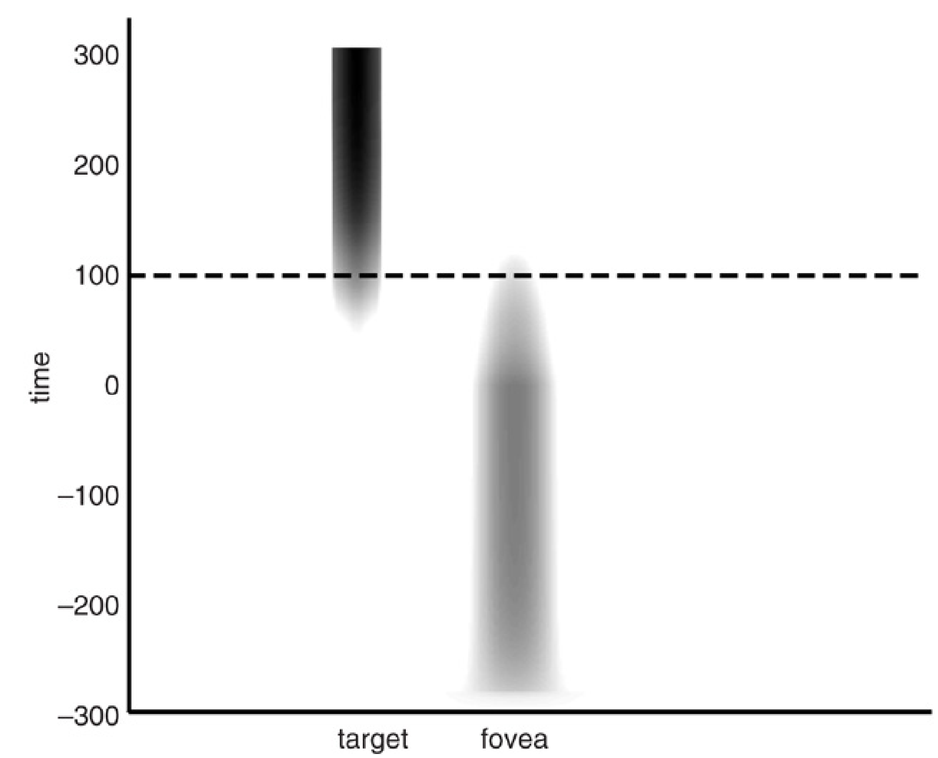
H. S. Hock, G. Schöner / Seeing and Perceiving 23 (2010) 173–195



overcoming fixation

- detection can be like selection: initiating an action means terminating the non-action=fixation or posture
- example: saccade initiation

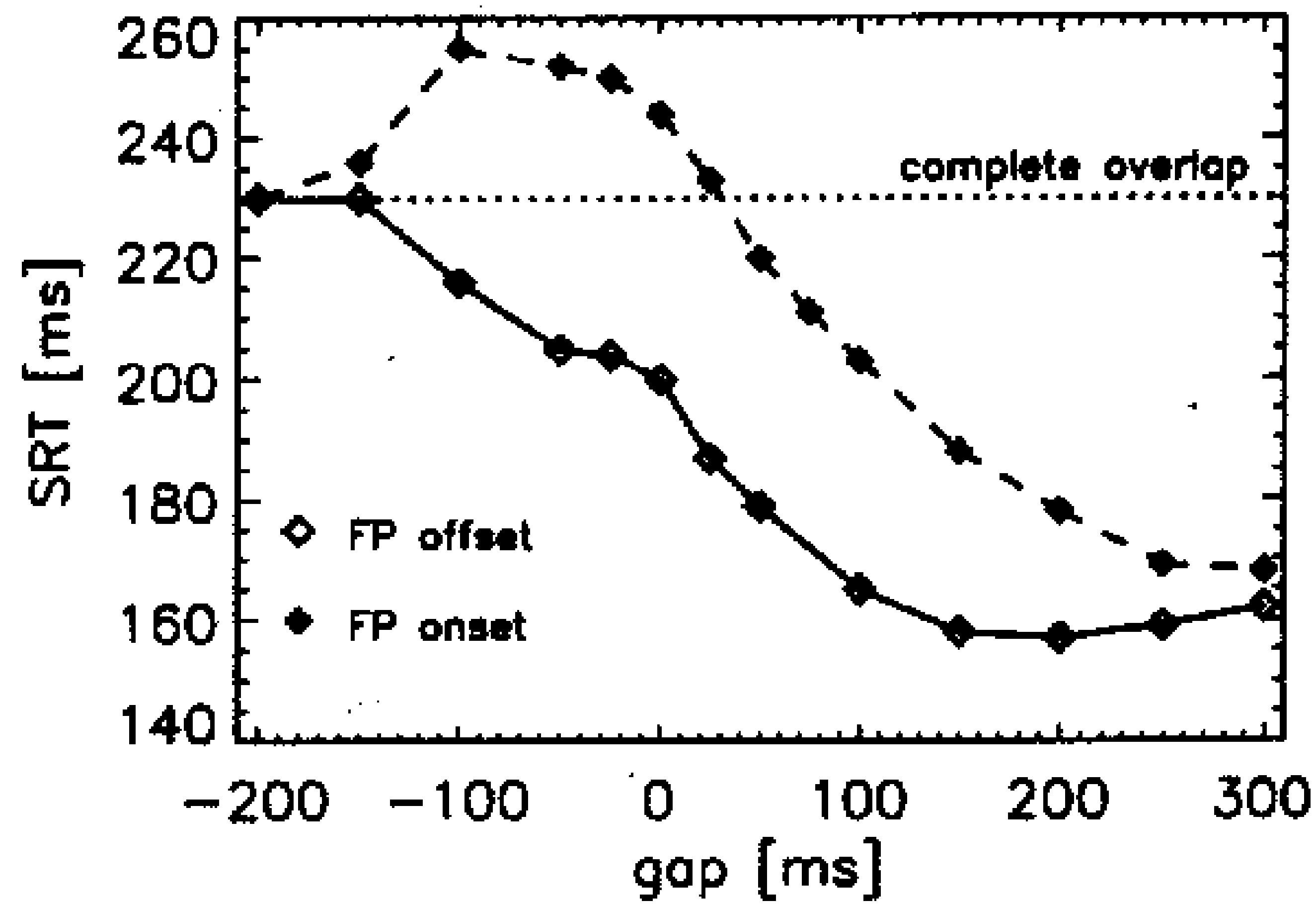


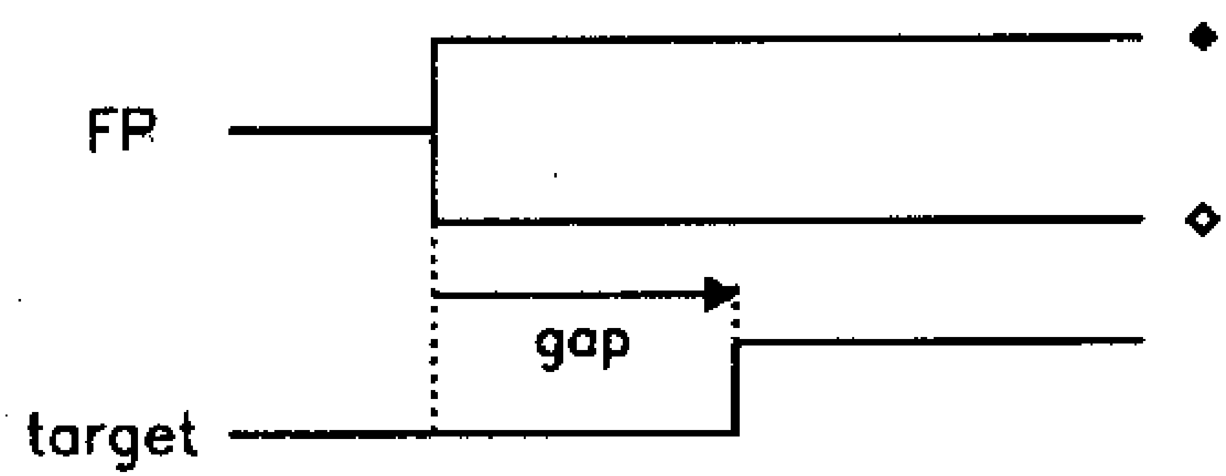


[Wilimzig, Schneider, Schöner, 2006]

initiation vs. fixation

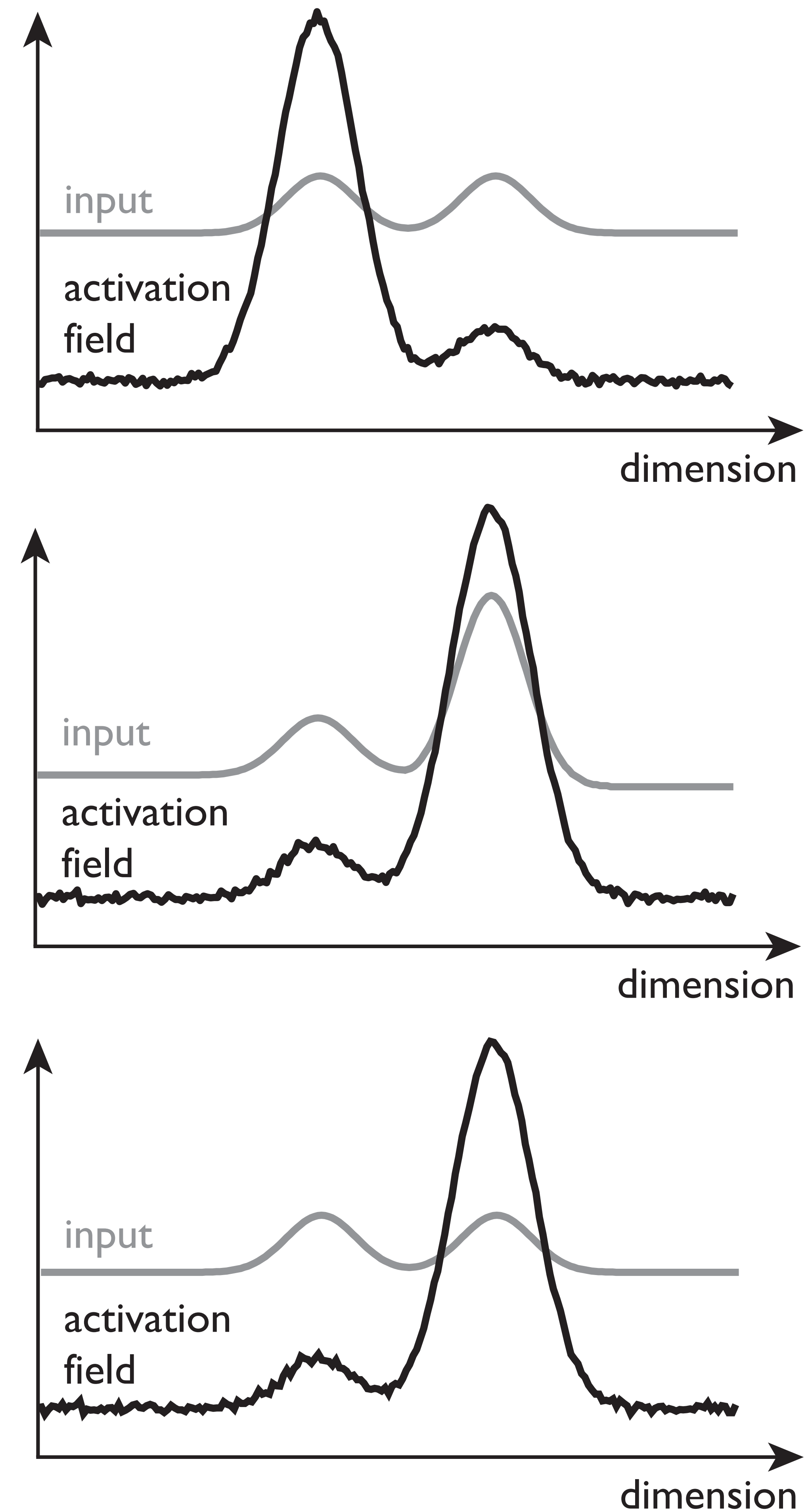
- such models account for the gap-step-overlap effect



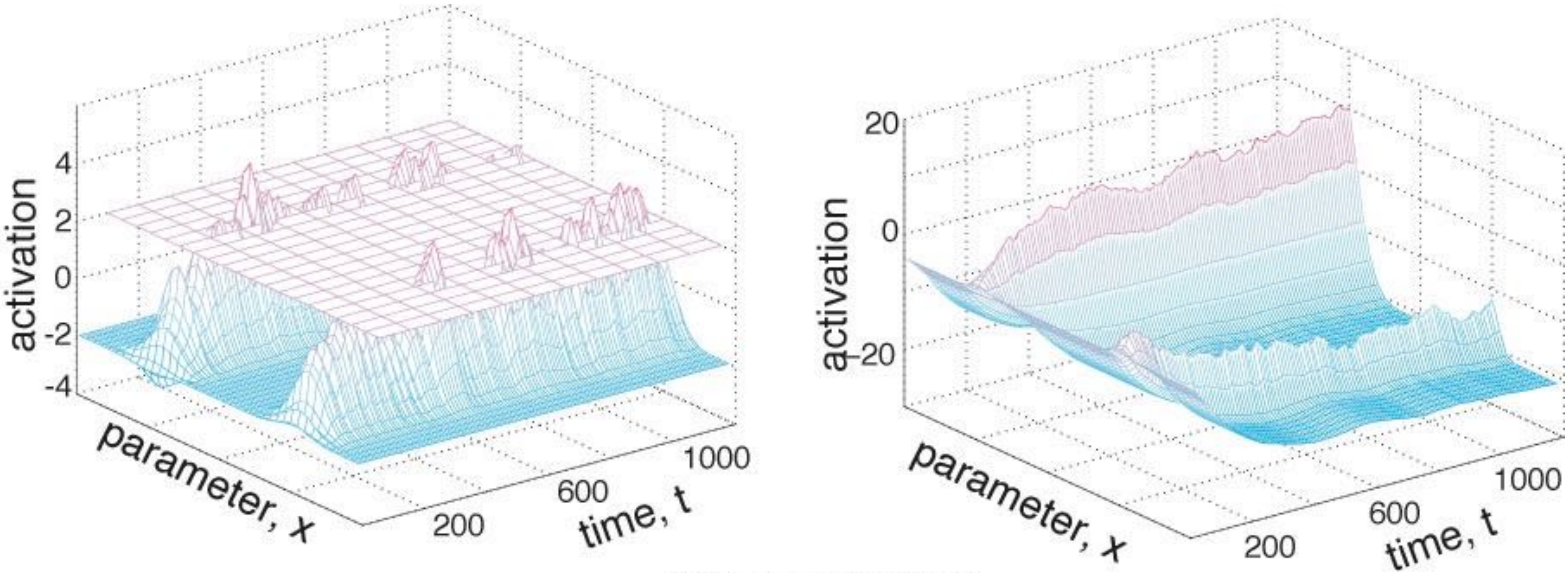


[Kopecz, 95]

selection instability



stabilizing selection decisions



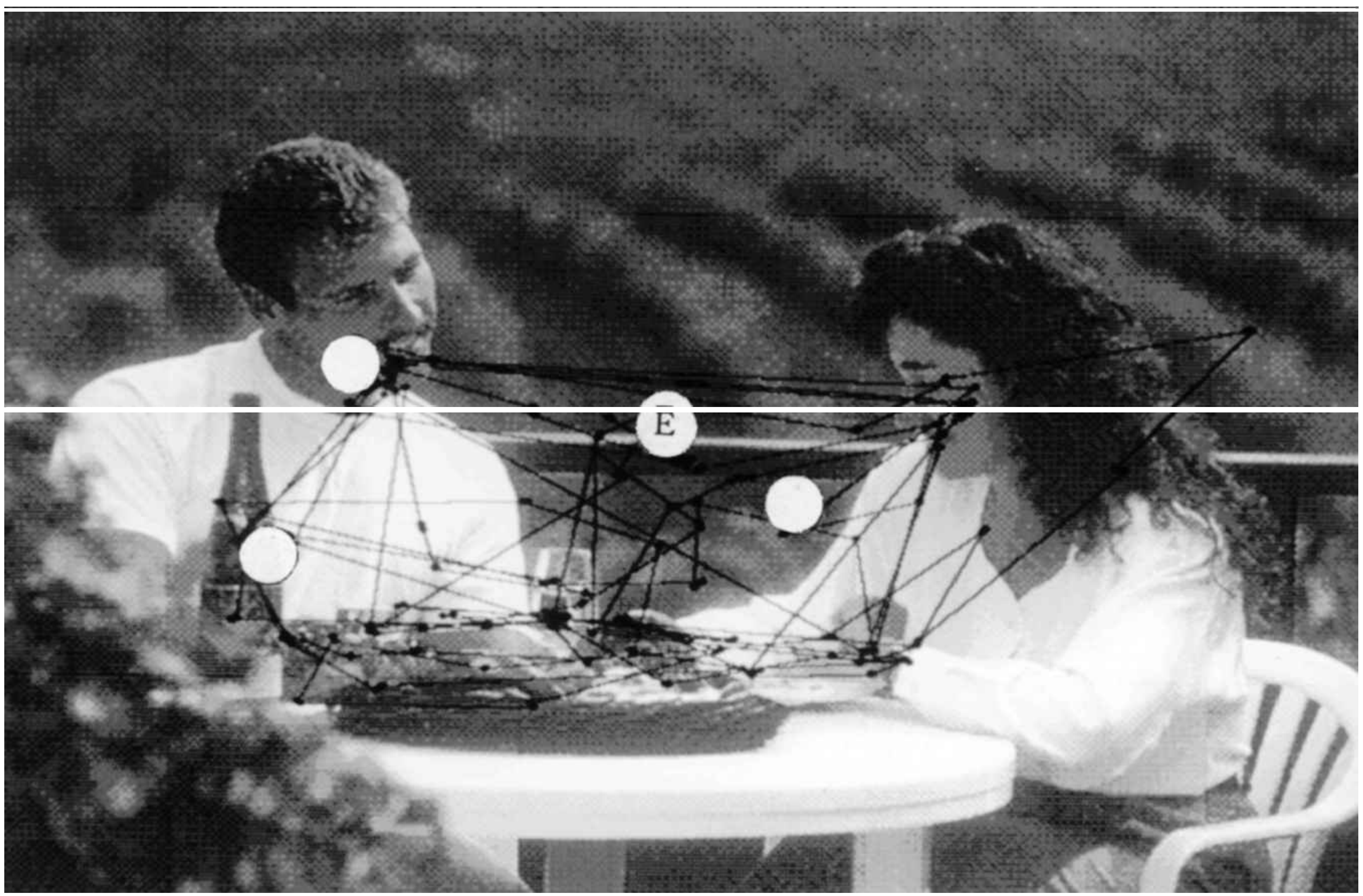
[Wilimzig, Schöner, 2006]

behavioral signatures of selection decisions

- in most experimental situations, the correct selection decision is cued by an “imperative signal” leaving no actual freedom of “choice” to the participant (only the freedom of “error”)
- reasons are experimental
- when performance approaches chance level, then close to “free choice”
- because task set plays a major role in such tasks, I will discuss these only a little later

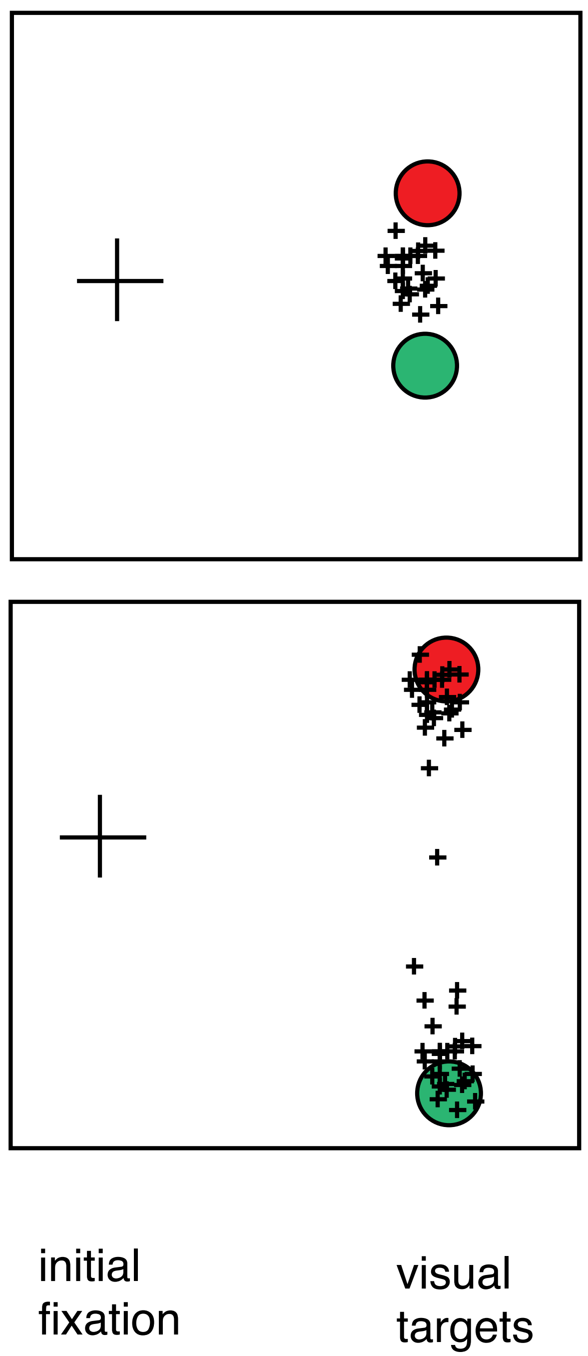
one system of "free choice"

- selecting a new saccadic location

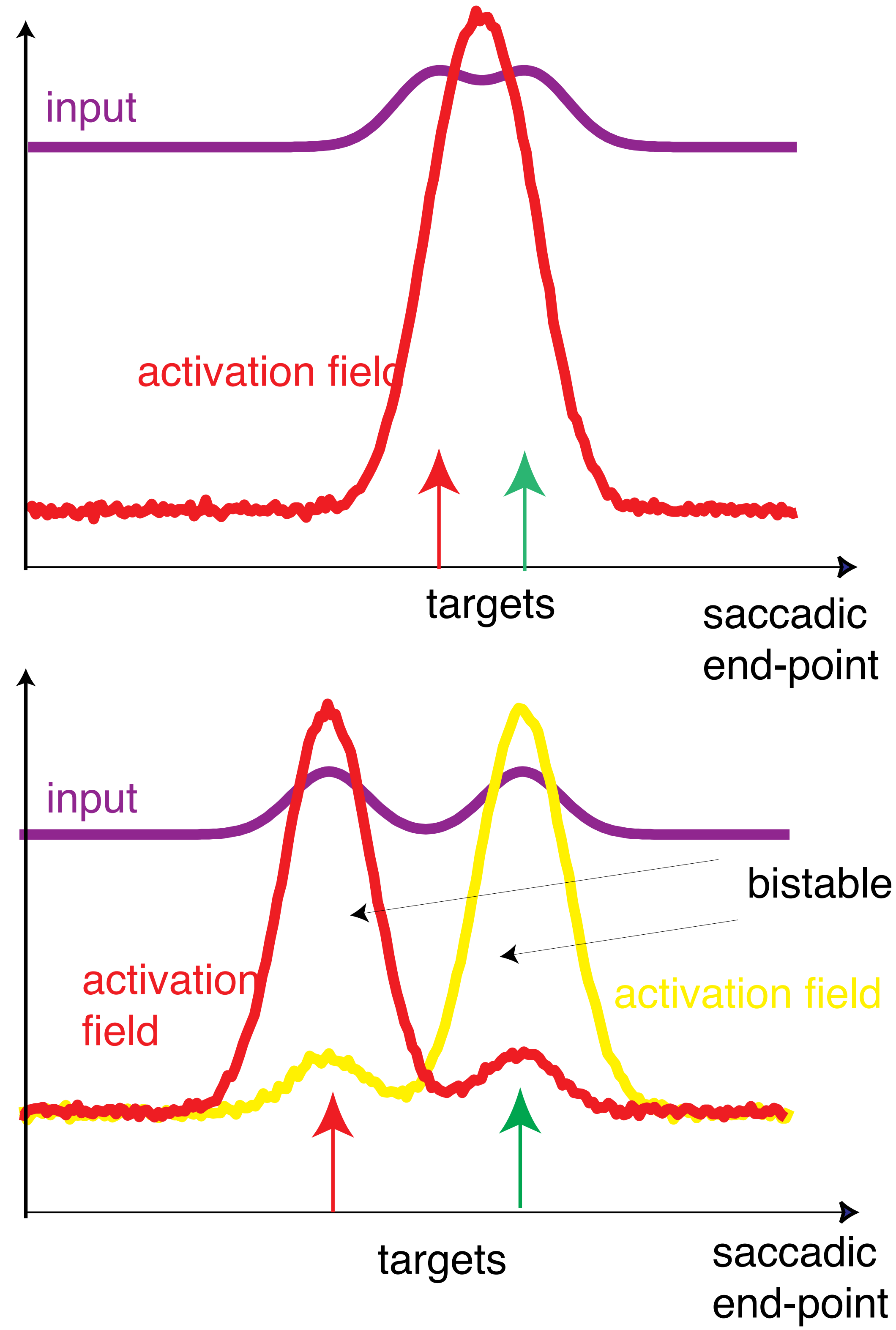


[O'Reagan et al., 2000]

saccade generation



[after: Ottes et al., Vis. Res. 25:825 (85)]

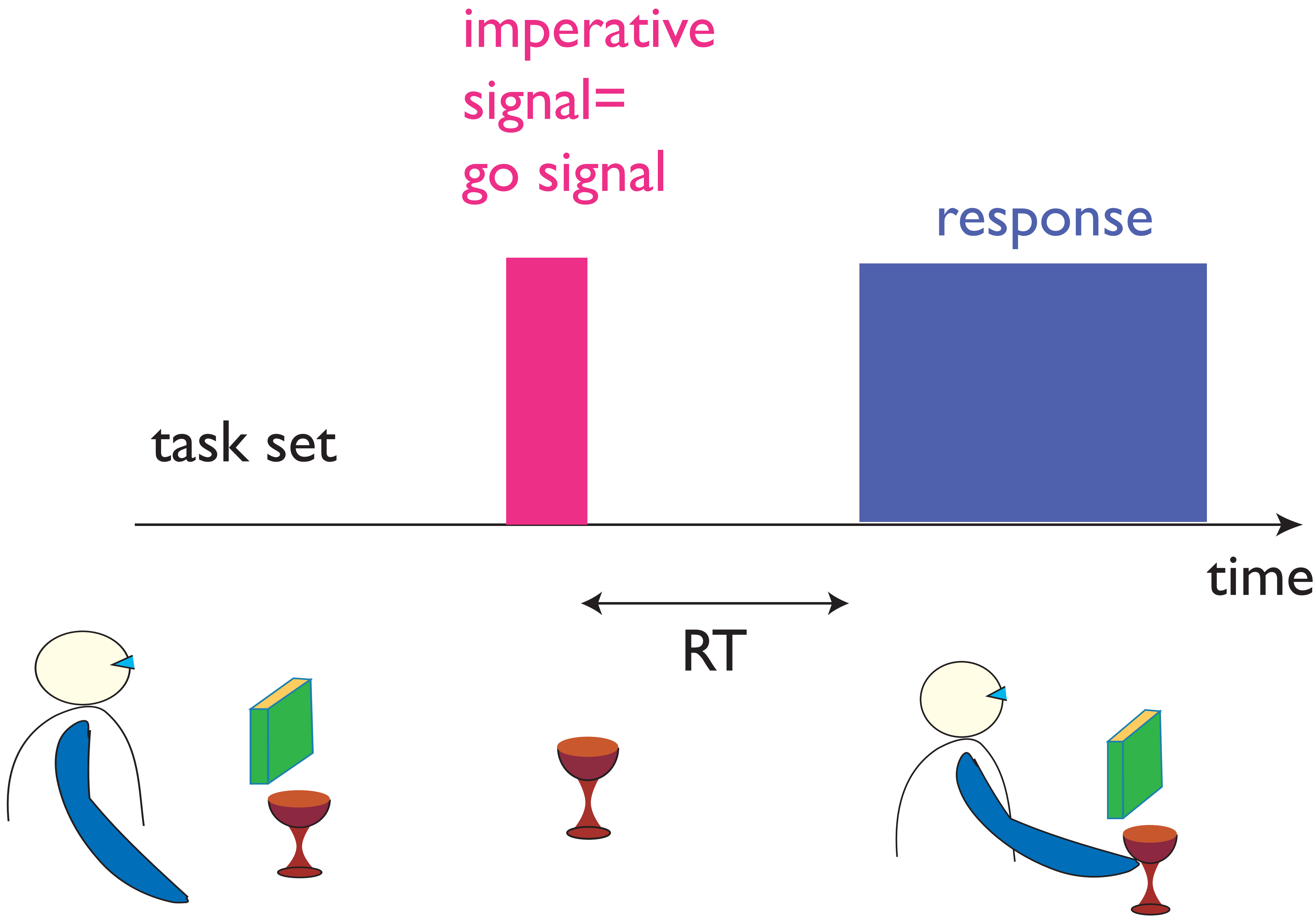


[after Kopecz, Schöner: Biol Cybern 73:49 (95)]

studying selection decisions in the laboratory

- using an imperative signal...

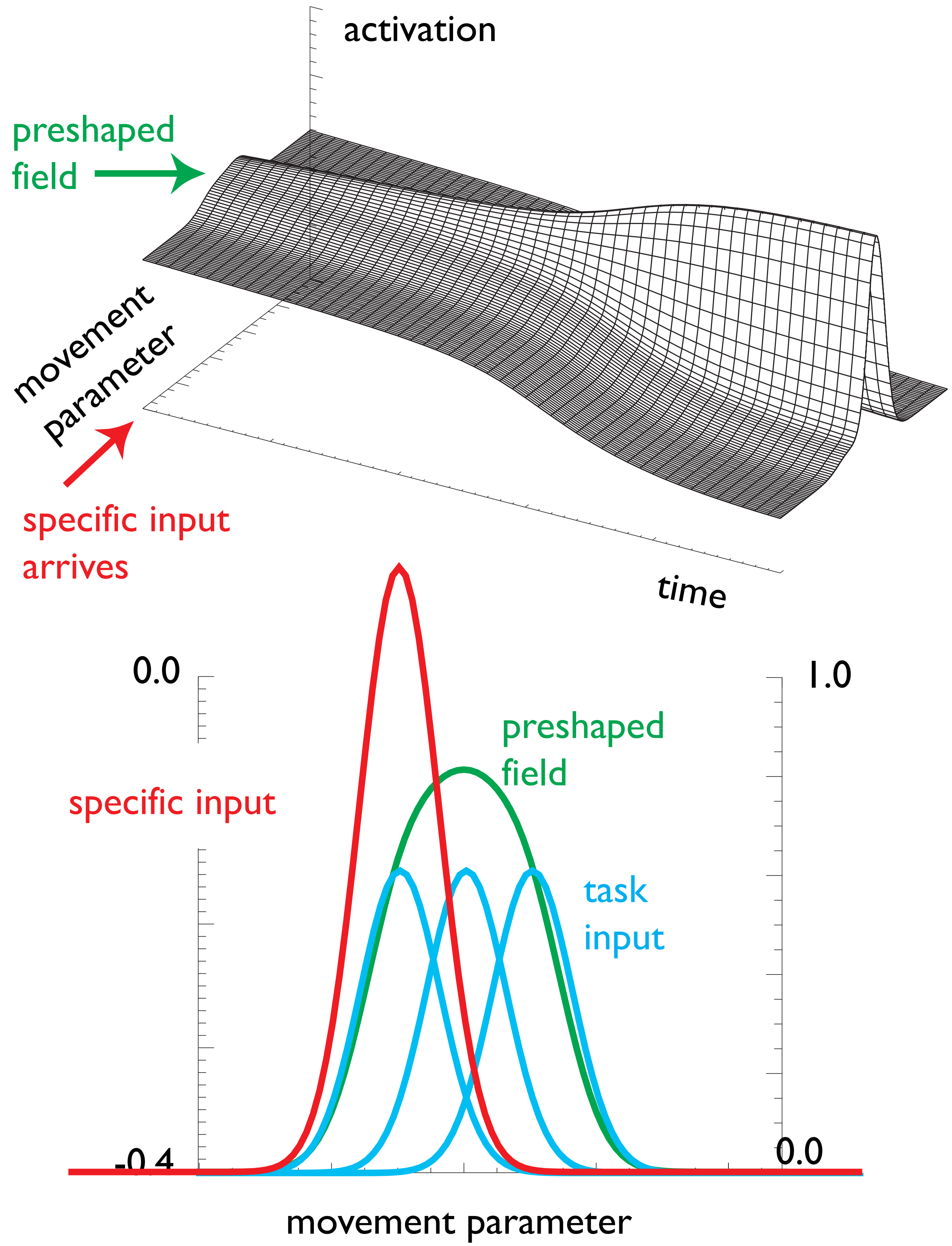
reaction time (RT) paradigm



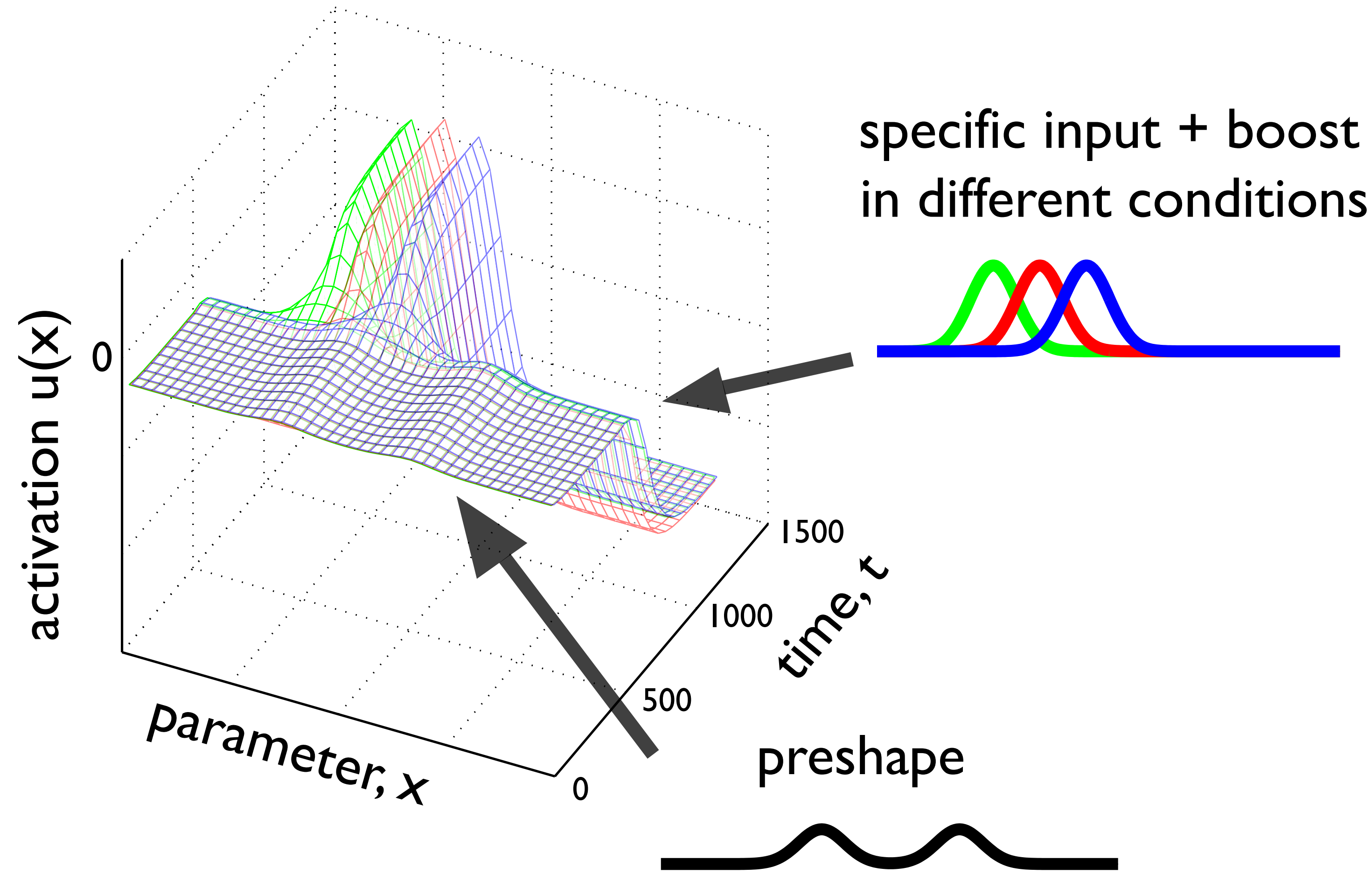
the task set

- is the critical factor in such studies of selection: which perceptual/action alternative/choices are available…
  - e.g., how many choices
  - e.g., how likely is each choice
  - e.g., how "easy" are the choices to recognize/perform
- because the task set is known to the participant prior to the presentation of the imperative signal, one may think of the task set as a "preshaping" of the underlying representation (pre=before the decision)

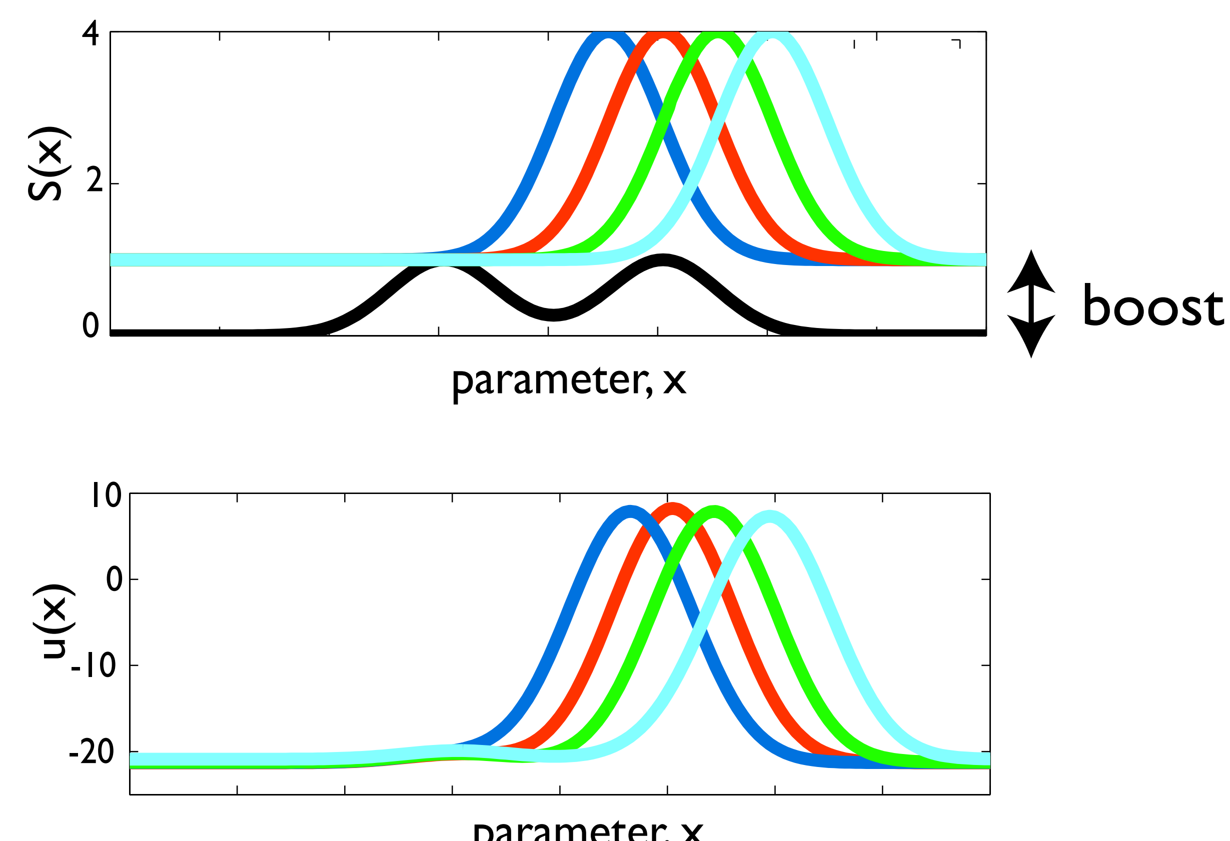
notion of preshape



weak preshape in selection



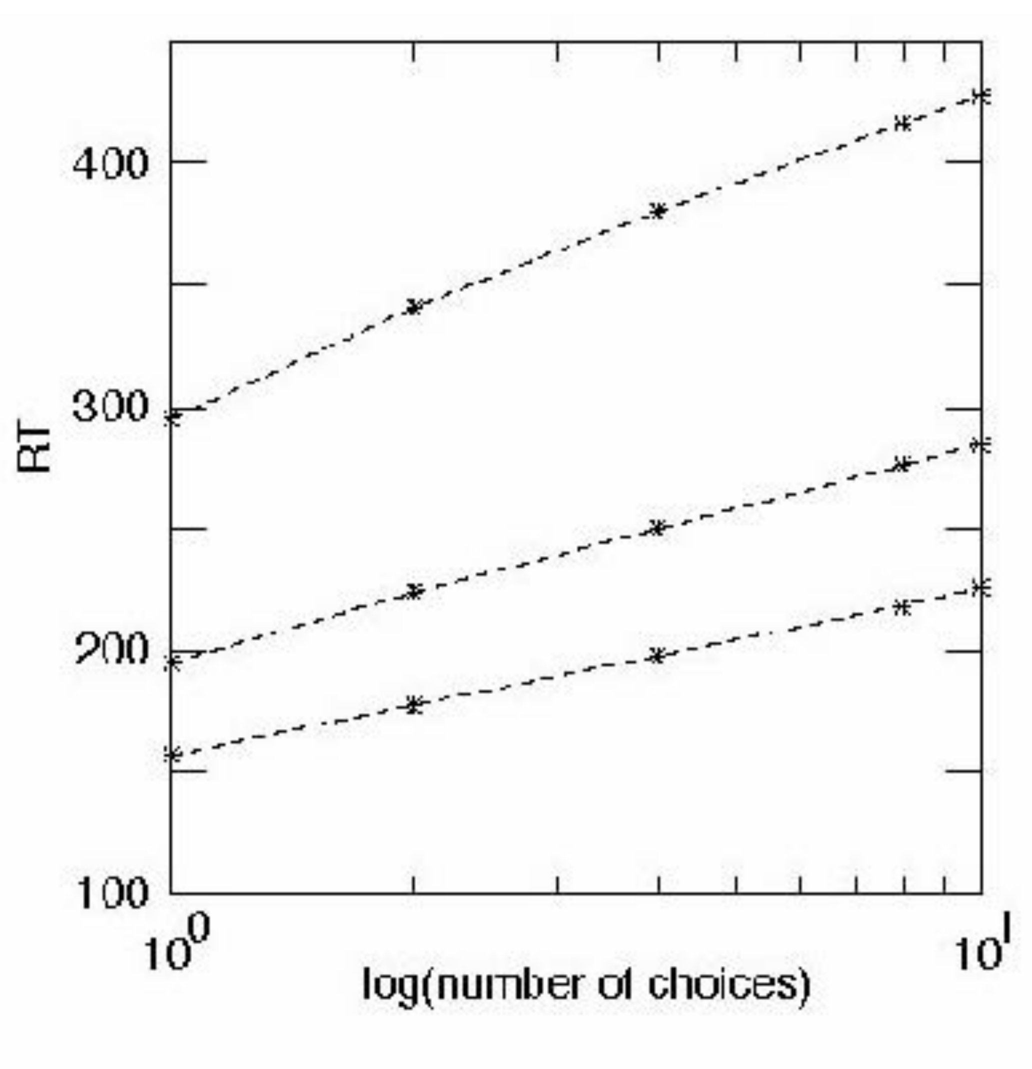
- specific (imperative) input dominates and drives detection instability

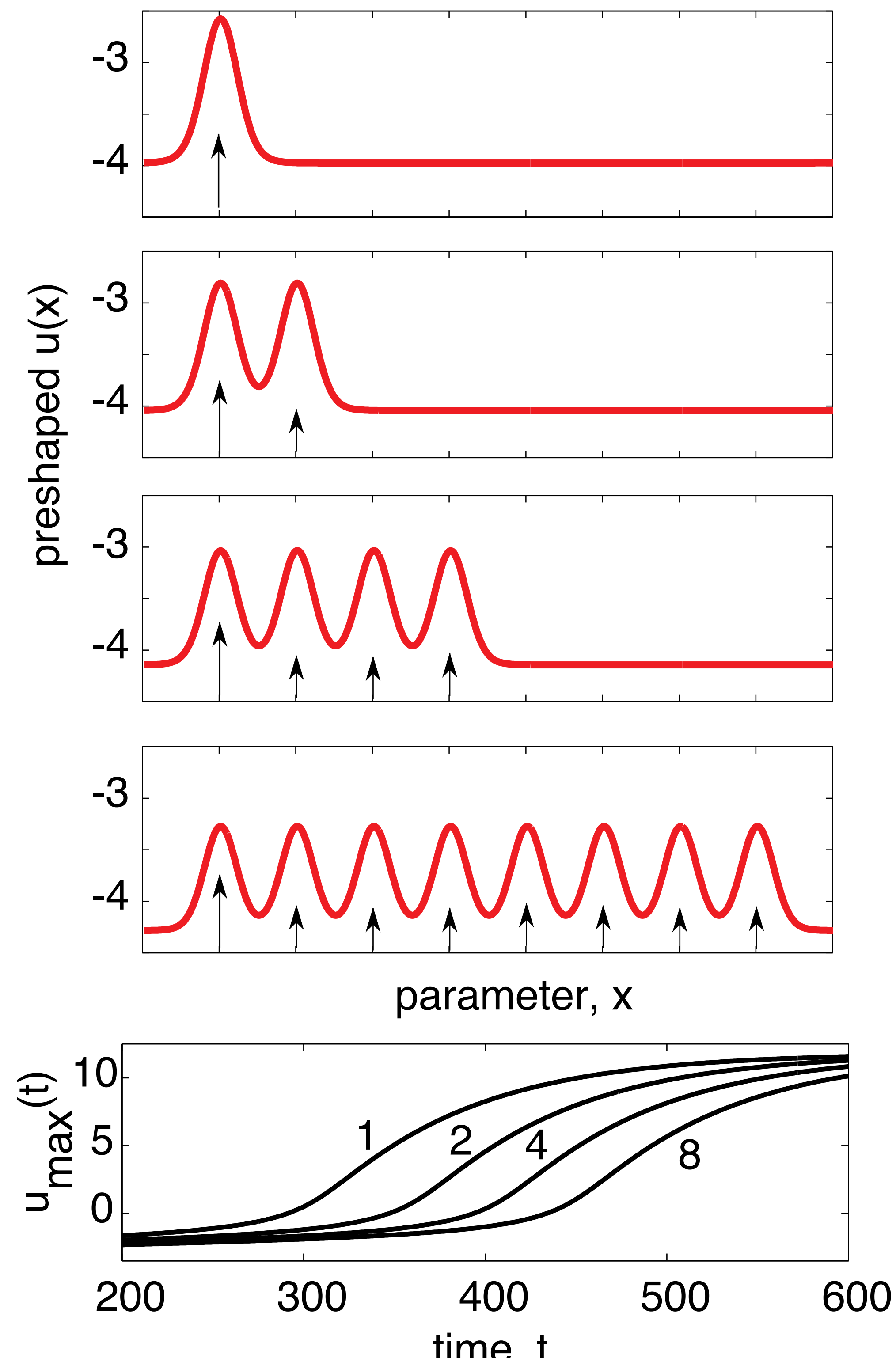


[Wilimzig, Schöner, 2006]

using preshape to account for classical RT data

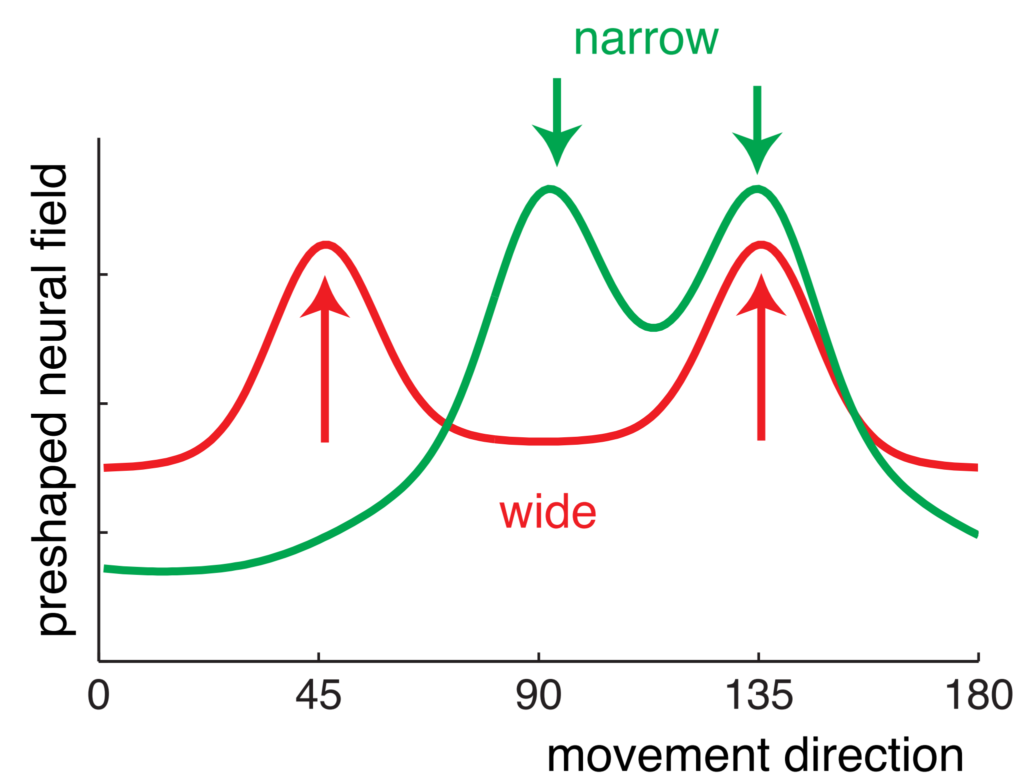
- Hick's law: RT increases with the number of choices



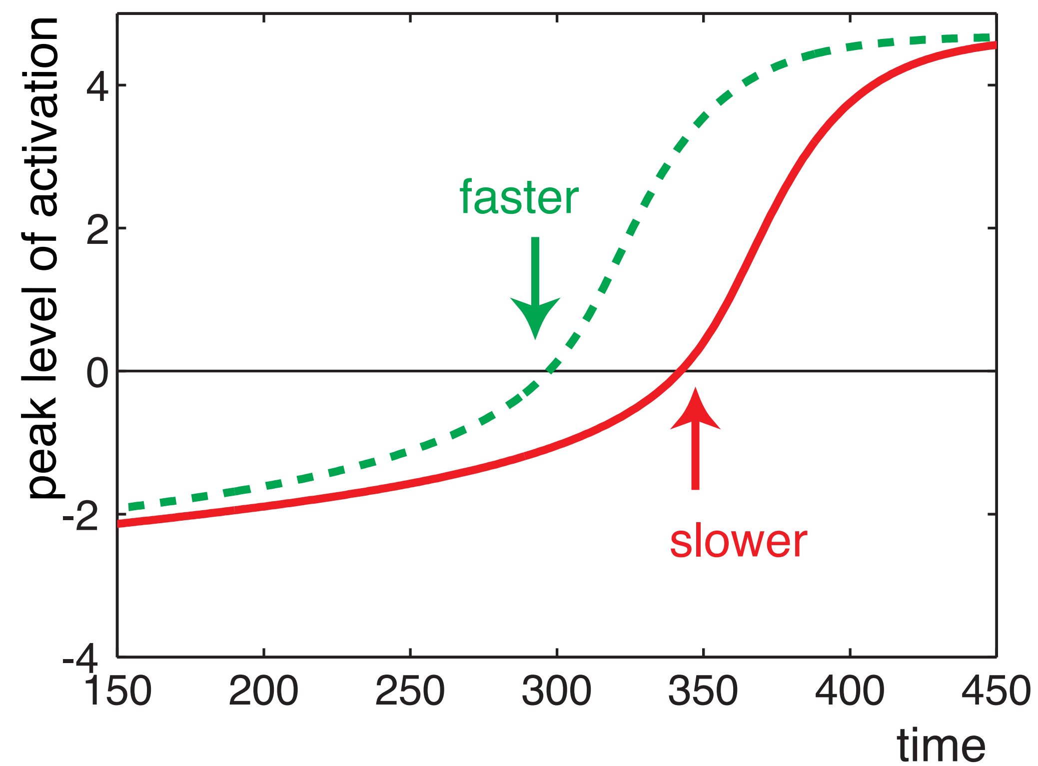


[Erlhagen, Schöner, Psych Rev 2002]

metric effect

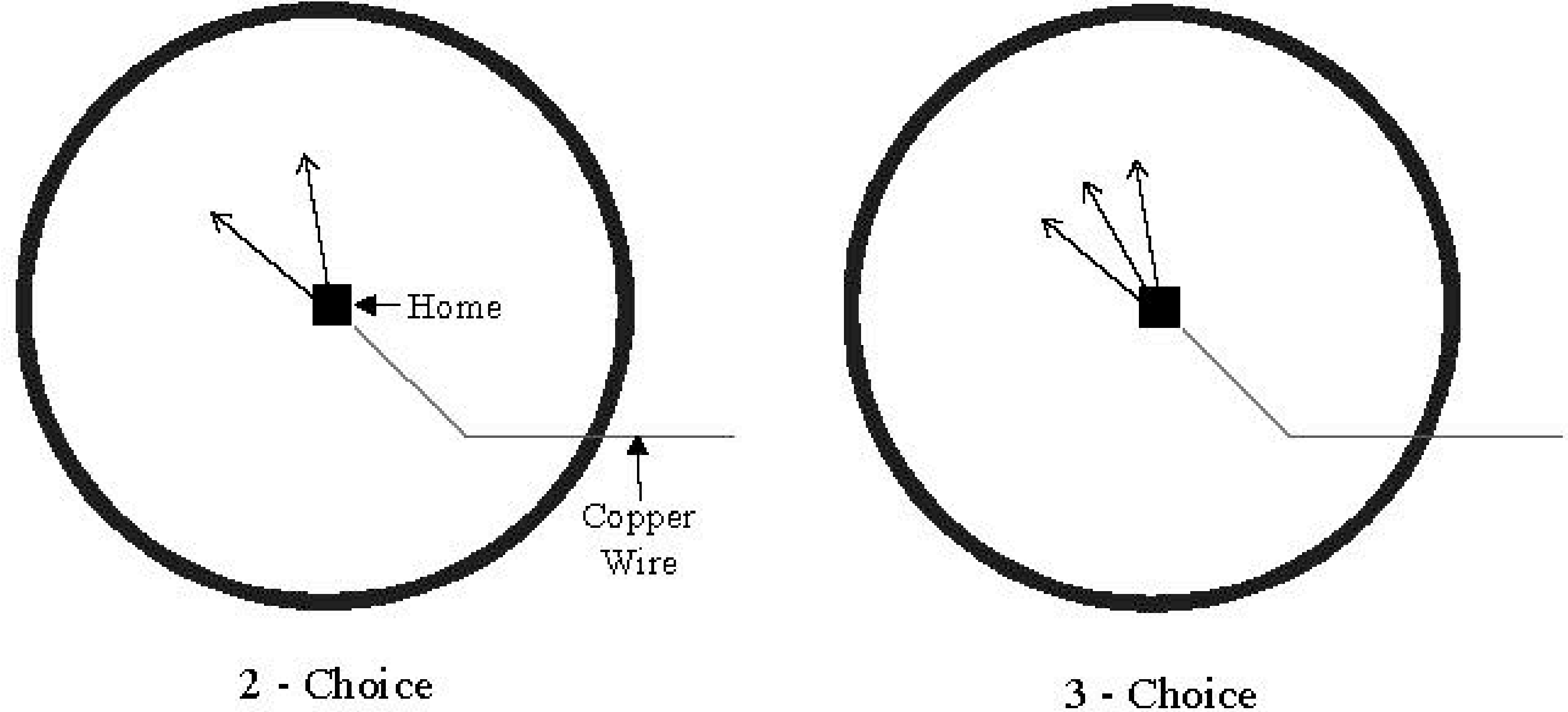


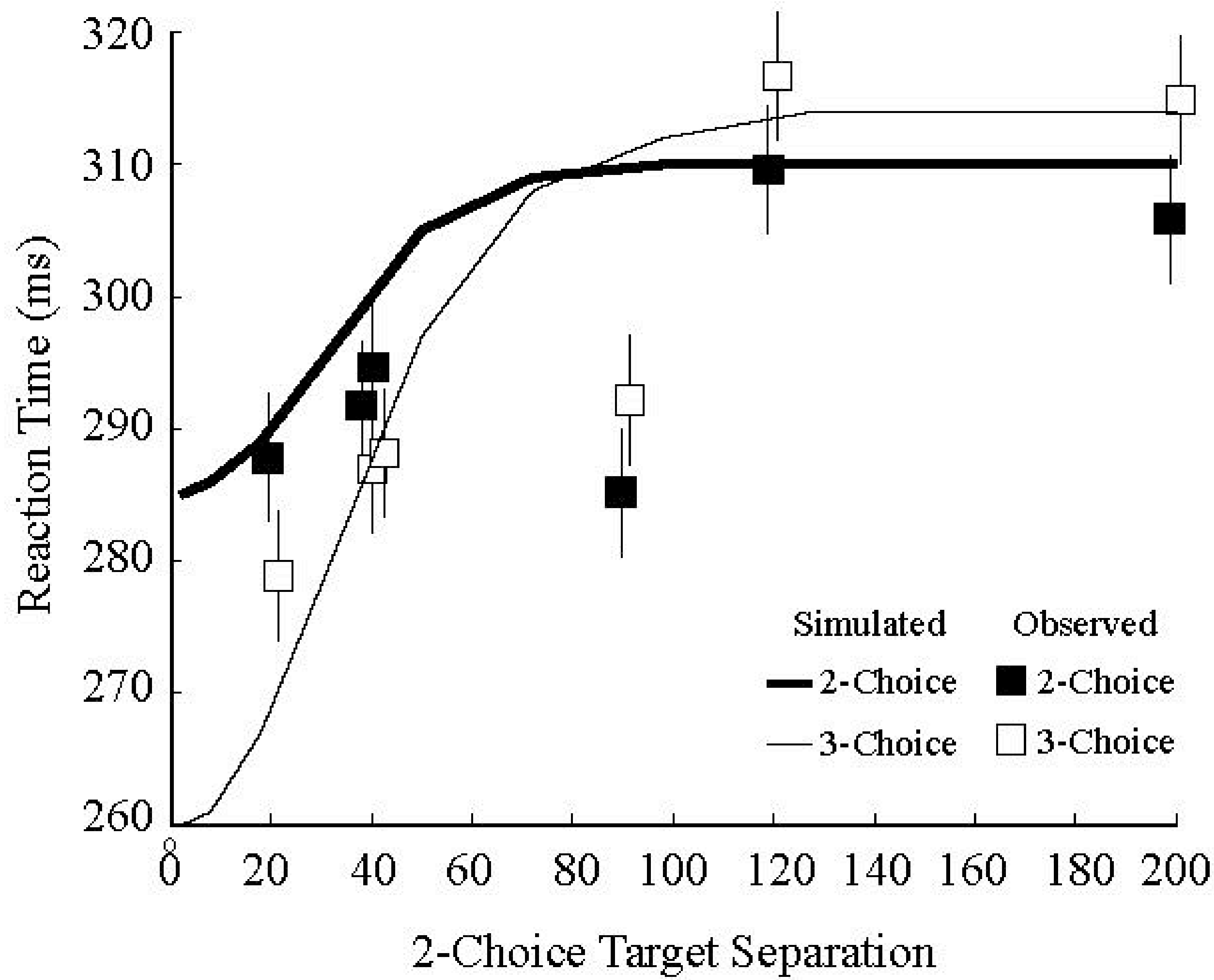
- predict faster response times for metrically close than for metrically far choices



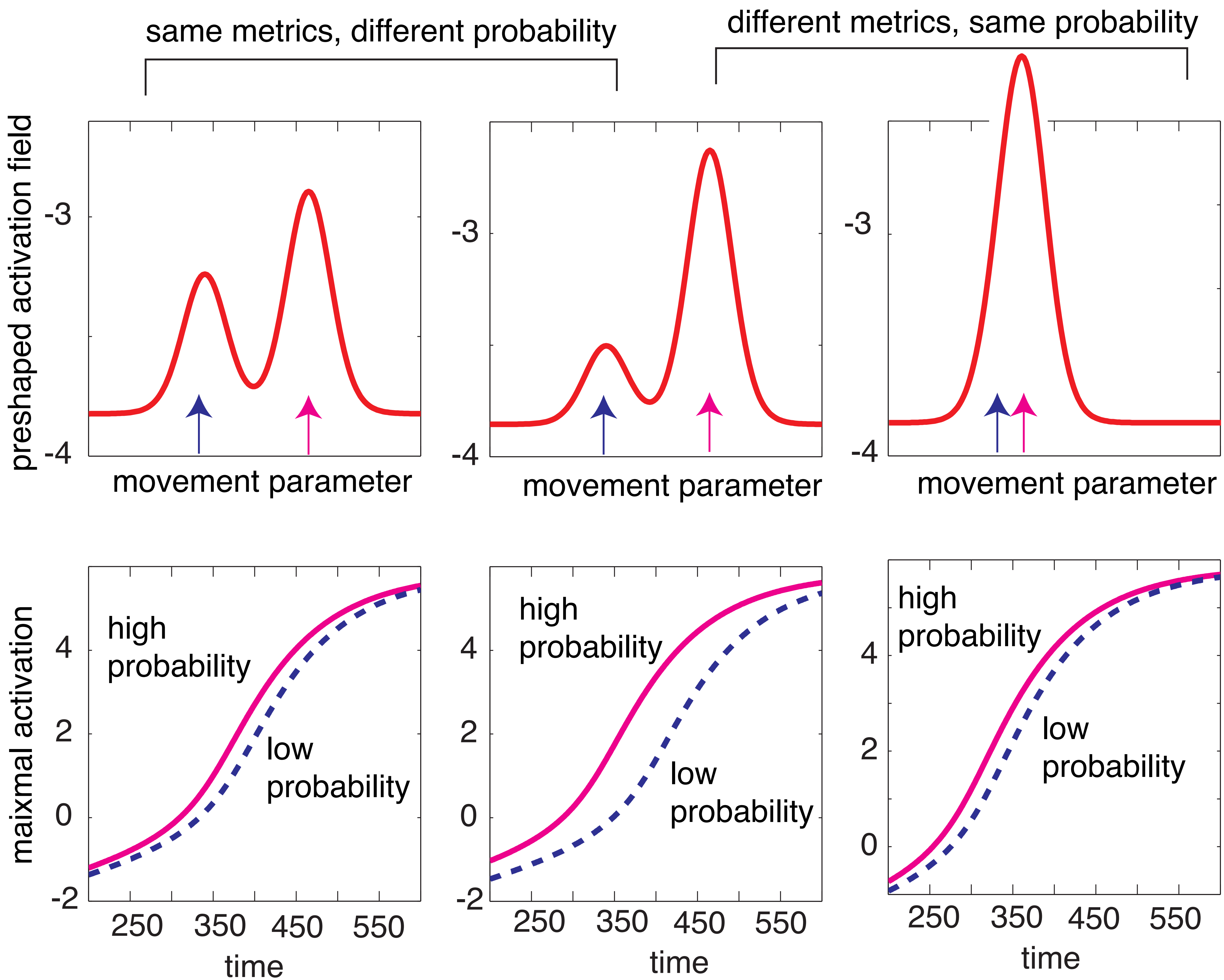
[from Schöner, Kopecz, Erlhagen, 1997]

experiment: metric effect

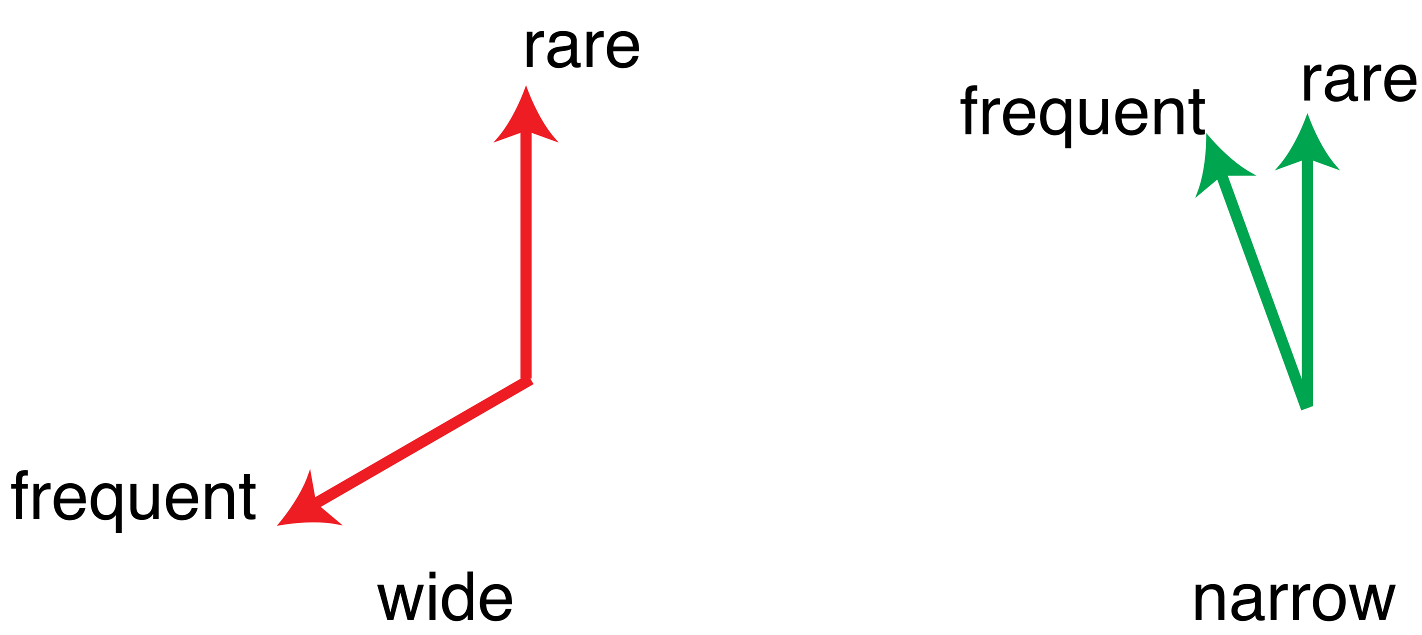


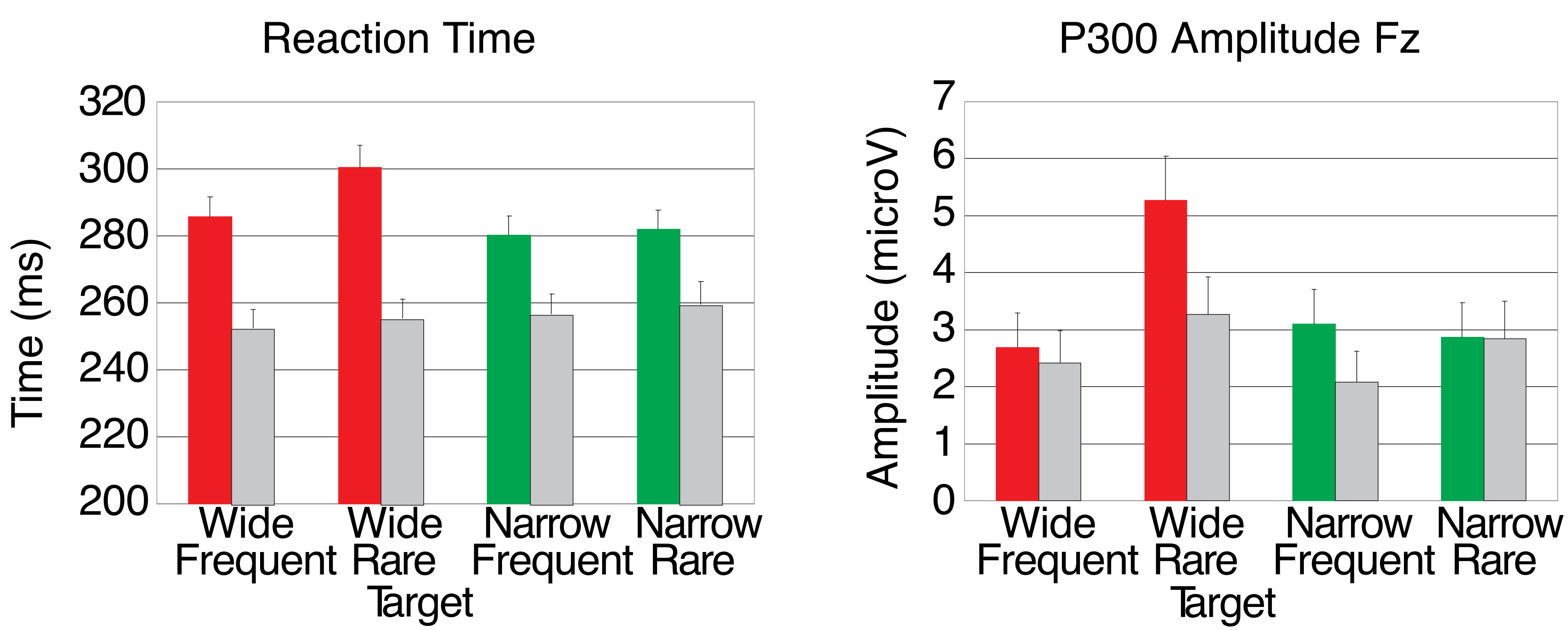


[McDowell, Jeka, Schöner]



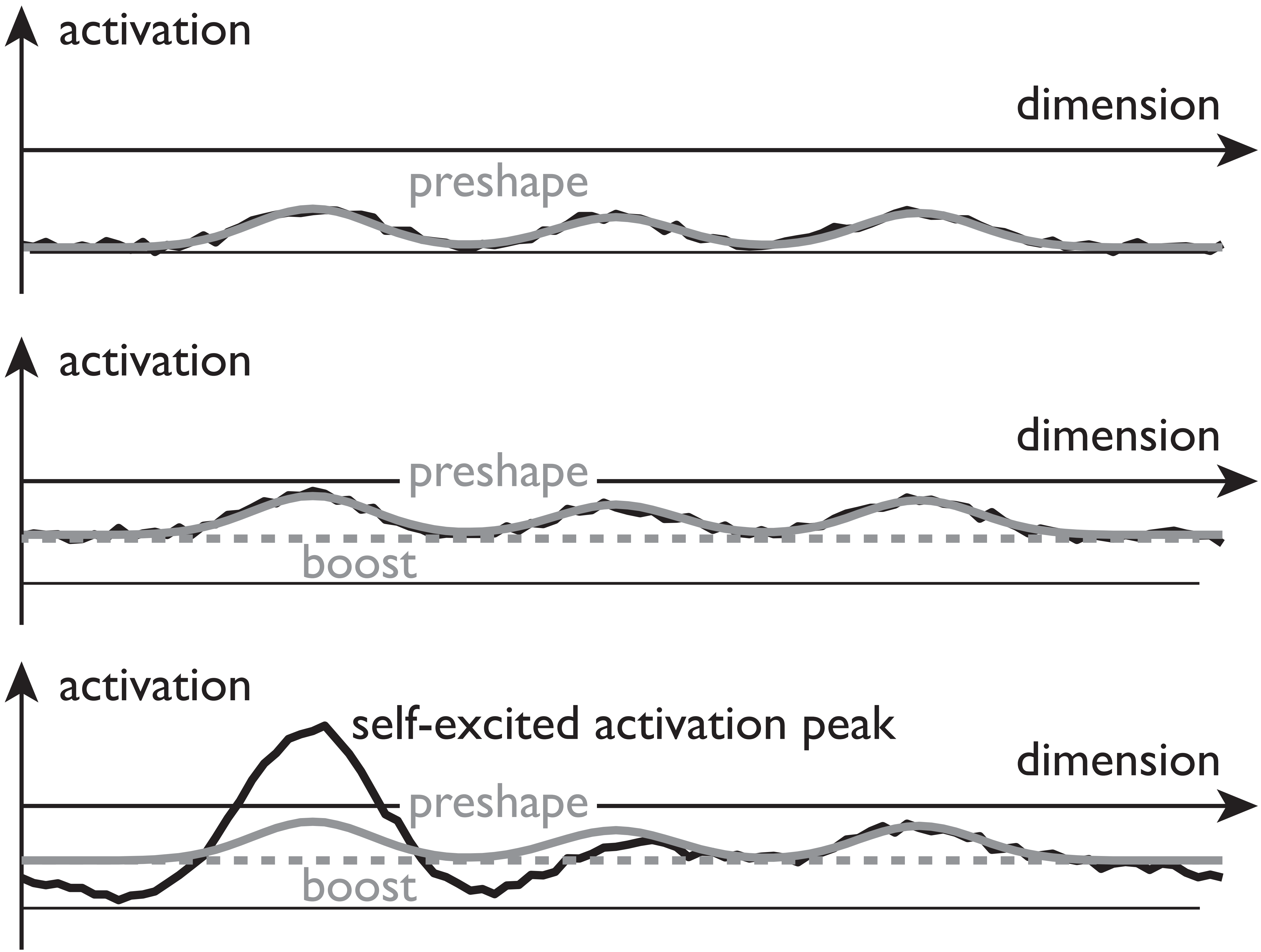
[from Erlhagen, Schöner: Psych. Rev. 2002]





[from McDowell, Jeka, Schöner, Hatfield, 2002]

boost-induced detection instability



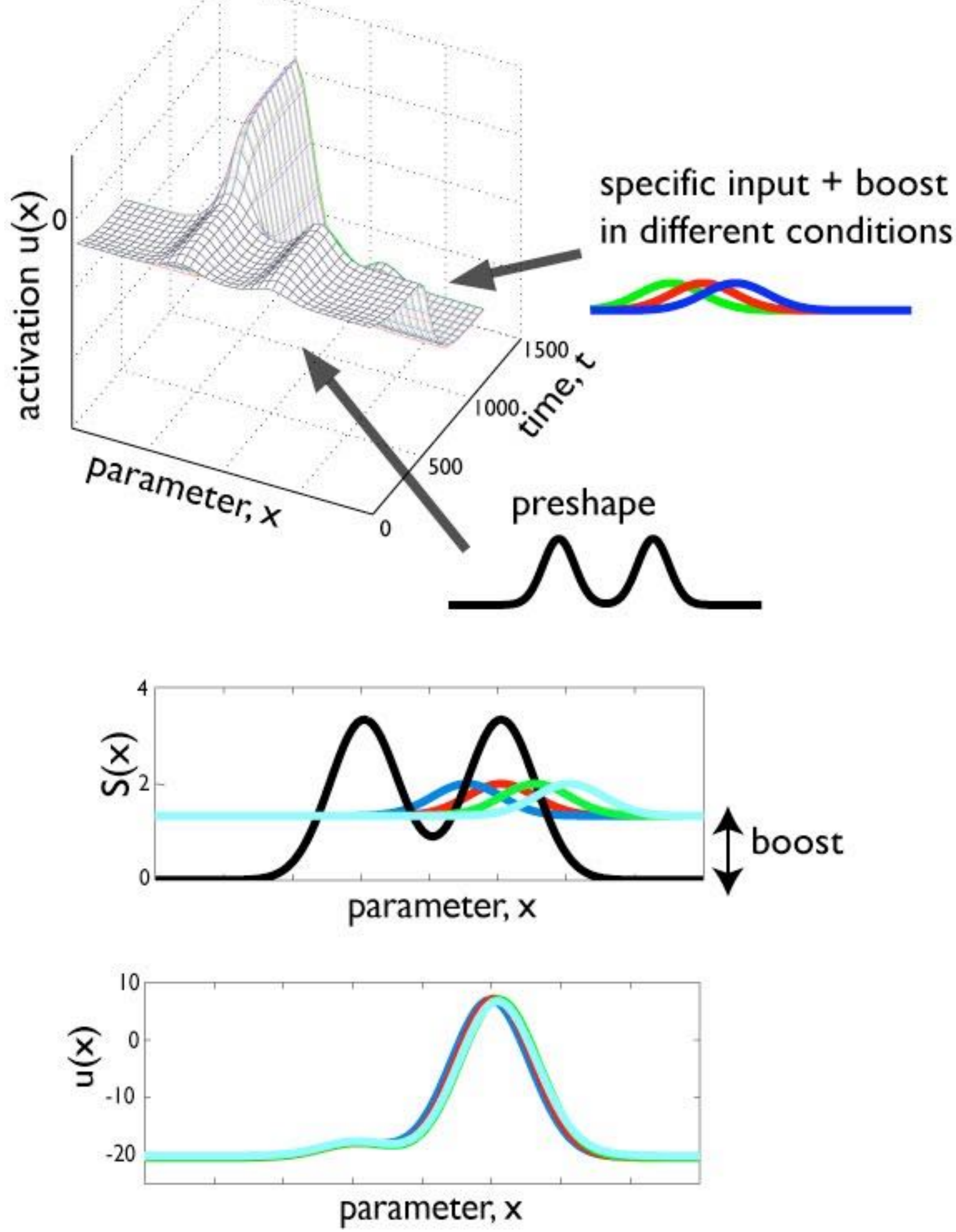
boost-driven detection instability

- inhomogeneities in the field existing prior to a signal/stimulus that leads to a macroscopic response="preshape"
- the boost-driven detection instability amplifies preshape into macroscopic selection decisions

… emergence of categories?

- if we understand, how such inhomogeneities come about, we understand the emergence of categories…

this supports categorical behavior

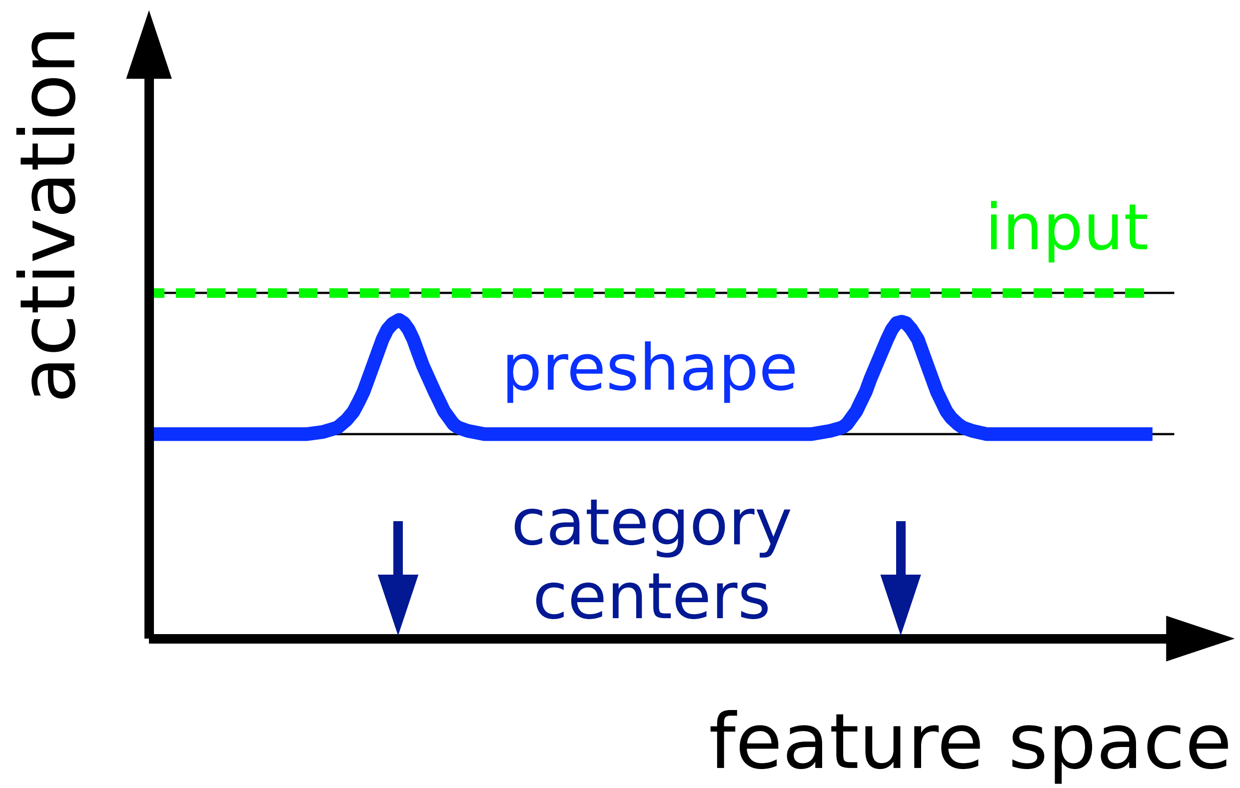


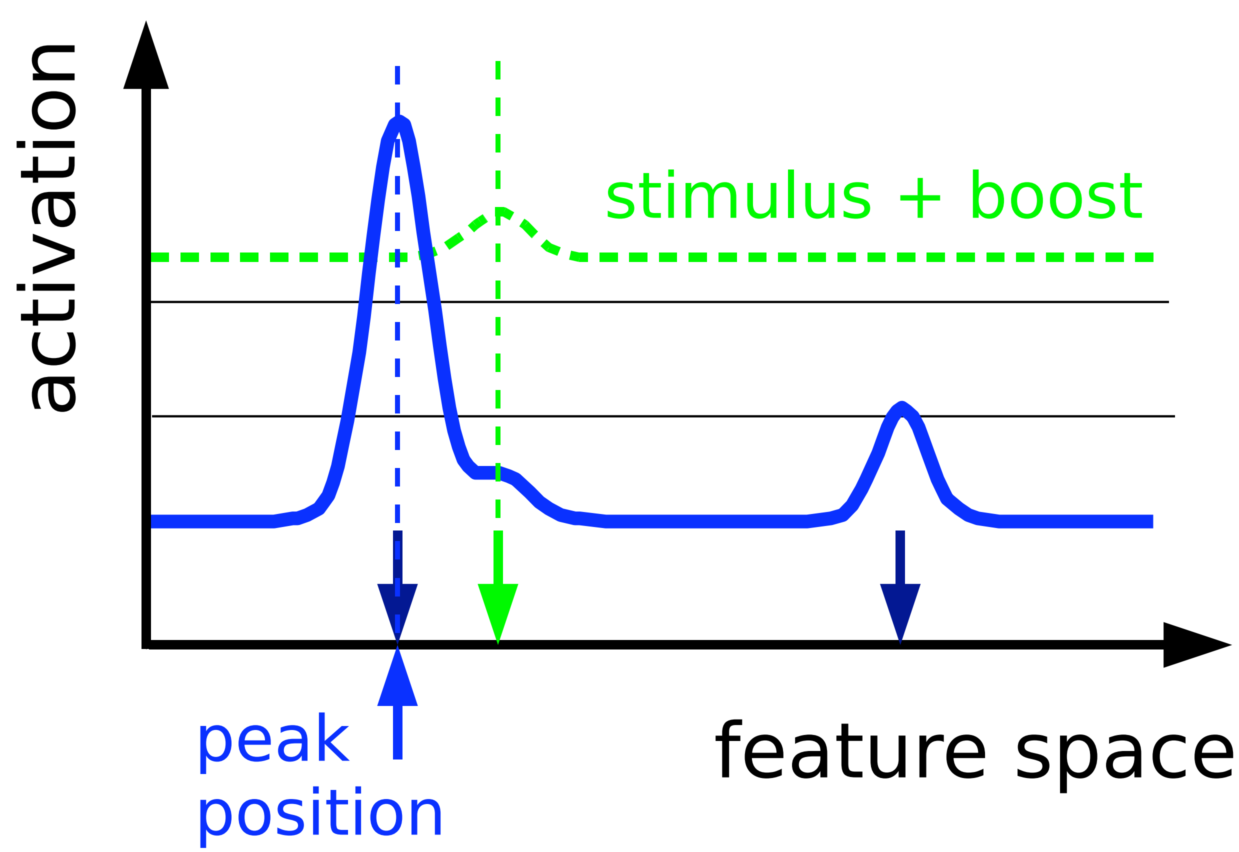
- when preshape dominates

[Wilimzig, Schöner, 2006]

categorical responding

- based on categorical memory trace and boost-driven detection instability



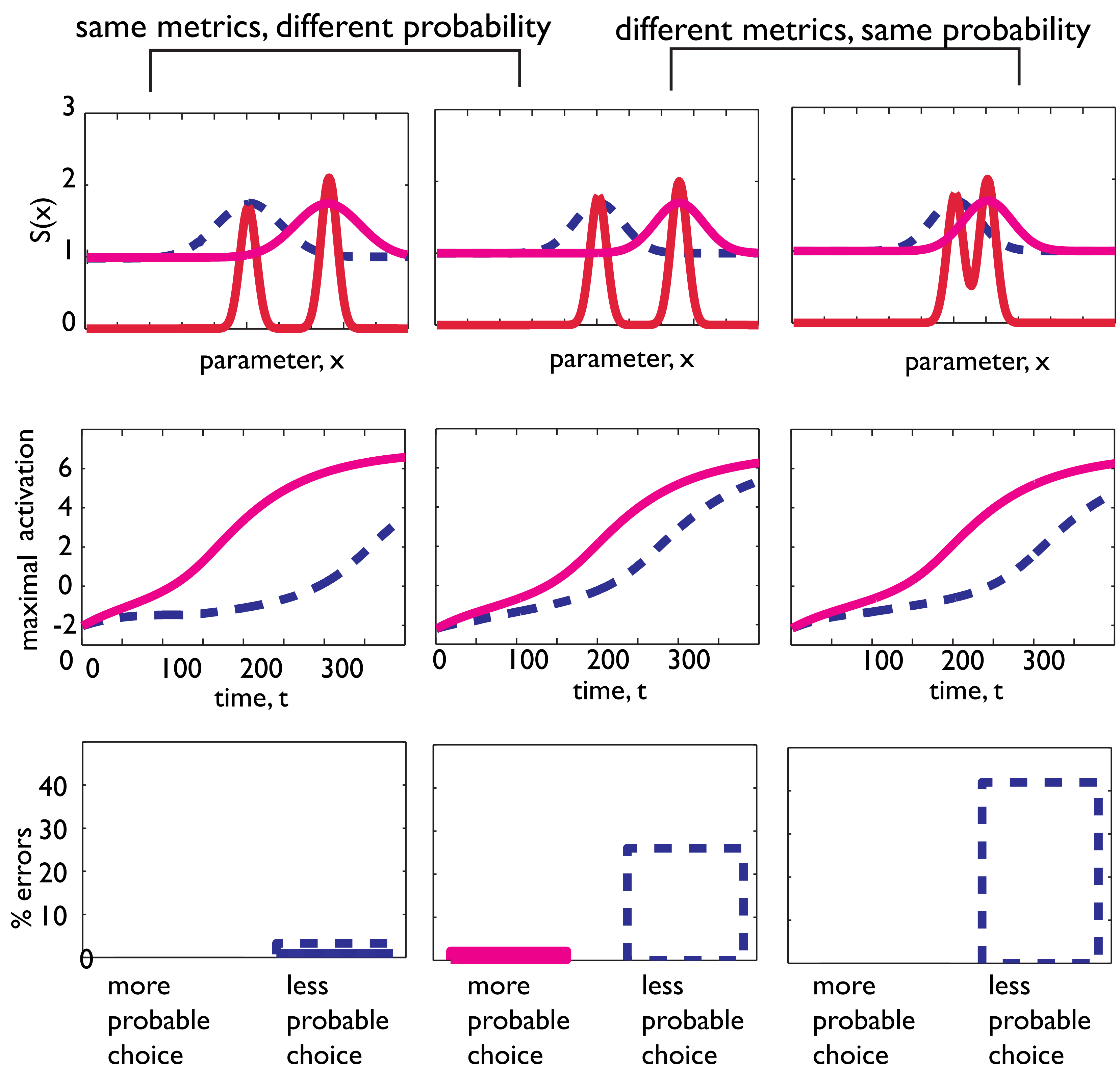


distance effect

- common in categorical tasks… e.g., decide which of two sticks is longer => RT is larger when sticks are more similar in length (1930s')

interaction metrics-probability

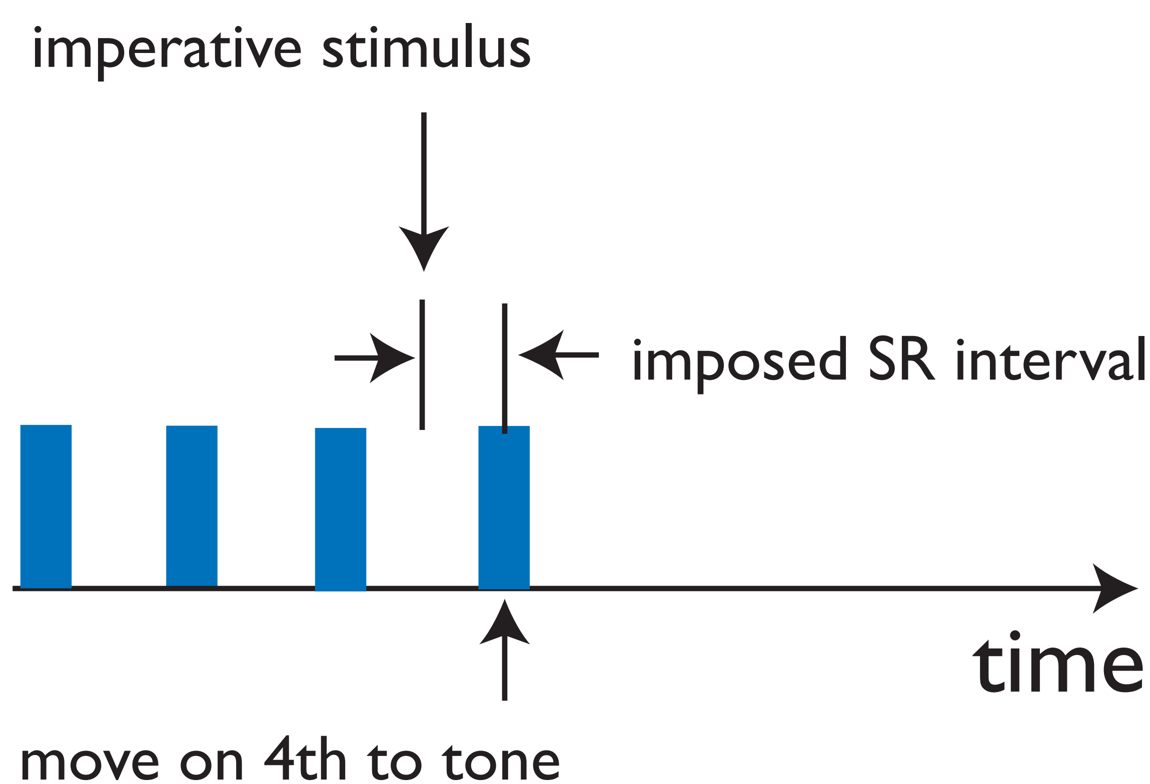
- opposite to that predicted for input-driven detection instabilities:
- metrically close choices show larger effect of probability



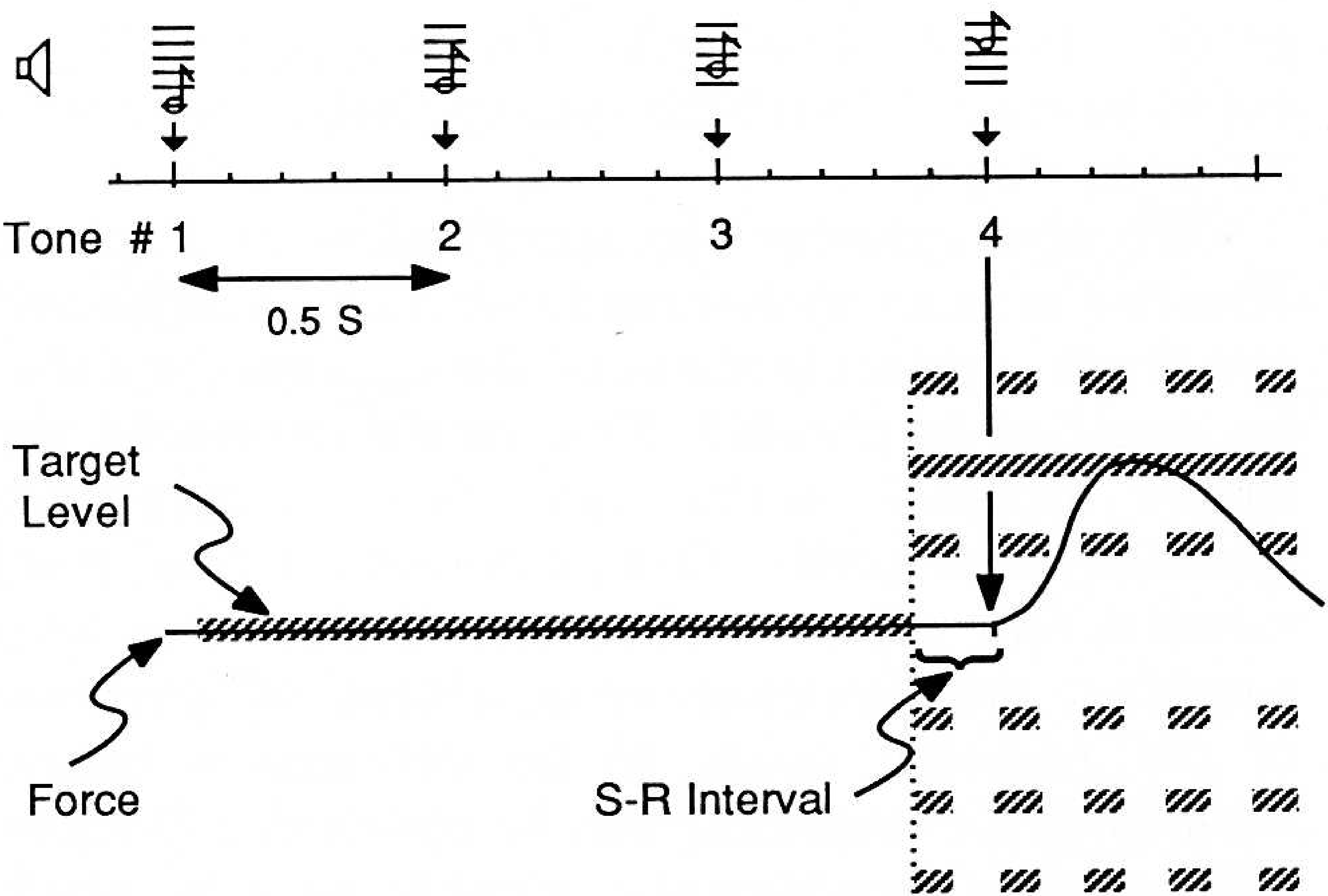
Wilimzig, Schöner, 2006

Behavioral evidence for the graded and continuous evolution of decision

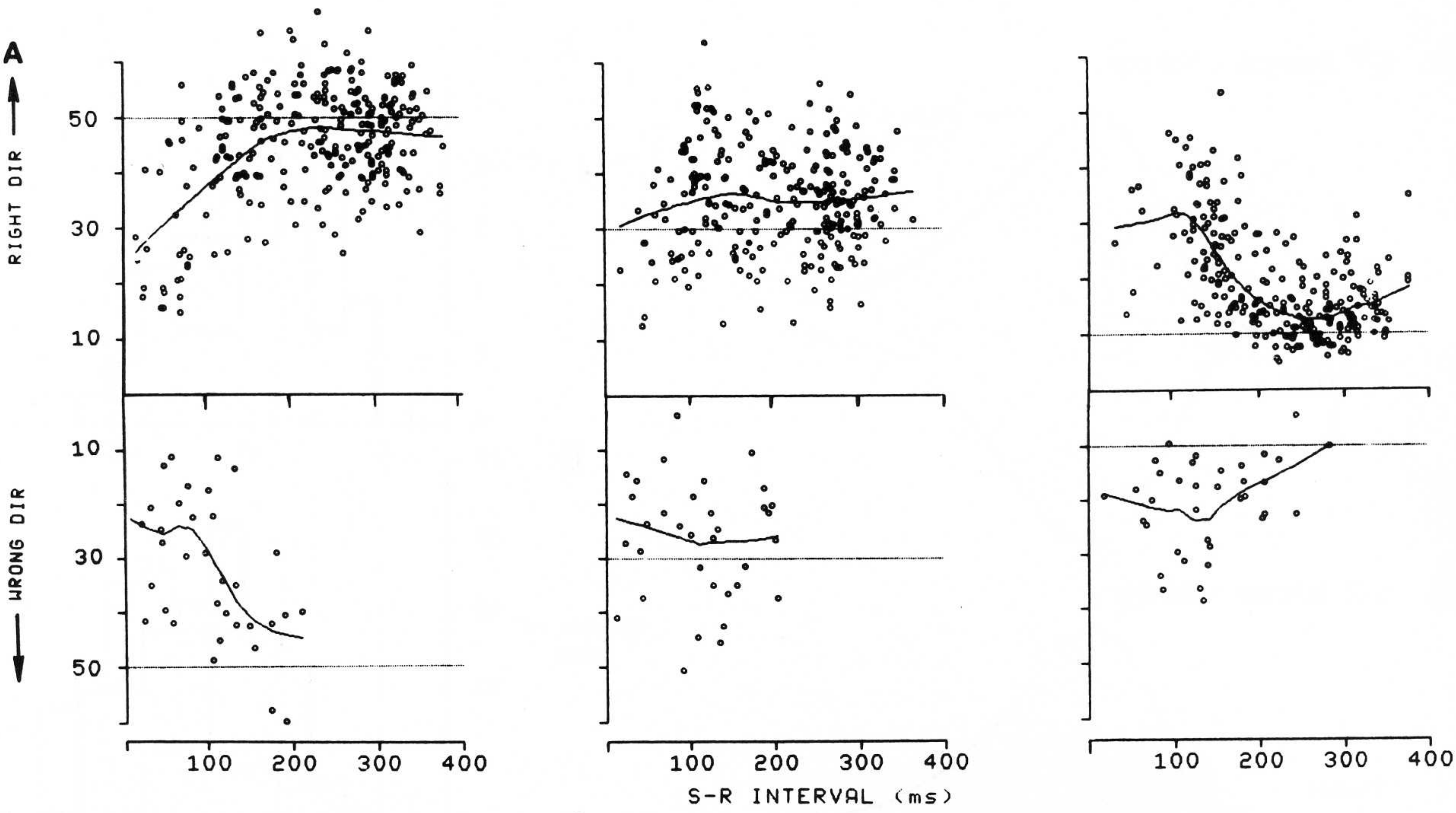
timed movement
initiation paradigm



[Ghez and colleagues, 1988 to 1990's]

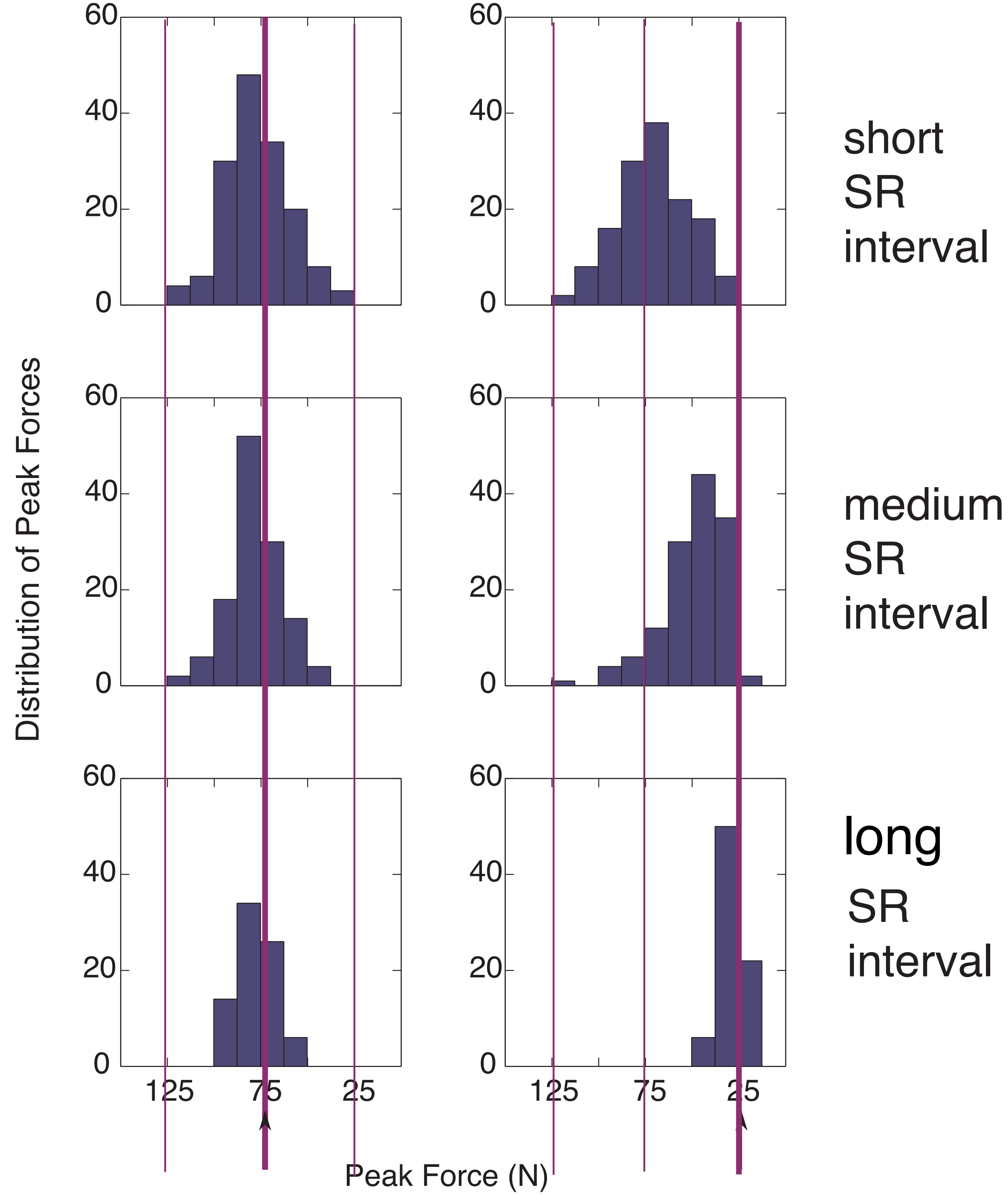


[Favilla et al. 1989]

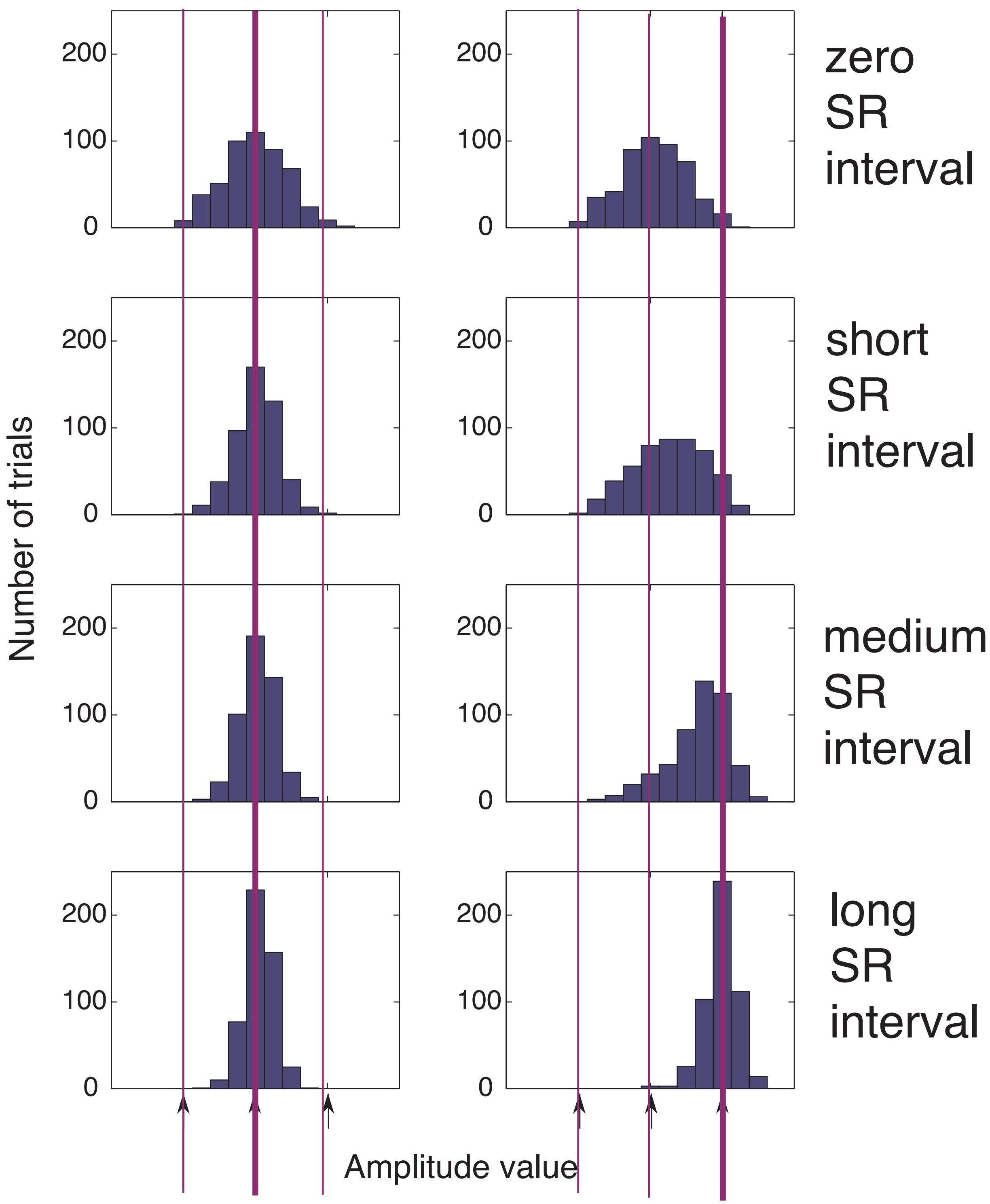


[Favilla et al. 1989]

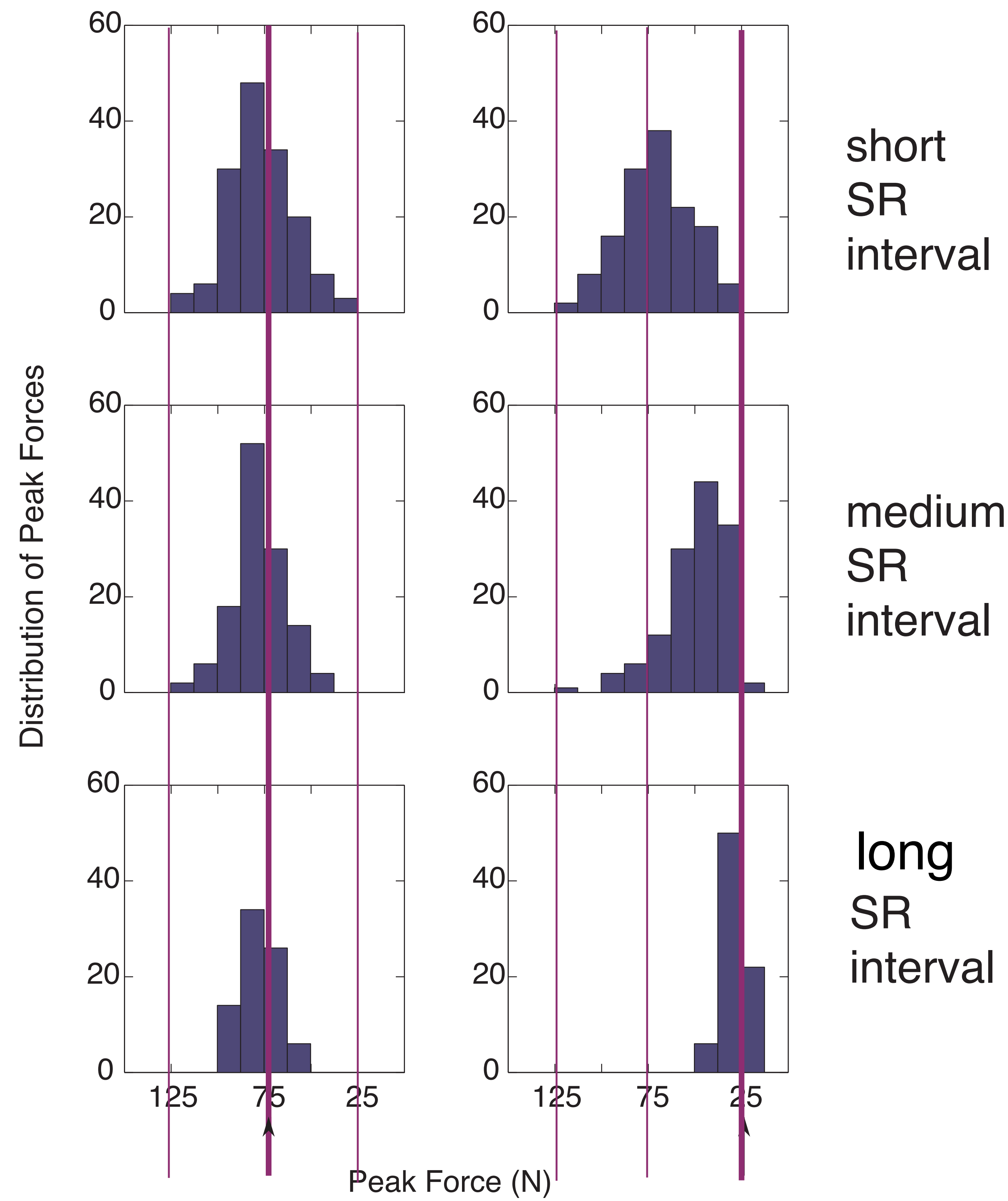
Experimental results of Henig et al



theoretical account for Henig et al.

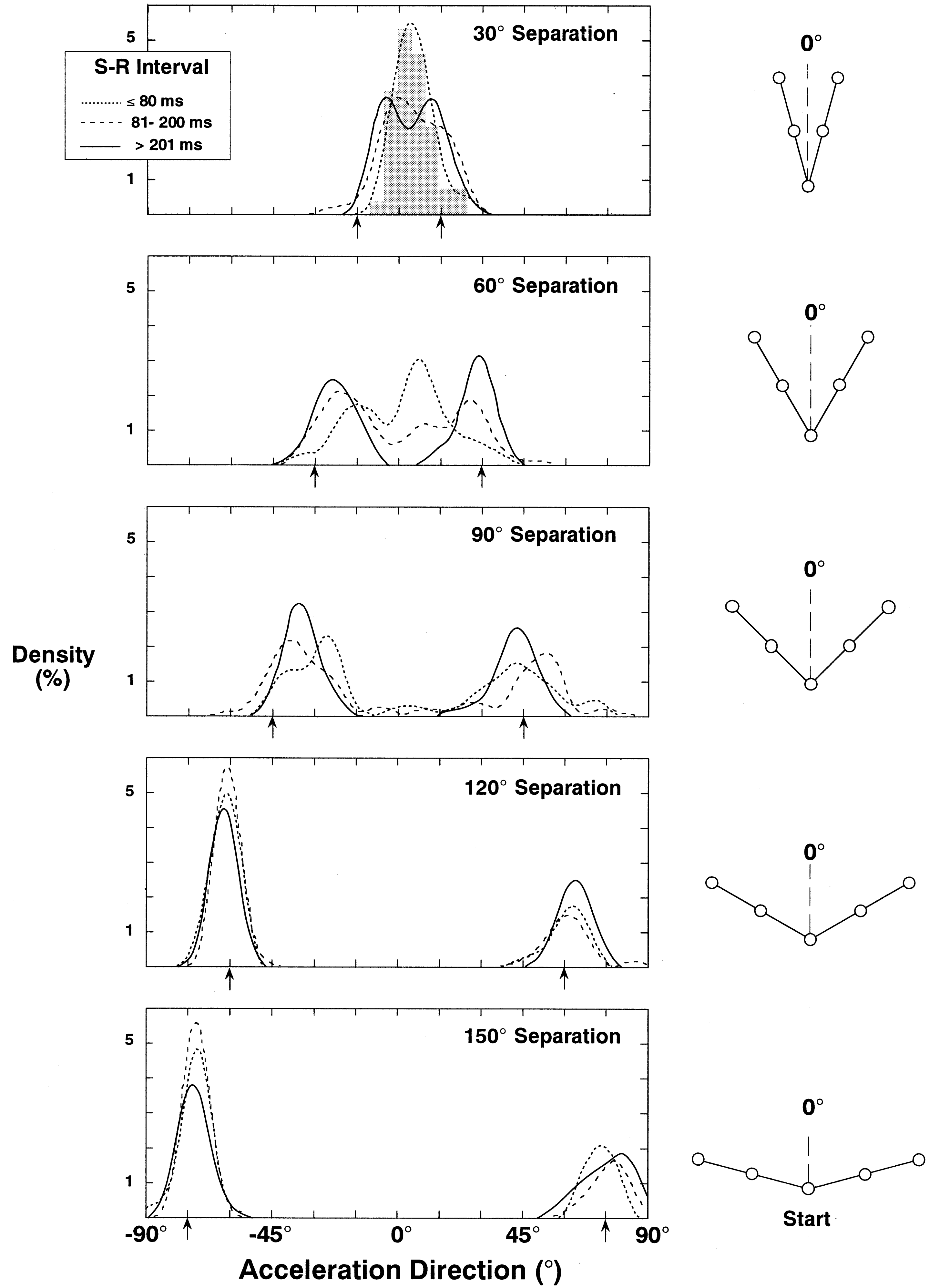


Experimental results of Henig et al



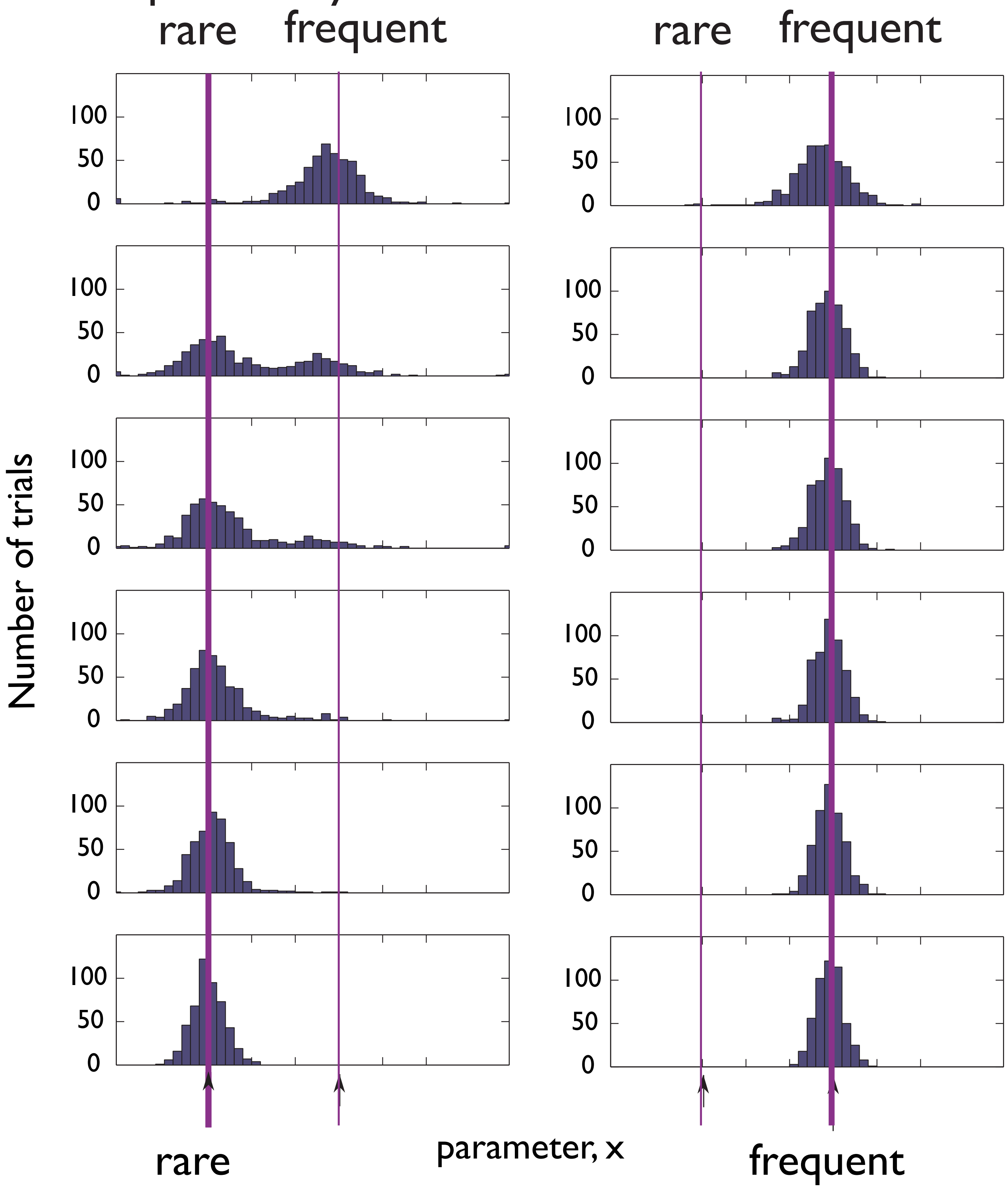
[Erlhagen, Schöner. 2002, Psychological Review 109, 545–572 (2002)]

- infer width of preshape peaks in field



[Ghez et al 1997]

probability in timed movement initiation

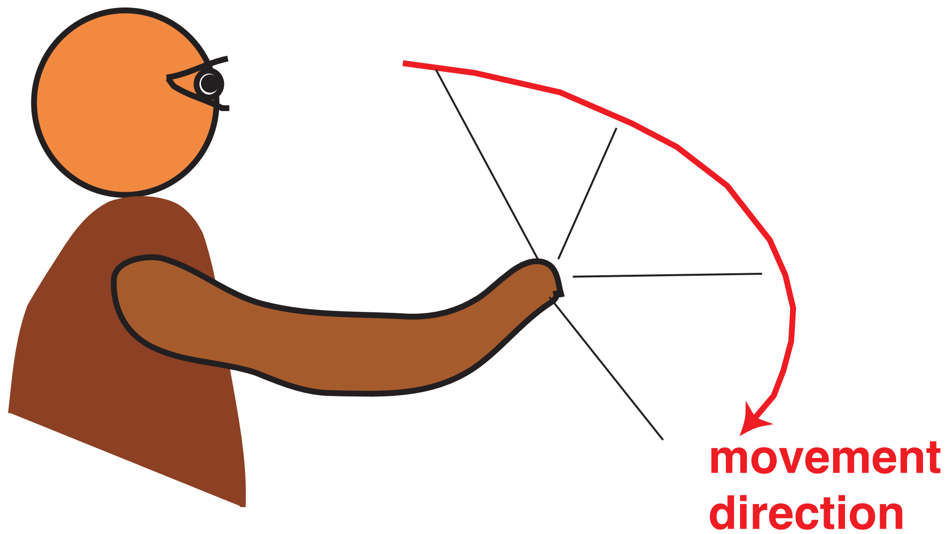


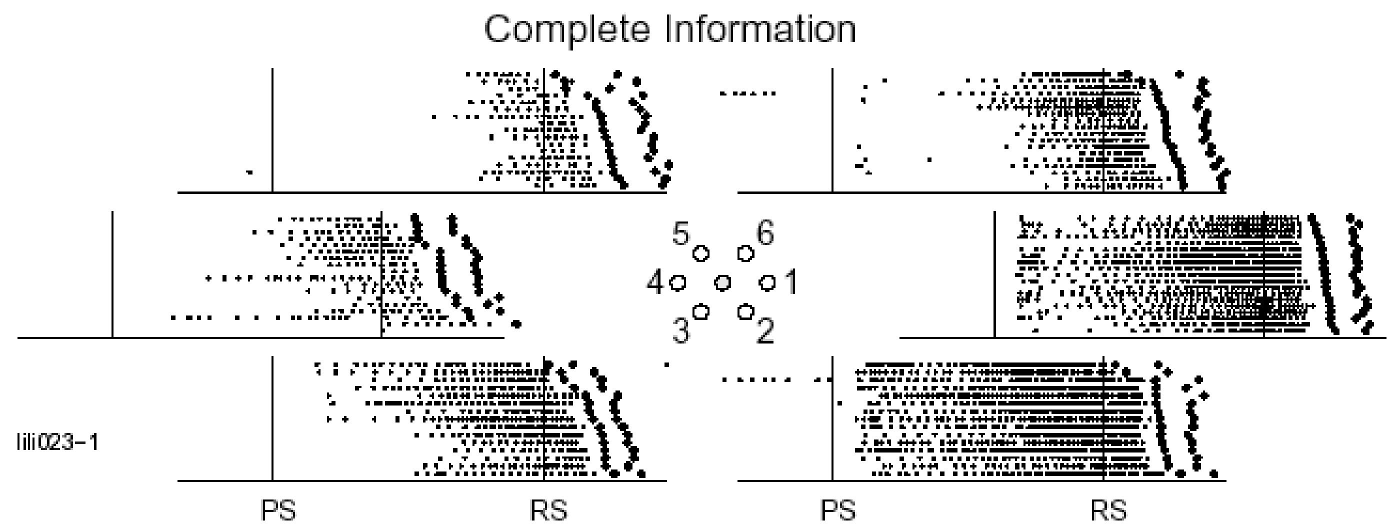
short SR interval:
observe preshape

long SR interval:
observe stimulus-defined
movement plan

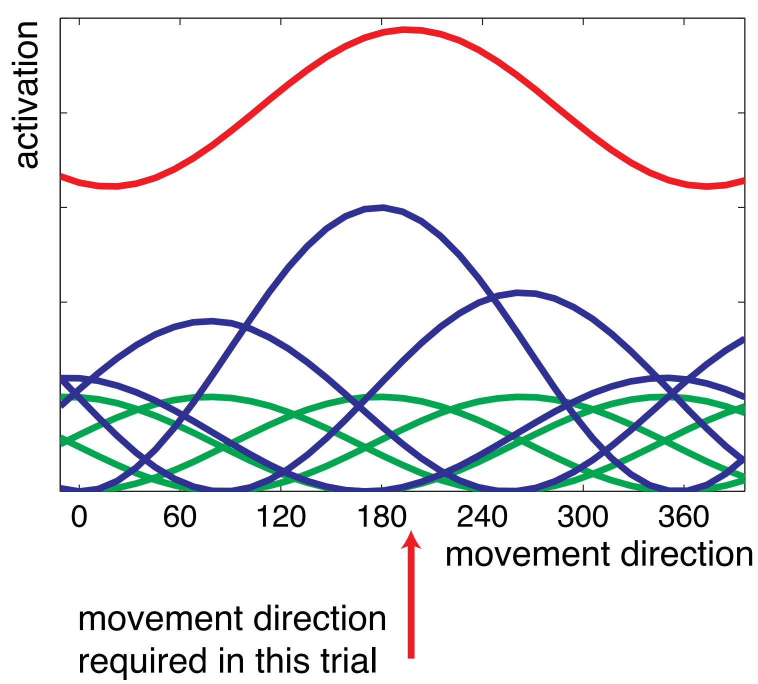
Ghez et al, 1997

Neural evidence for preshape

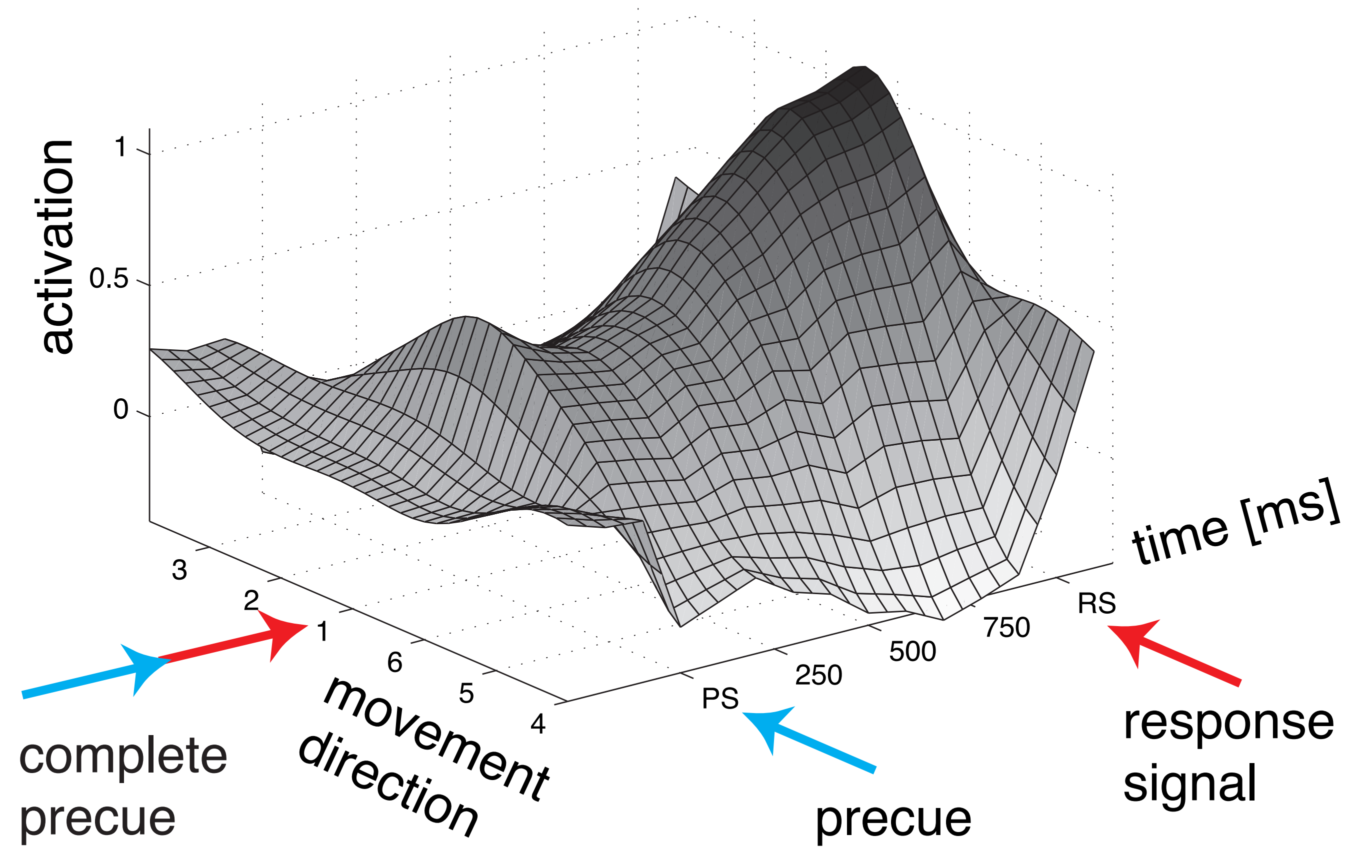




Distribution of population activation = $\sum_{\text{neurons}}$ tuning curve * current firing rate

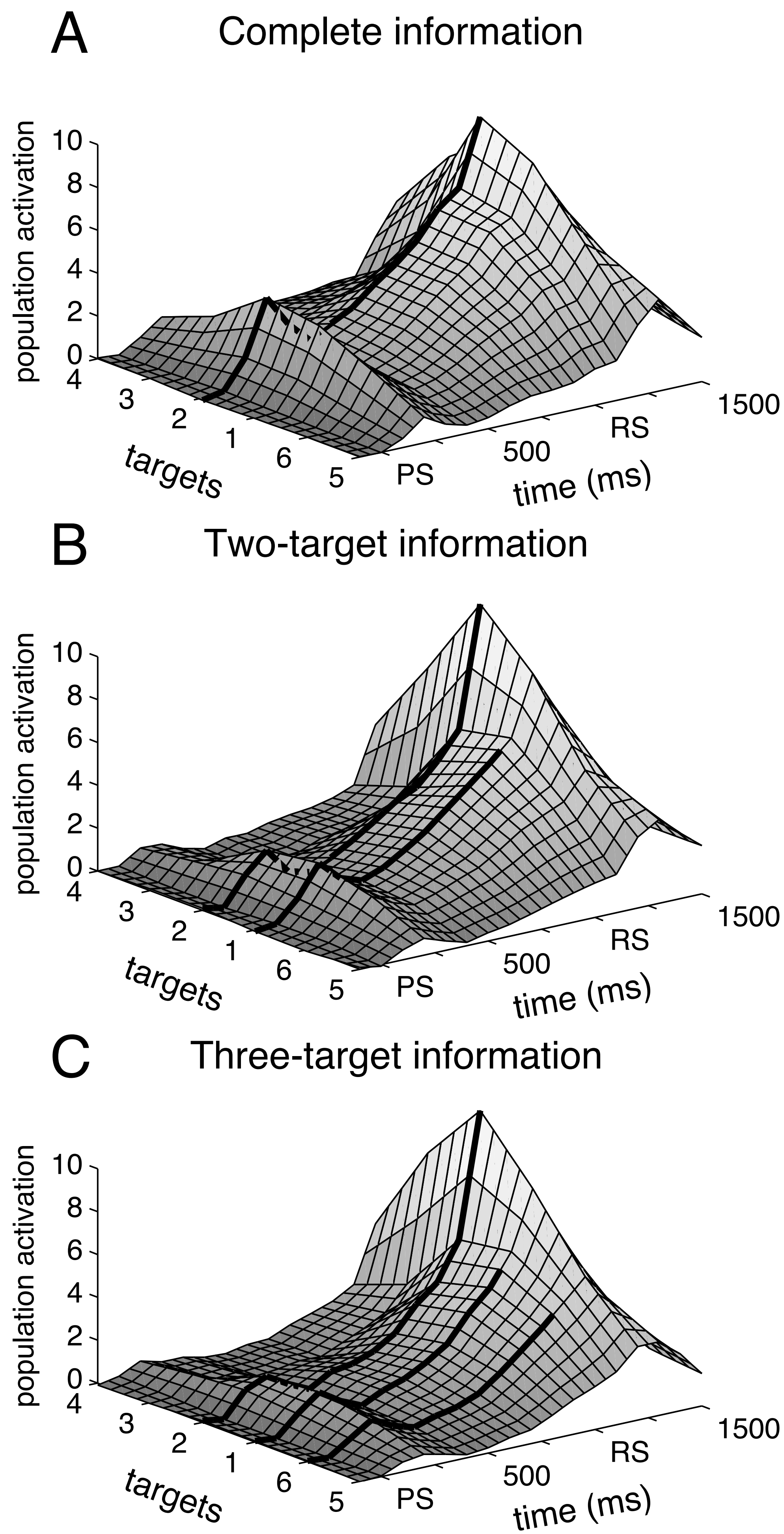


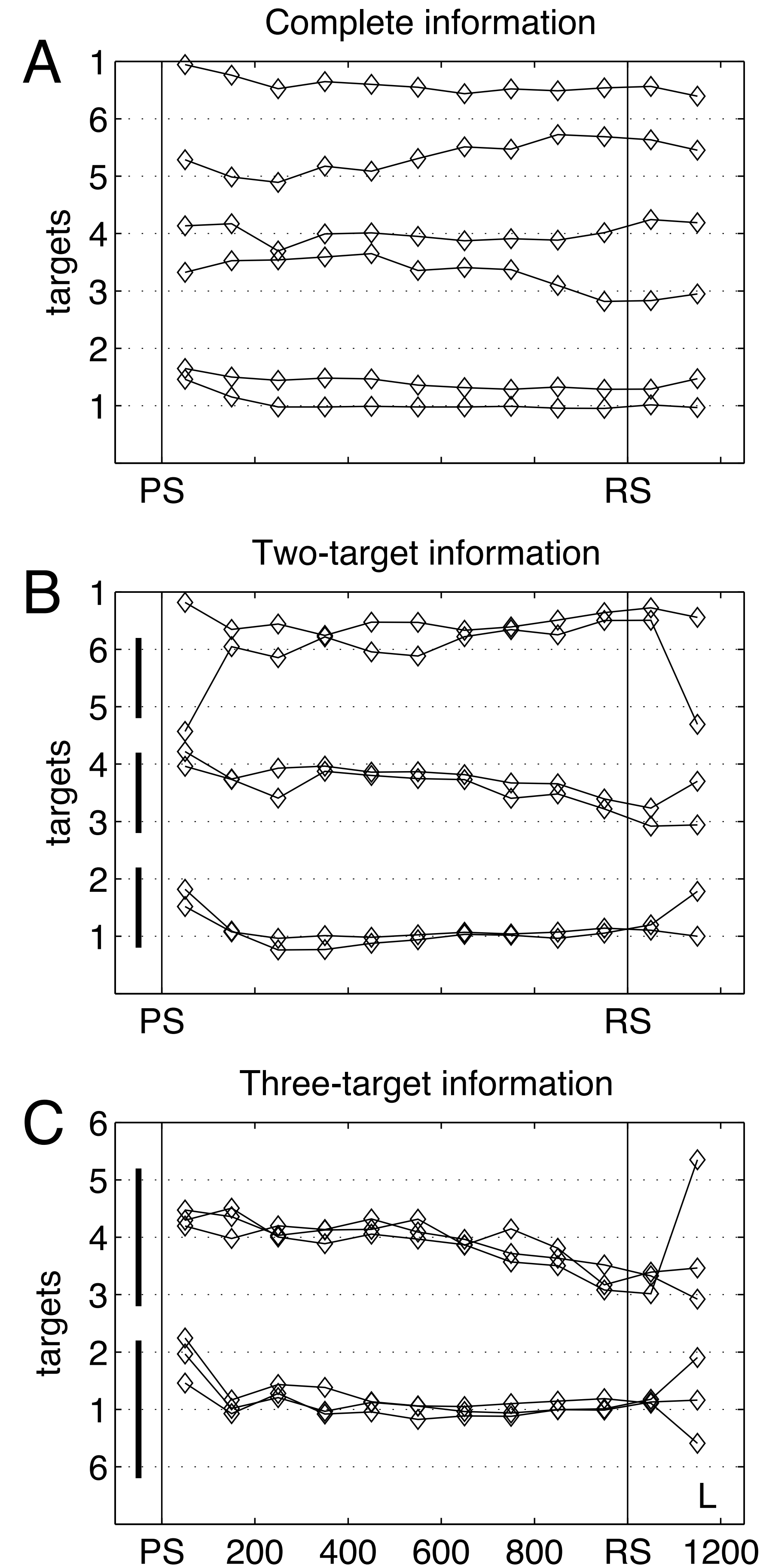
[after Bastian, Riehle, Schöner, submitted]



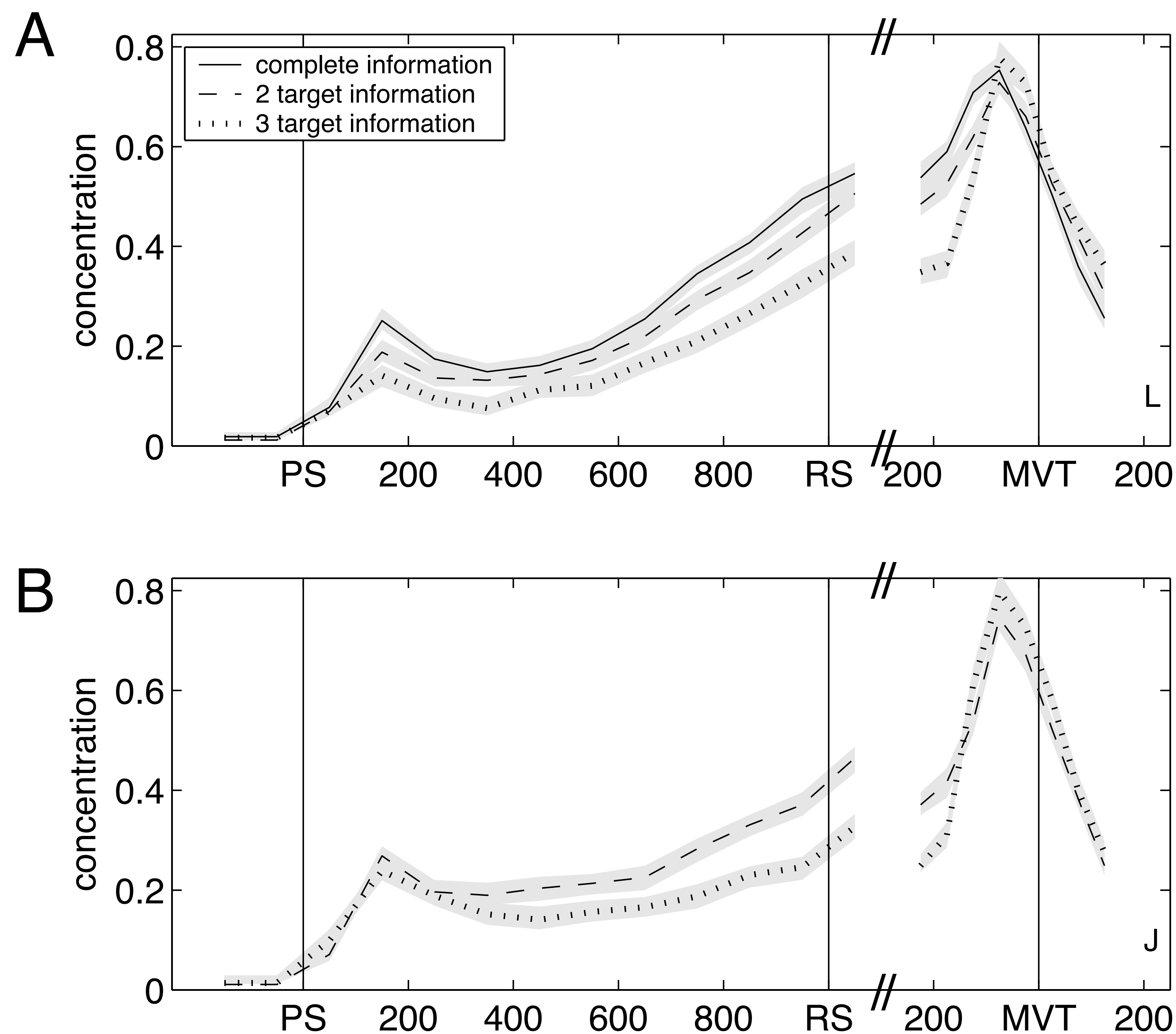
[Bastian, Riehle, Schöner: Europ J Neurosci 18: 2047 (2003)]

DPA reflects prior information





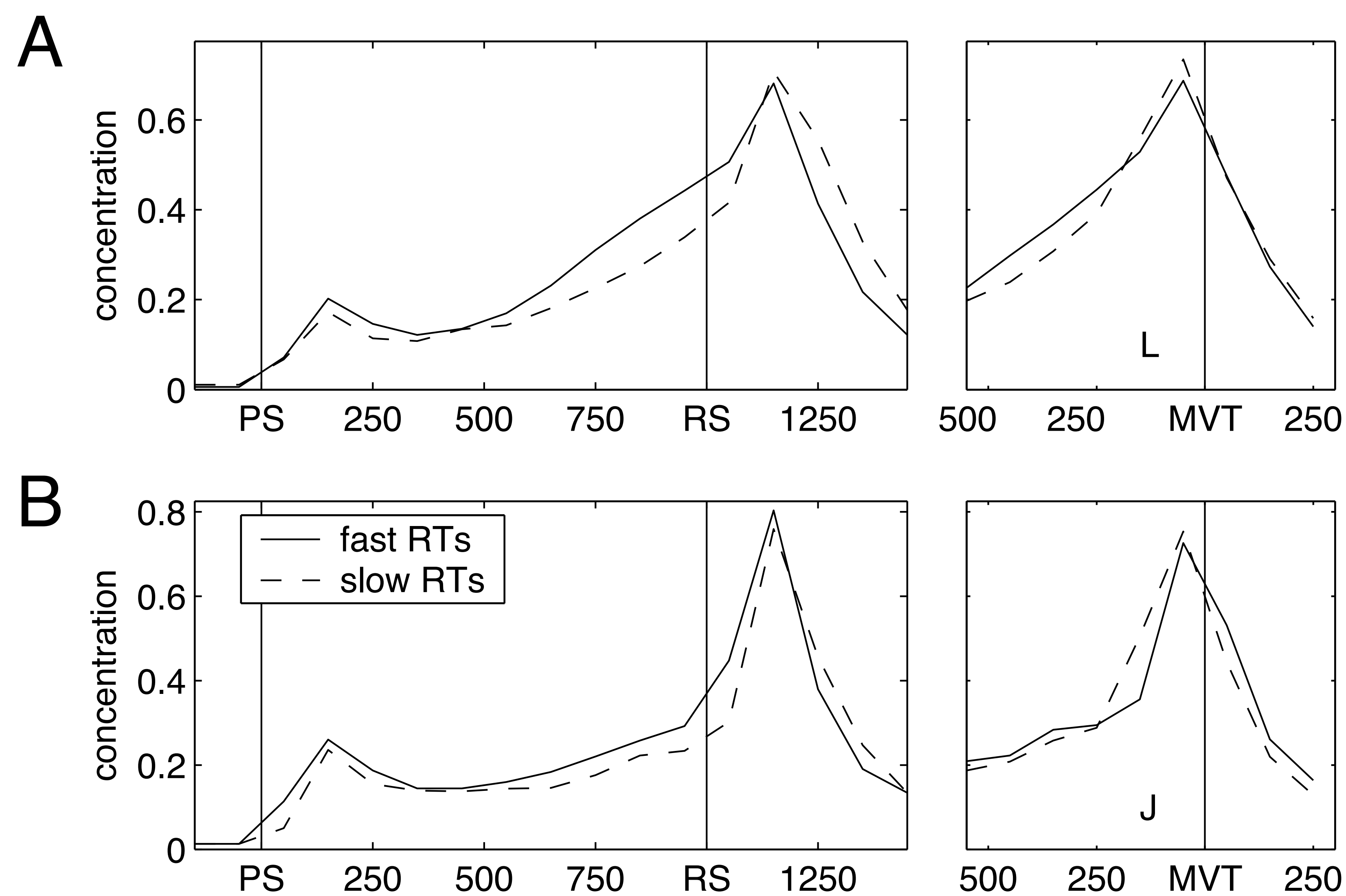
[Bastian, Schöner, Riehle 2003]



- DPA reflects prior information

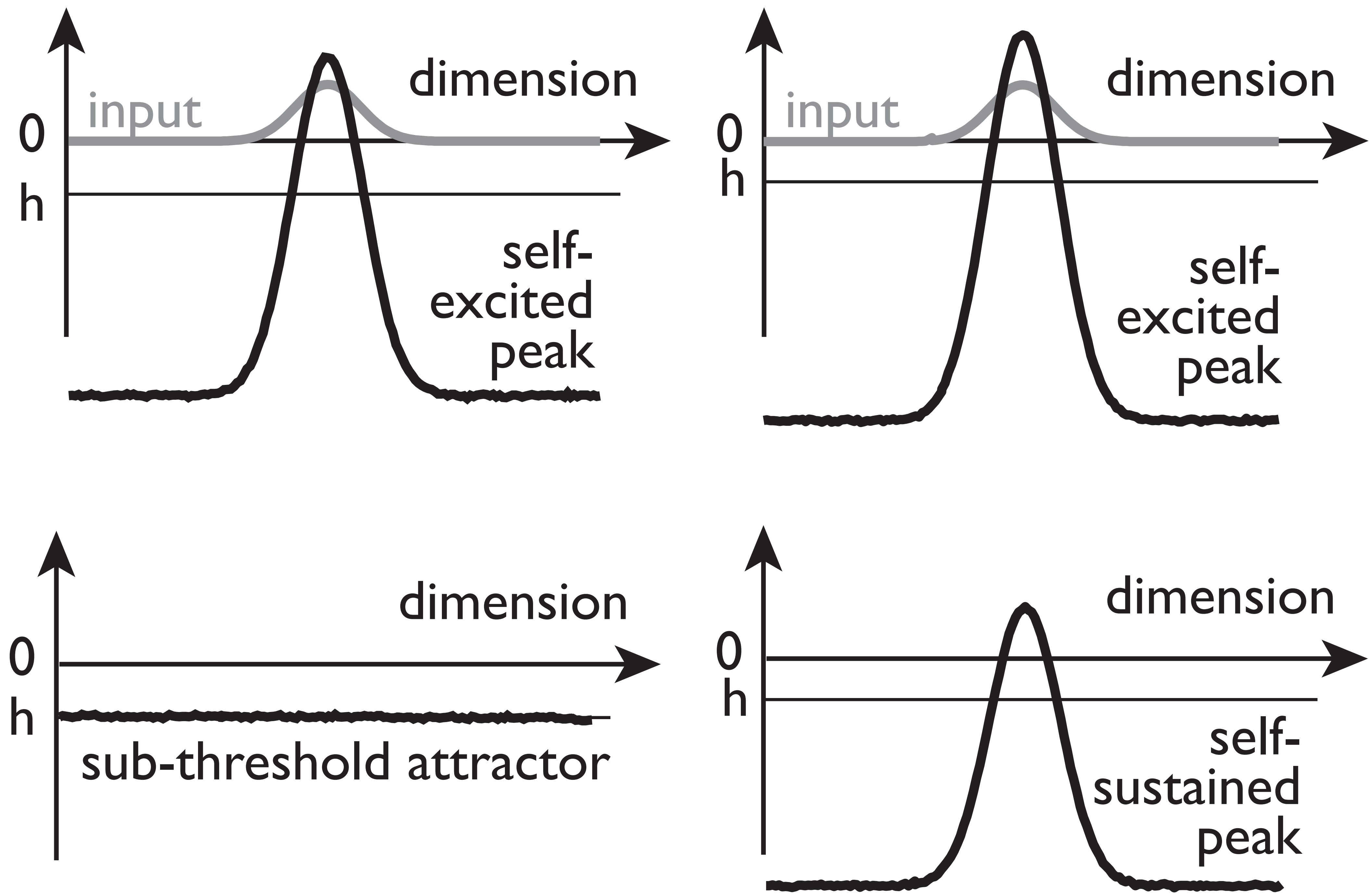
[Bastian, Schöner, Riehle 2003]

- preshape correlates with RT

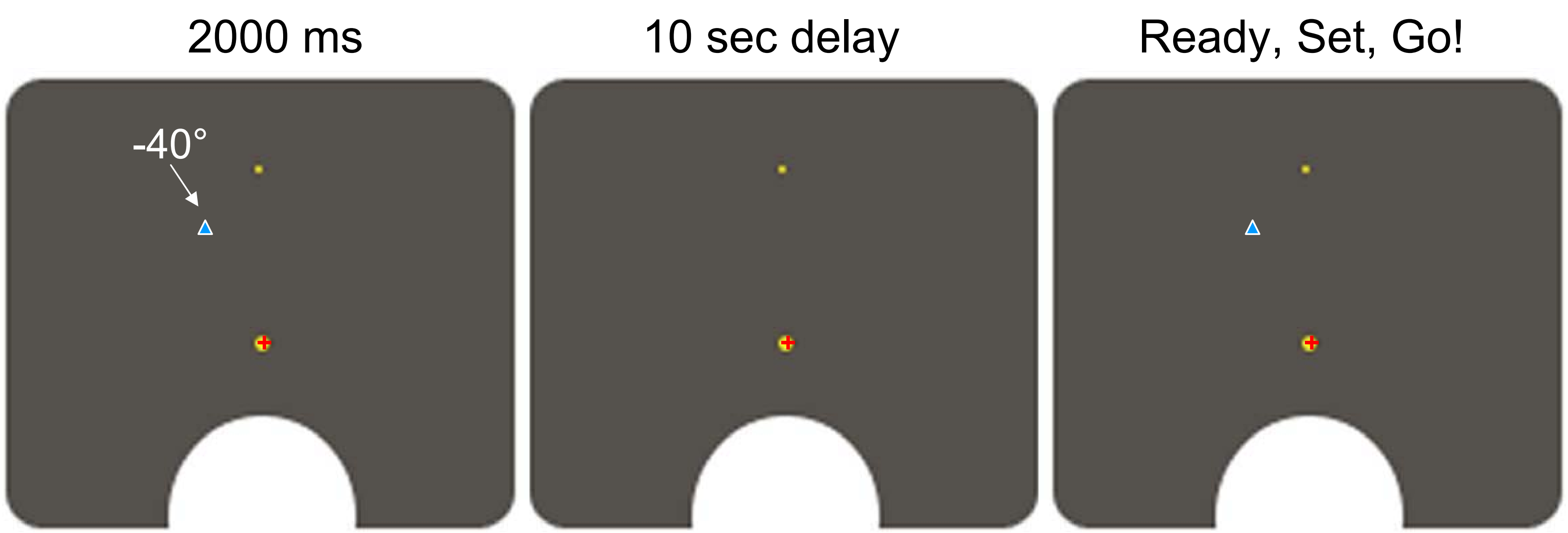


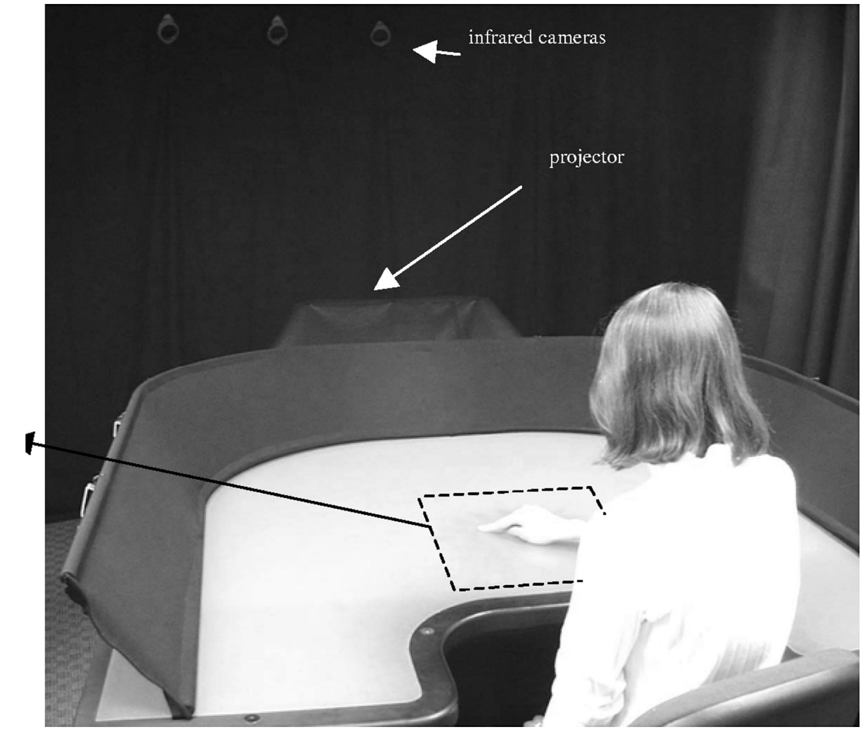
[Bastian, Schöner, Riehle 2003]

Memory instability

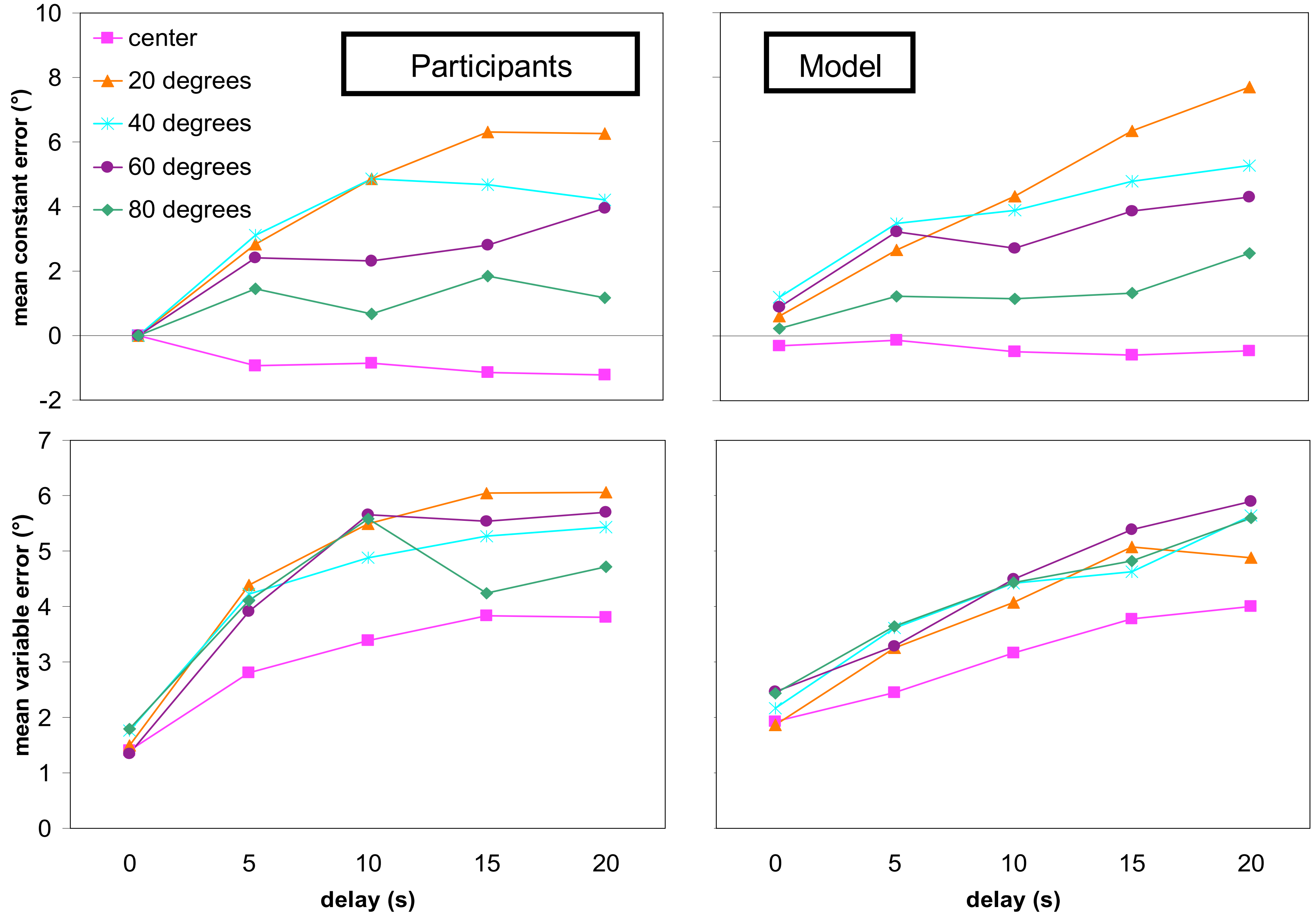


“space ship” task probing spatial working memory

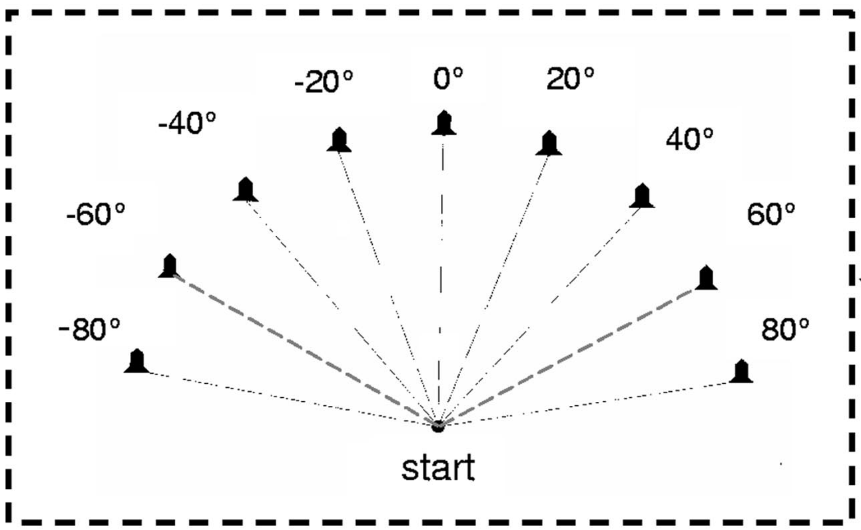


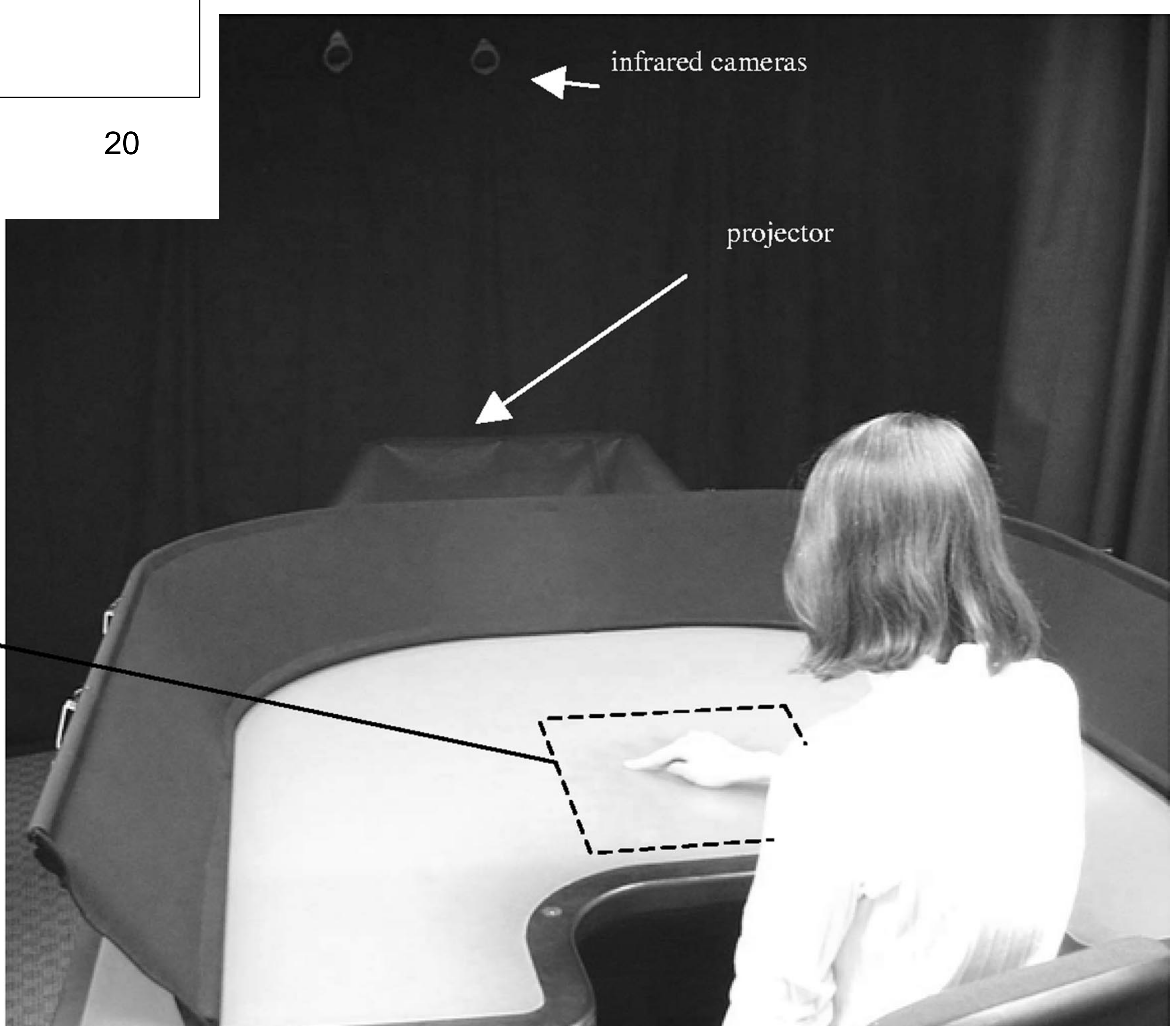


[Schutte, Spencer, JEP:HPP 2009]



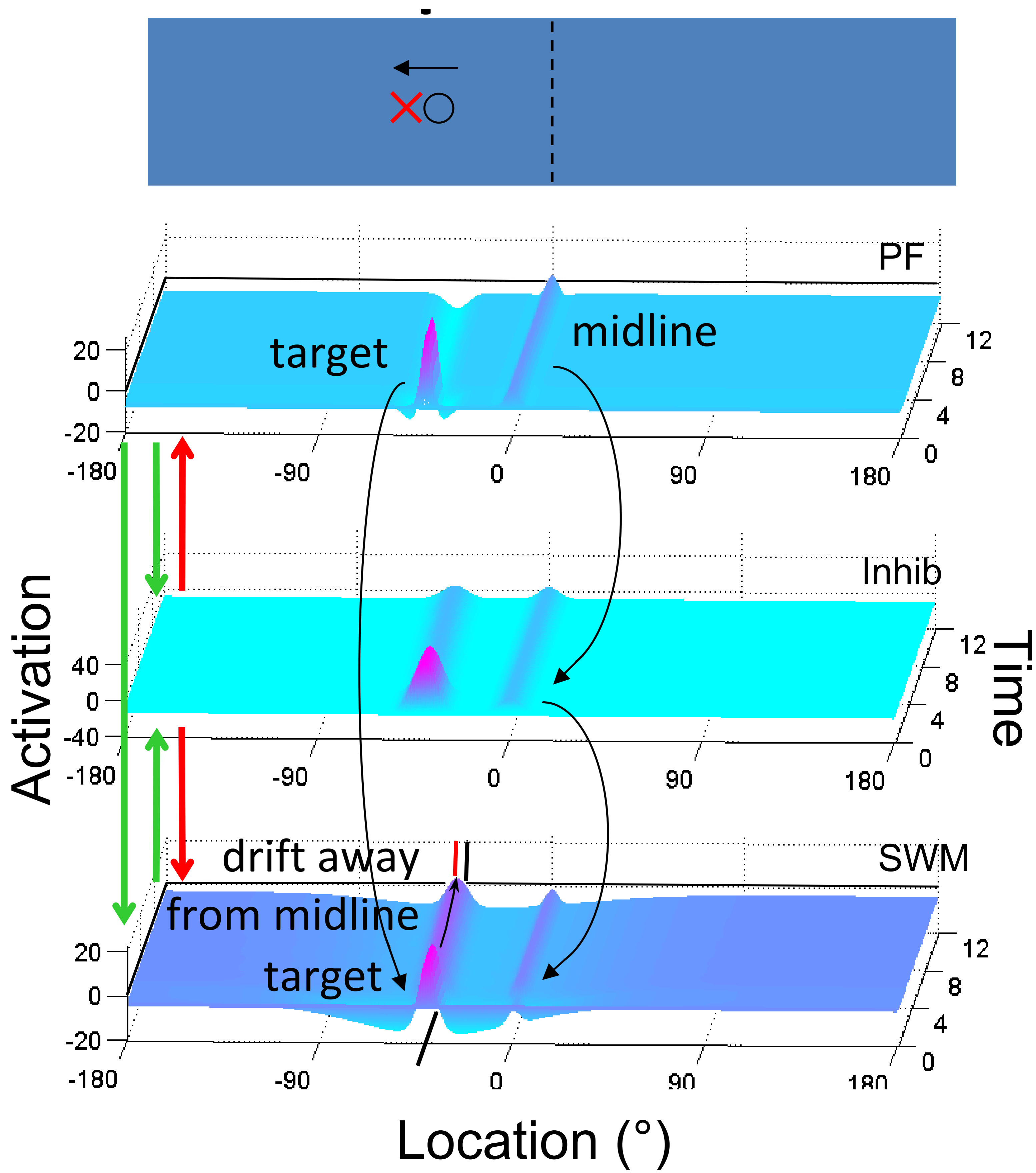
repulsion from mid-line





[Spencer, Schöner, 2006]

- DFT account of repulsion: inhibitory interaction with peak representing landmark



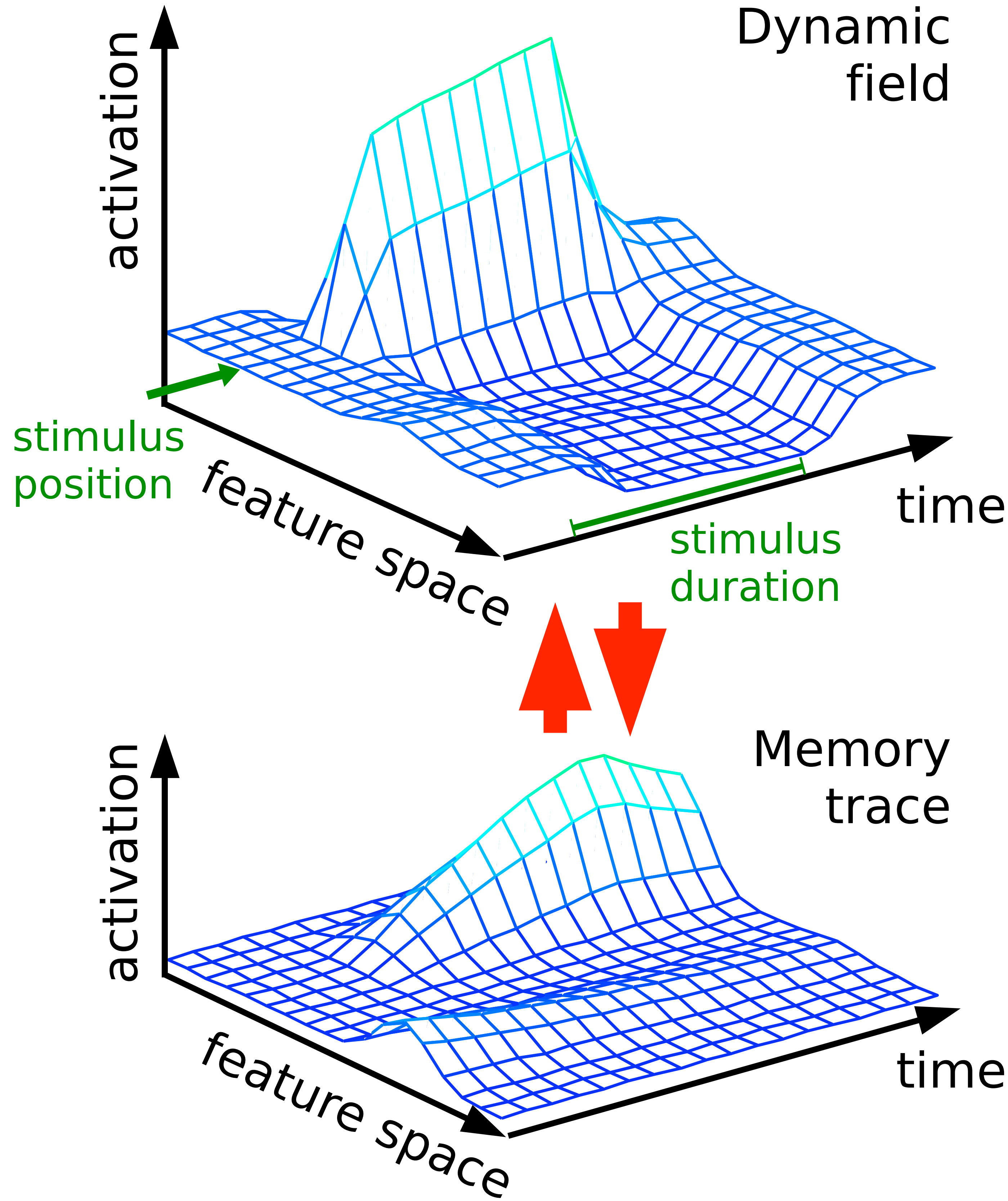
[Simmering, Schutte, Spencer: Brain Research, 2007]

Working memory as sustained peaks

- implies metric drift of WM, which is a marginally stable state (one direction in which it is not asymptotically stable)
- => empirically real..

the memory trace

- inhomogeneities from simplest from the memory trace
- ~ habit formation (?) William James: habit formation as the simplest form of learning
- habituation: the memory trace for inhibition..



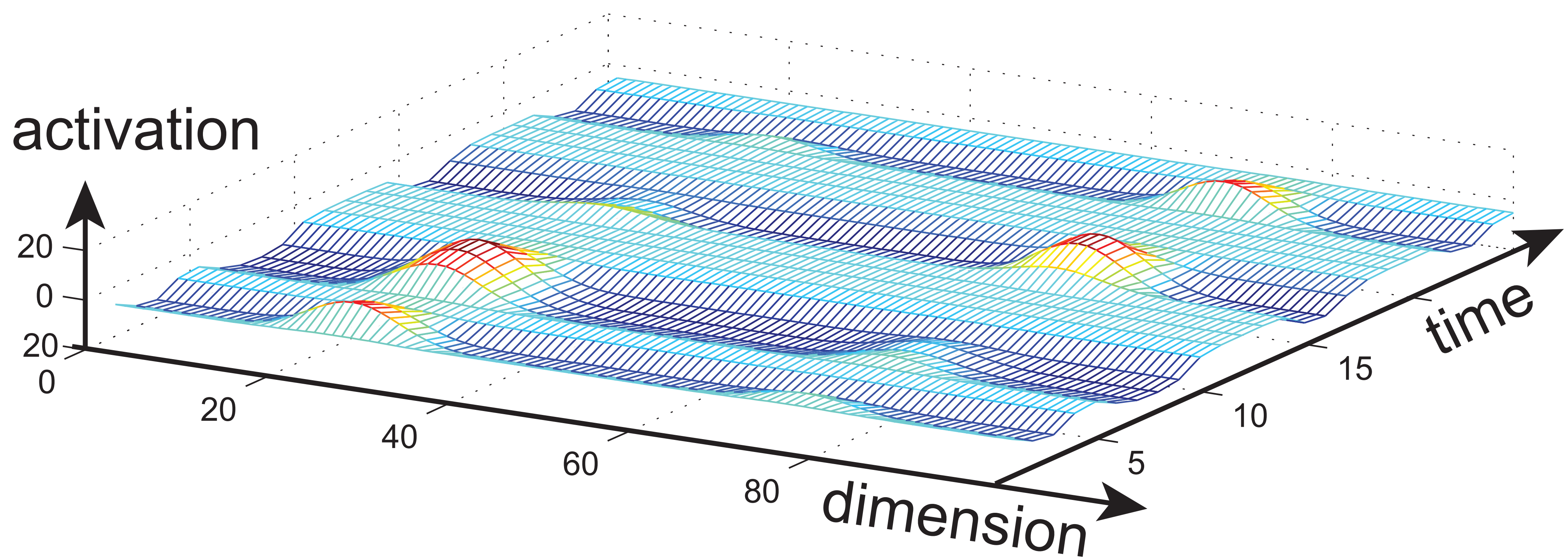
mathematics of the memory trace

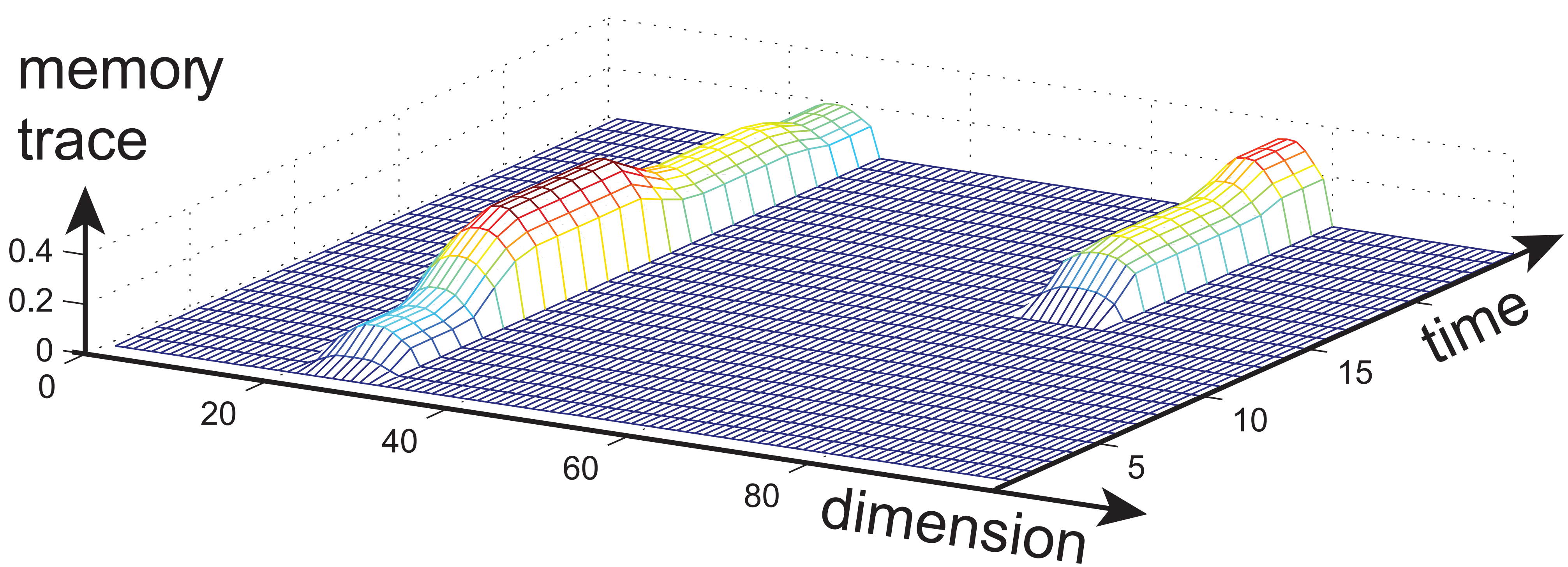
$$\begin{aligned}\tau \dot{u}(x,t) &= -u(x,t) + h + S(x,t) + u_{\rm mem}(x,t) \\ &+ \int dx'\ w(x-x')\ \sigma(u(x'))\end{aligned}$$

$$\begin{aligned}\tau_{\rm mem}\ \dot{u}_{\rm mem}(x,t) &= -u_{\rm mem}(x,t) \\ &+ \int dx'\ w_{\rm mem}(x-x')\sigma(u(x',t))\end{aligned}$$

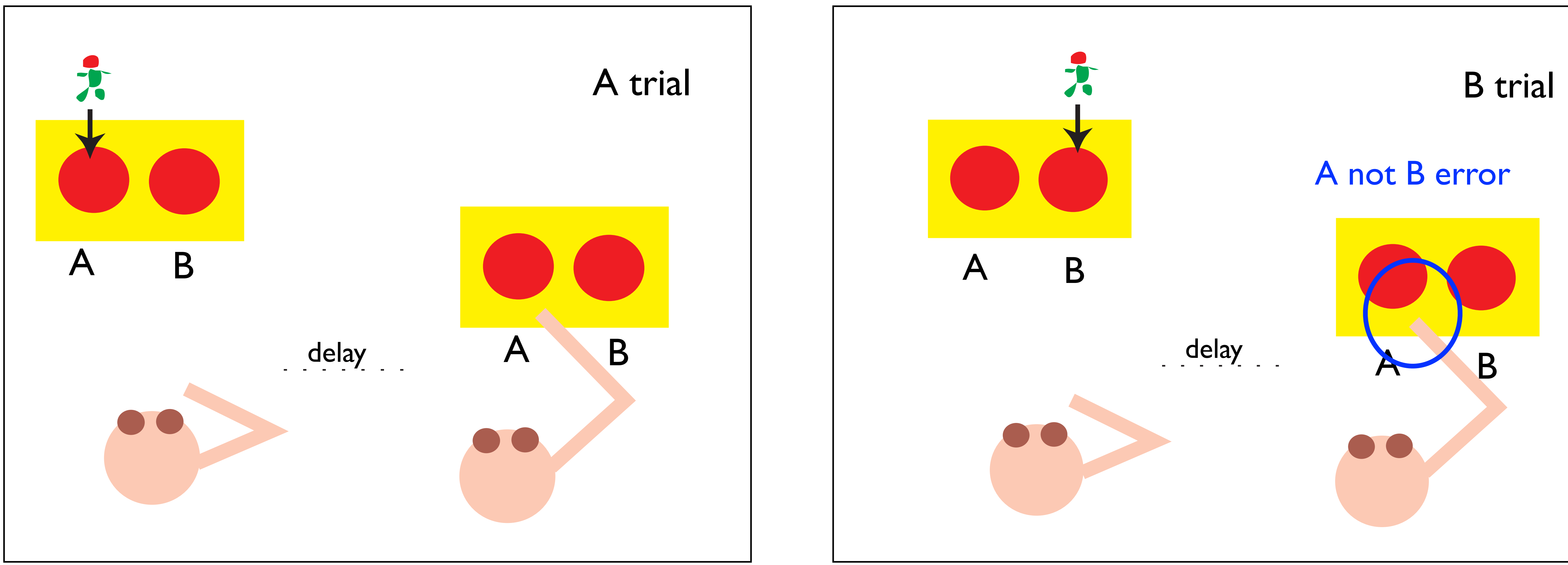
- memory trace only evolves while activation is excited
- potentially different growth and decay rates

memory trace reflects history of decisions formation





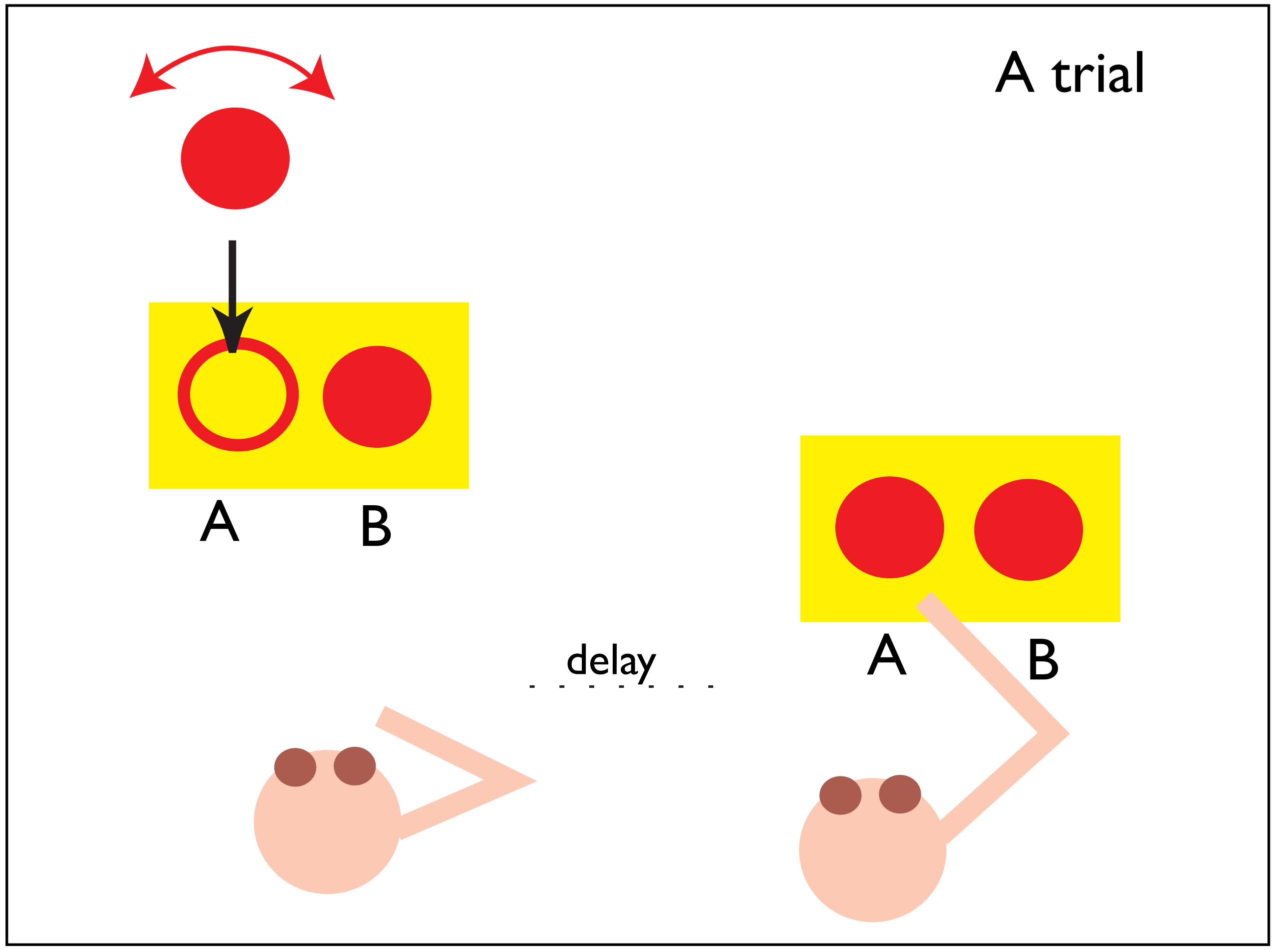
Piaget's A not B paradigm: "out-of-sight -- out of mind"

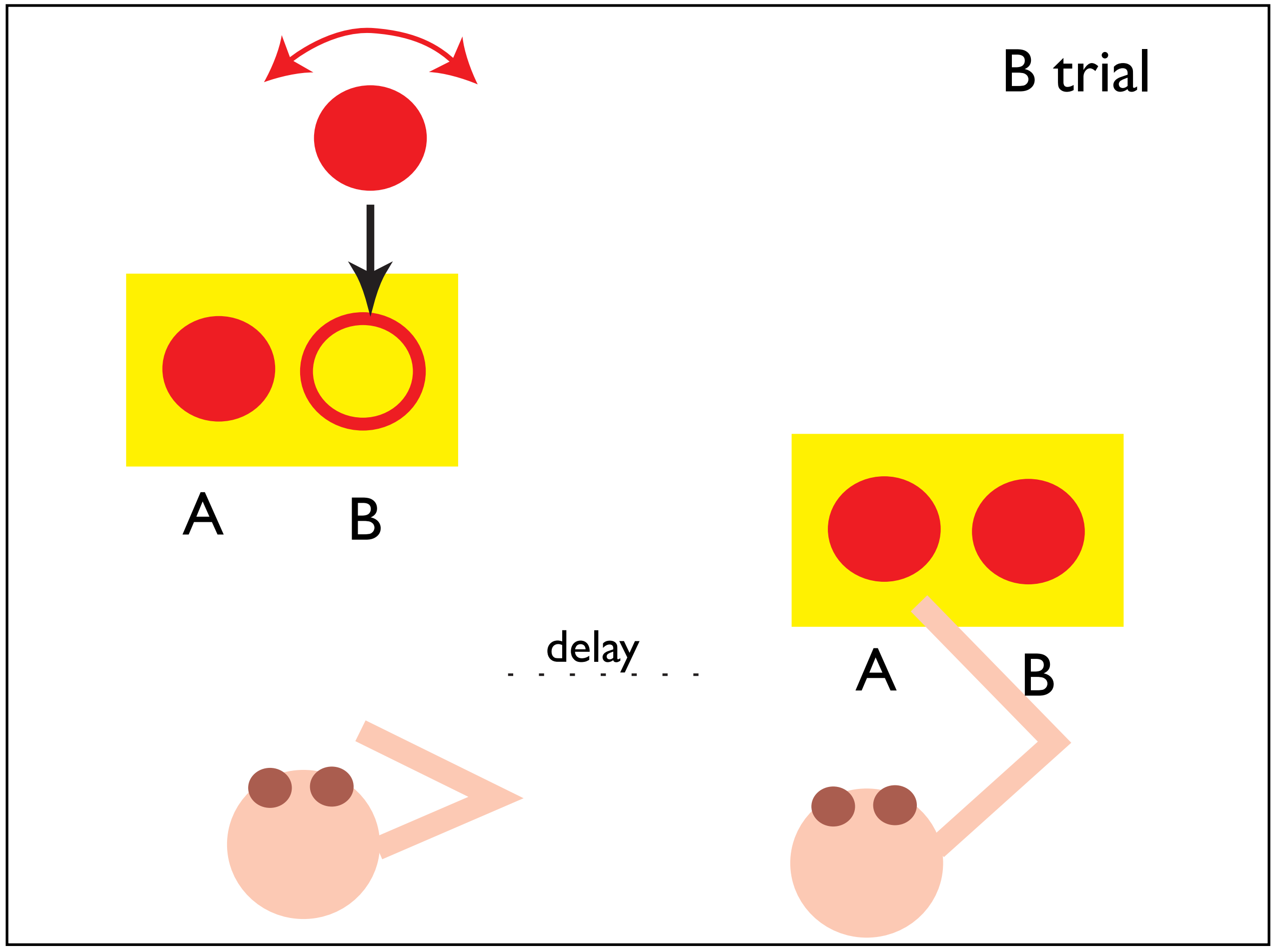


Toyless variant of A not B task

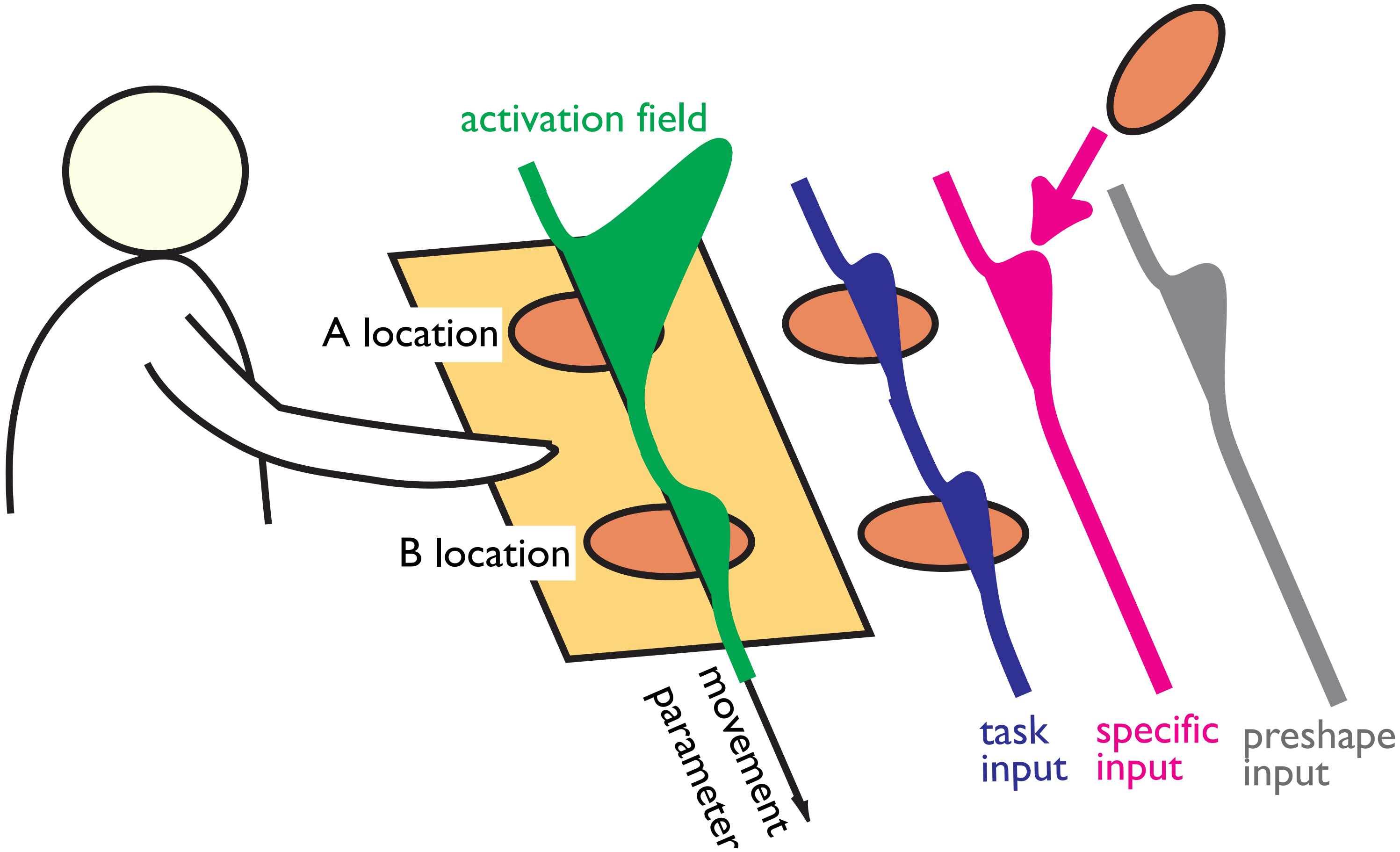
[Smith, Thelen et al.: Psychological Review (1999)]

Toyless variant of A not B task reveals that A not B is essentially a decision task!

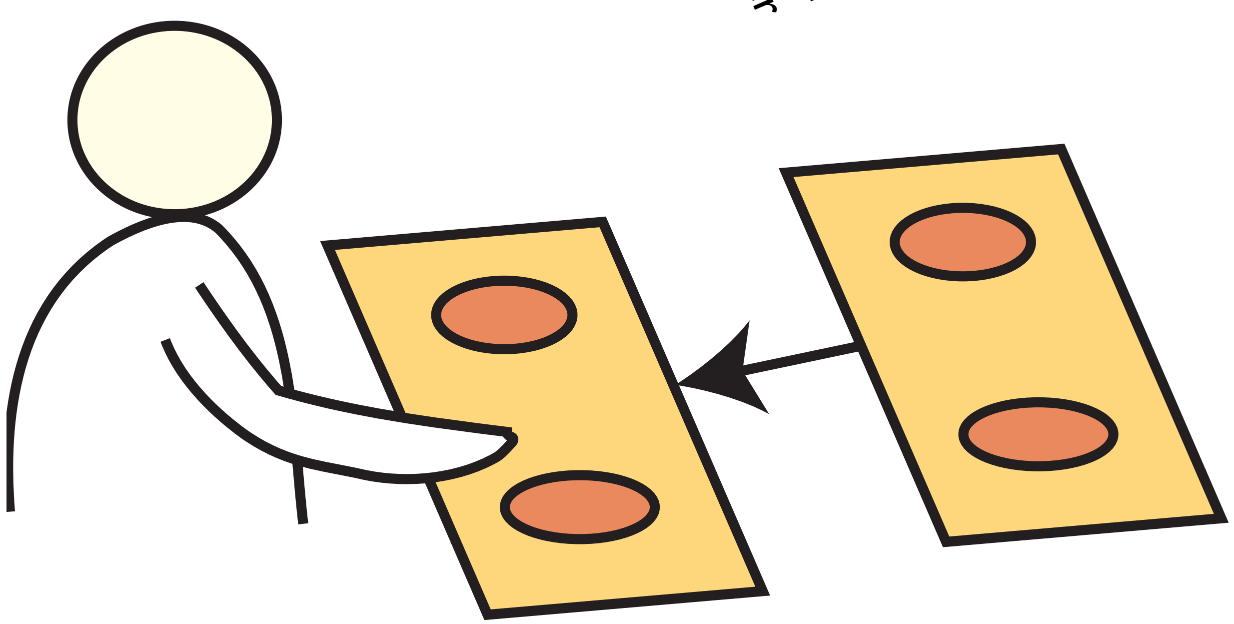




[Smith, Thelen et al.: Psychological Review (1999)]



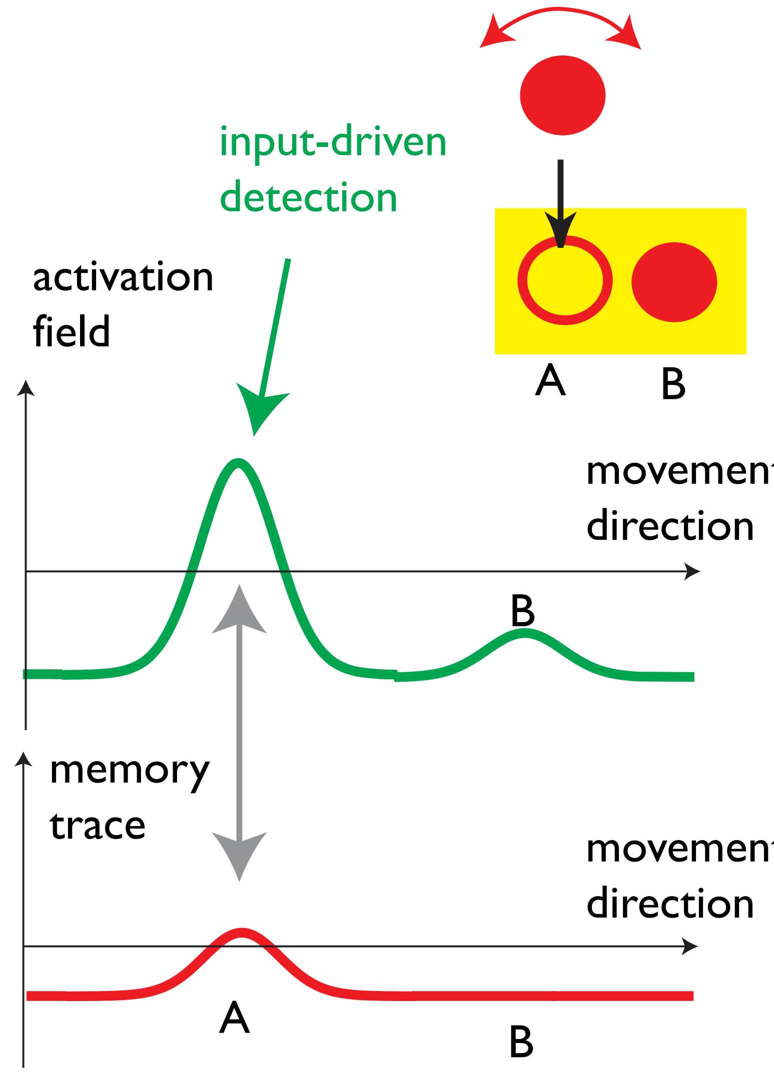
[Thelen, et al., BBS (2001)]



[Dinveva, Schöner, Dev. Science 2007]

Instabilities

- detection: forming and initiating a movement goal
- selection: making sensori-motor decisions
- (learning: memory trace)
- boost-driven detection: initiating the action
- memory instability: old infants sustain during the delay, young infants do not



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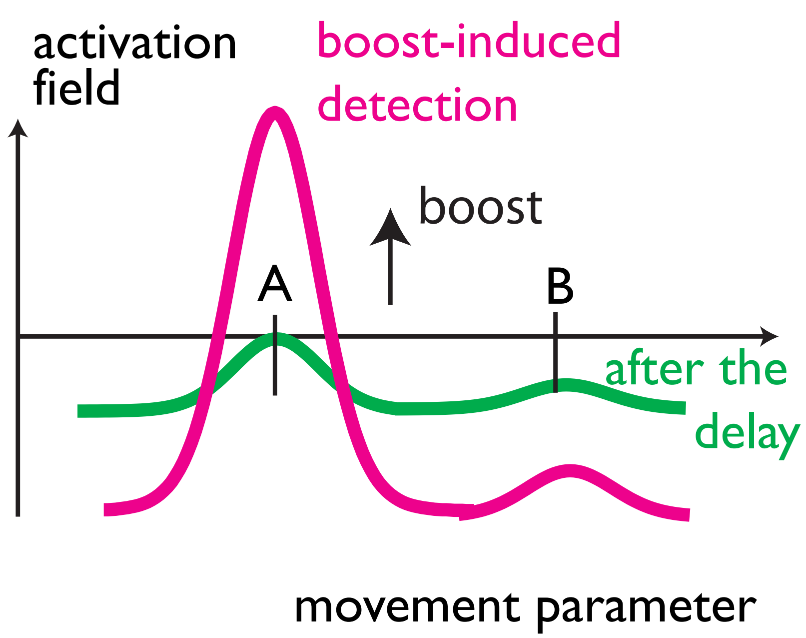

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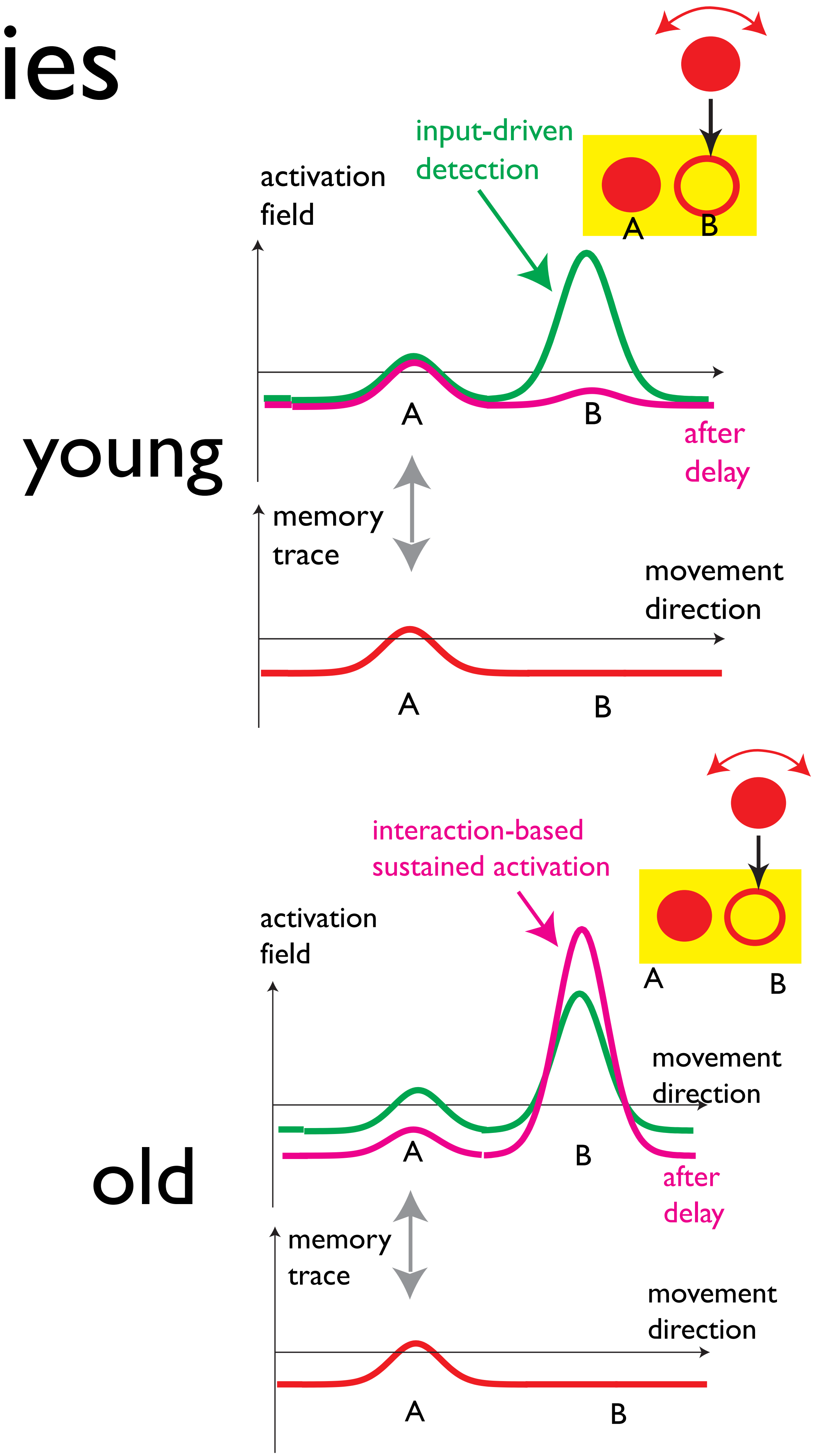
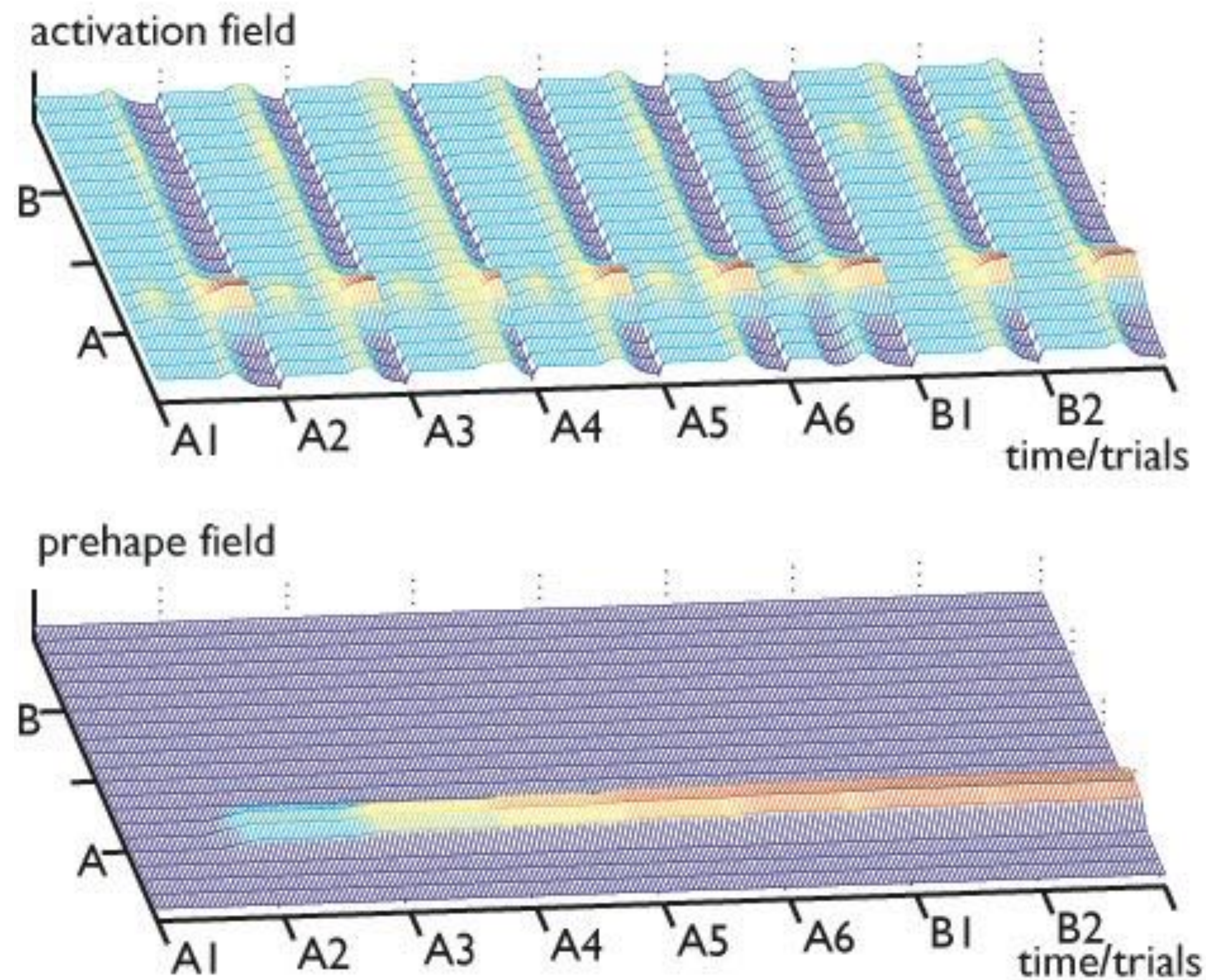
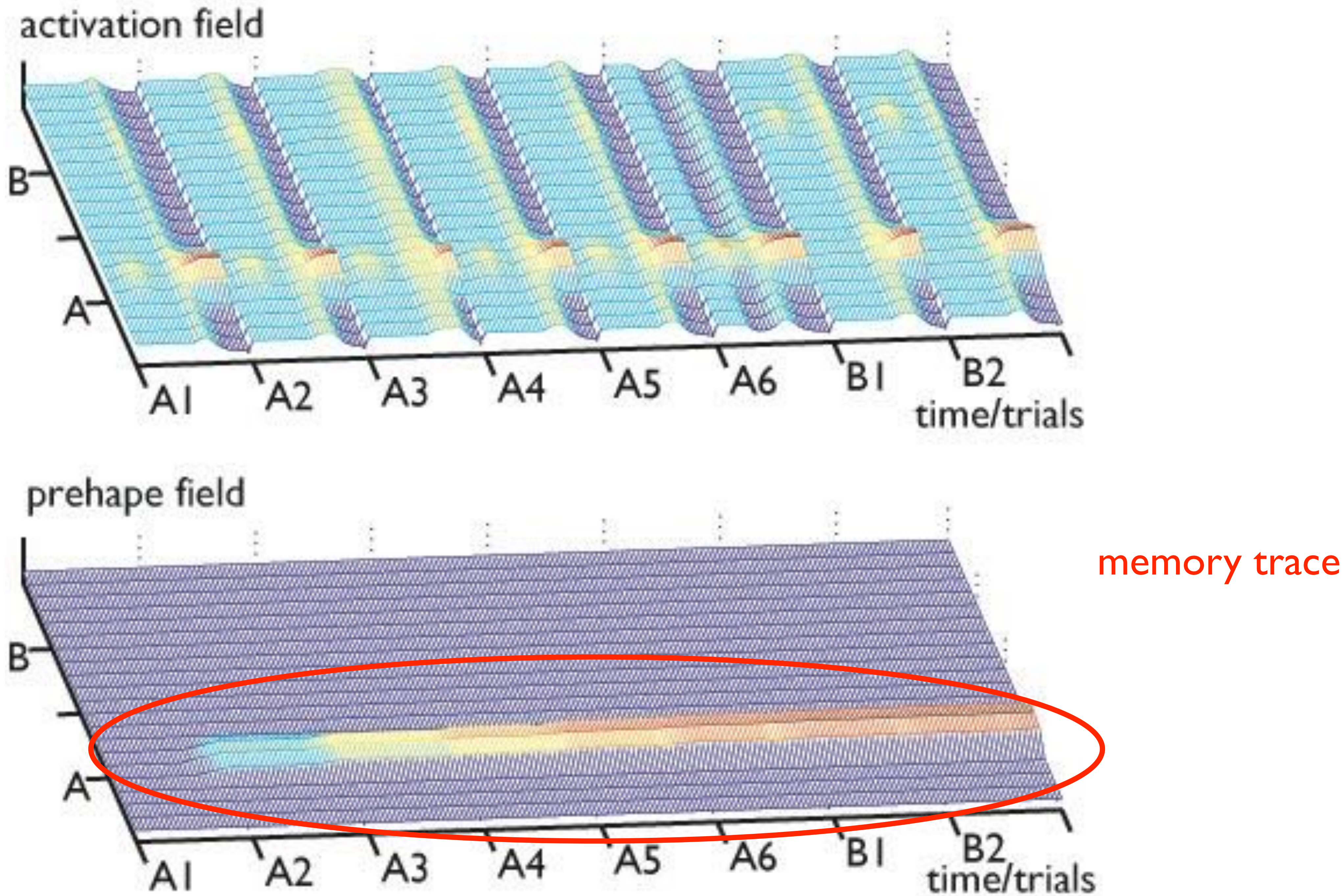


DFT of infant perseverative reaching



[Dinveva, Schöner, Dev. Science 2007]

DFT of infant perseverative reaching



[Dinveva, Schöner, Dev. Science 2007]

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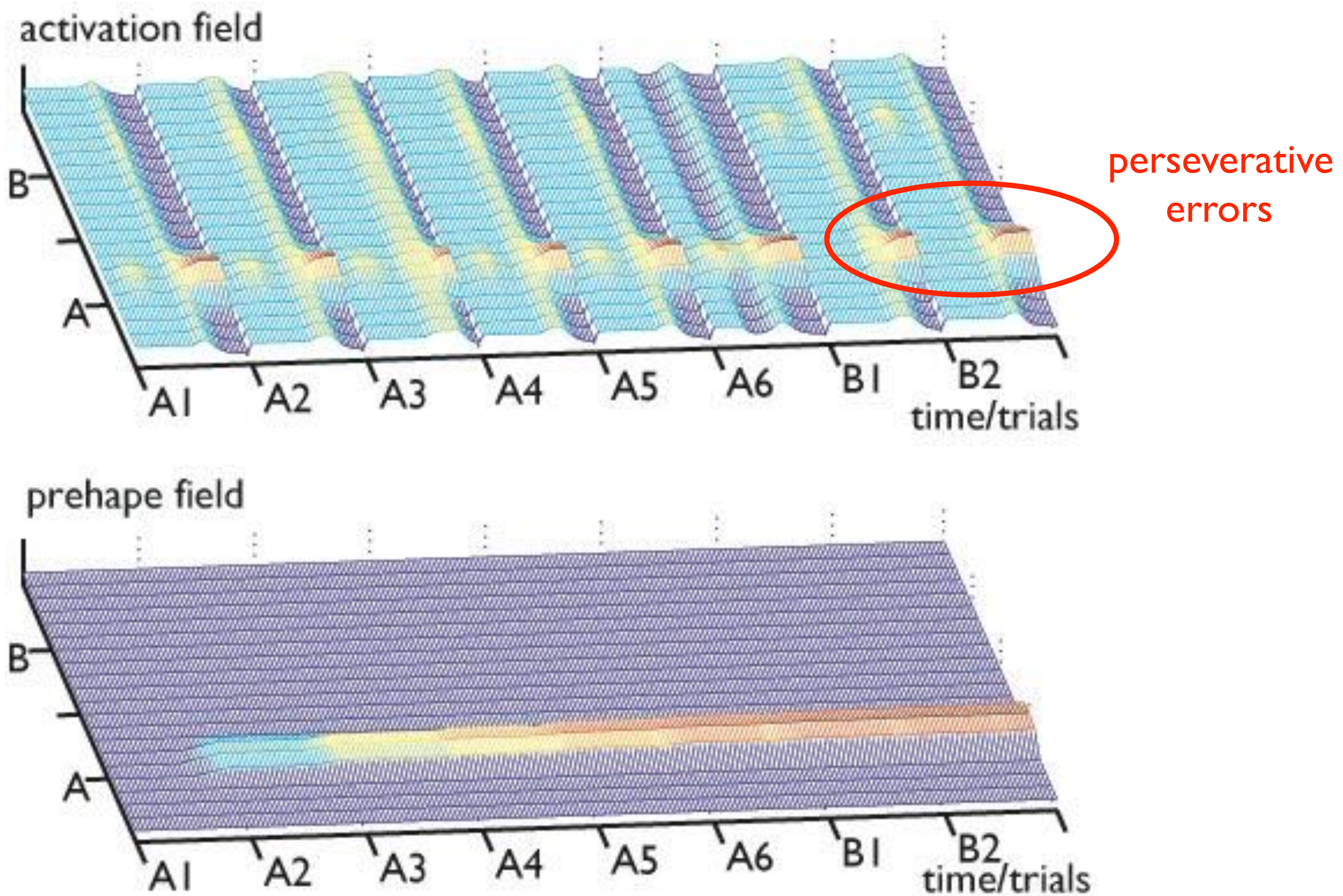
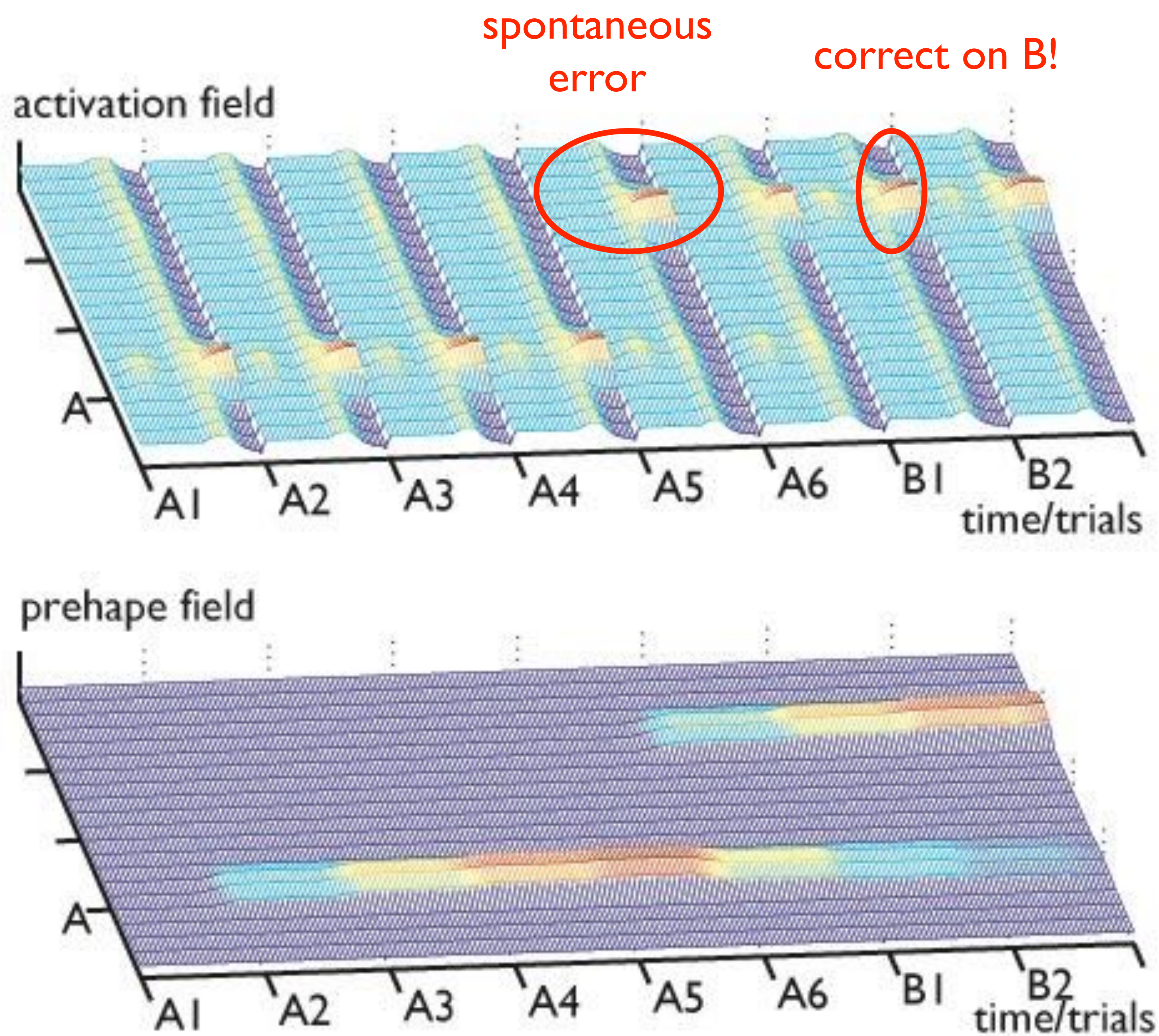


[Dinveva, Schöner, Dev. Science 2007]

DFT of infant perseverative reaching

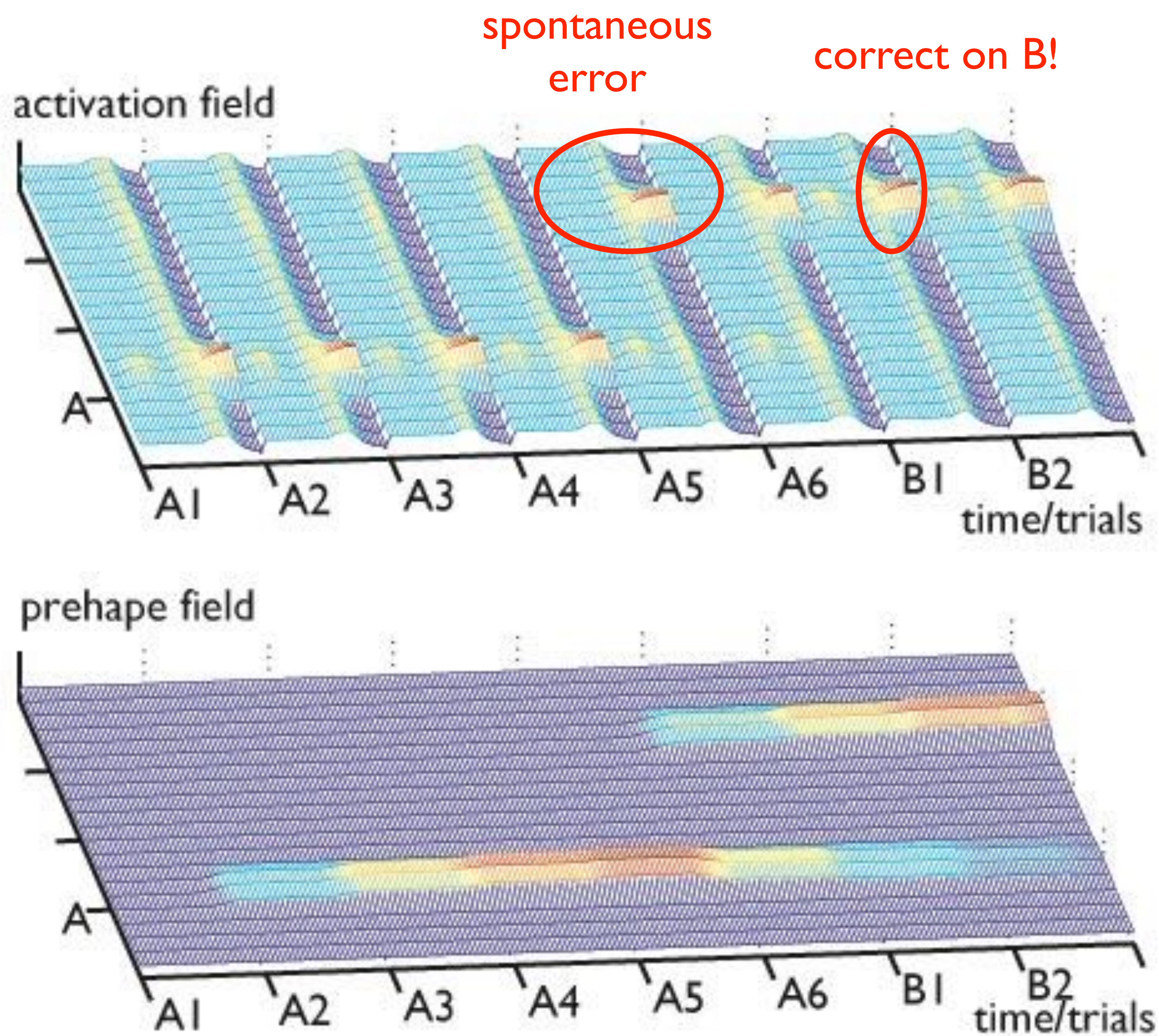
- in spotaneous errors, activation arises at B on an A trial
- which leads to correct reaching on B trial



[Dinveva, Schöner, Dev. Science 2007]

DFT of infant perseverative reaching

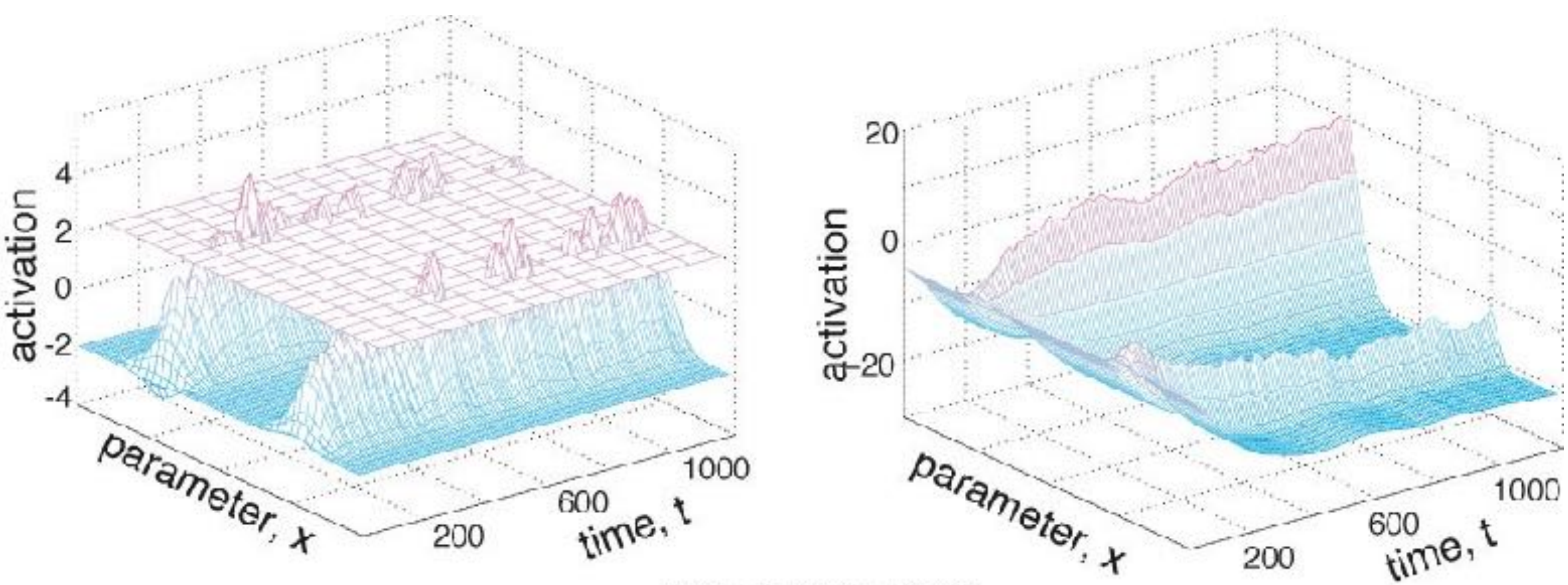
- that is because reaches to B on A trials leave memory trace at B



[Dinveva, Schöner, Dev. Science 2007]

DFT is a neural process model

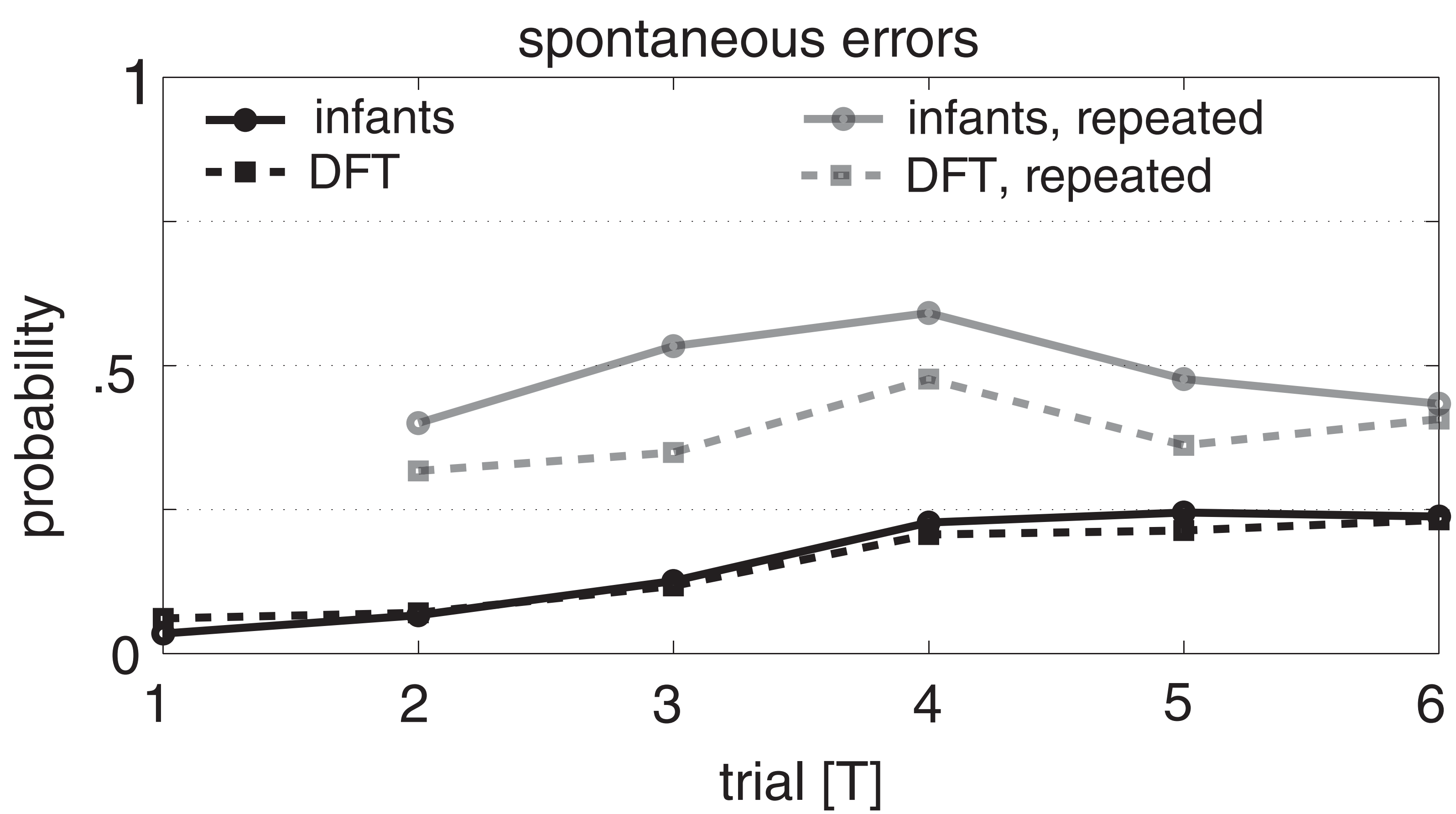
- that makes the decisions in each individual trial, by amplifying small differences into a macroscopic stable state
- and that's how decisions leave traces, have consequences



[Wilimzig, Schöner, 2006]

Decisions have consequences

- a spontaneous error doubles probability to make the spontaneous error again



[Dineva, Schöner: Connection Science 2018]

Conclusions

- action, perception, and embodied cognition takes place in continuous spaces. peaks = units of representation are attractors of the neural dynamics
- neural fields link neural representations to these continua
- stable activation peaks are the units of neural representation
- peaks arise and disappear through instabilities through which elementary cognitive functions (e.g. detection, selection, memory) emerge

The conceptual framework of DFT