Dynamic Field Theory

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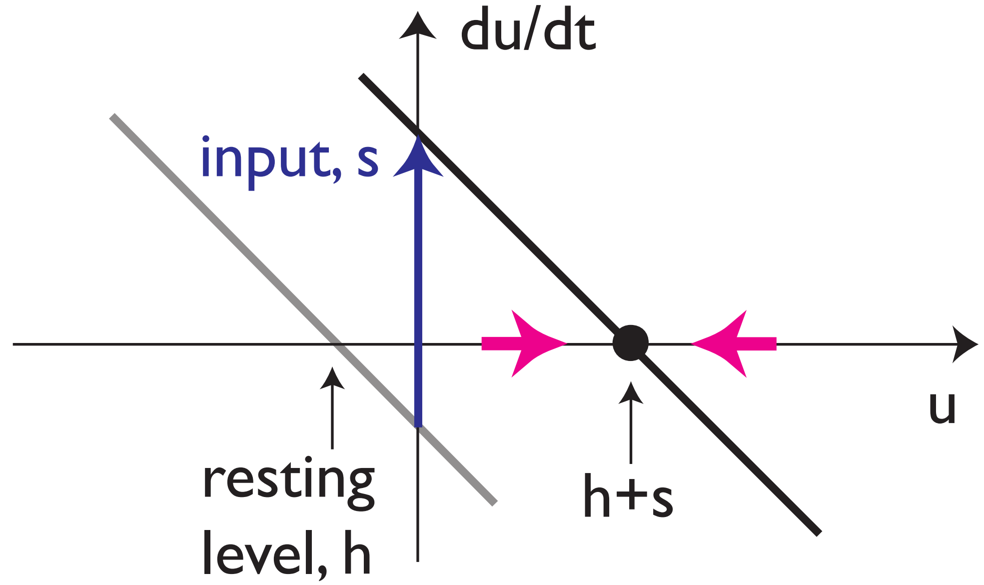
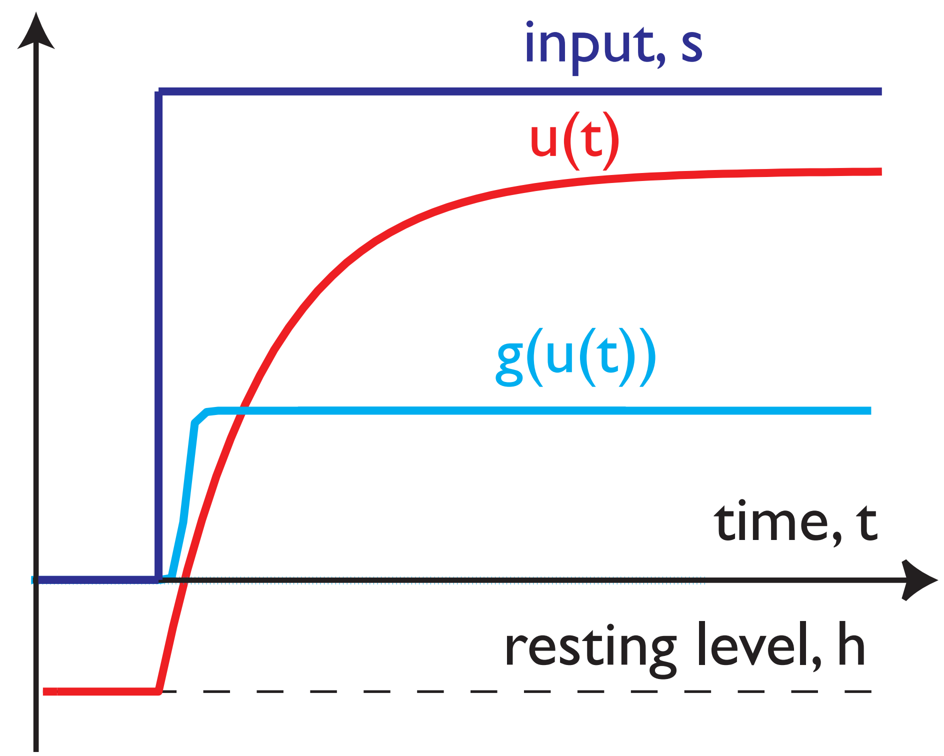
Recall: neural dynamics



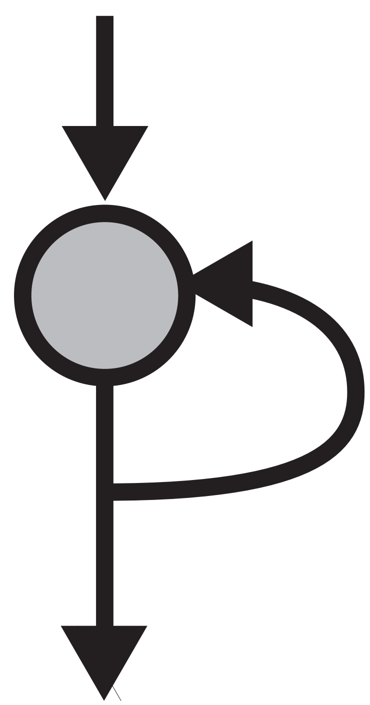
- activation dynamics of individual “neurons”

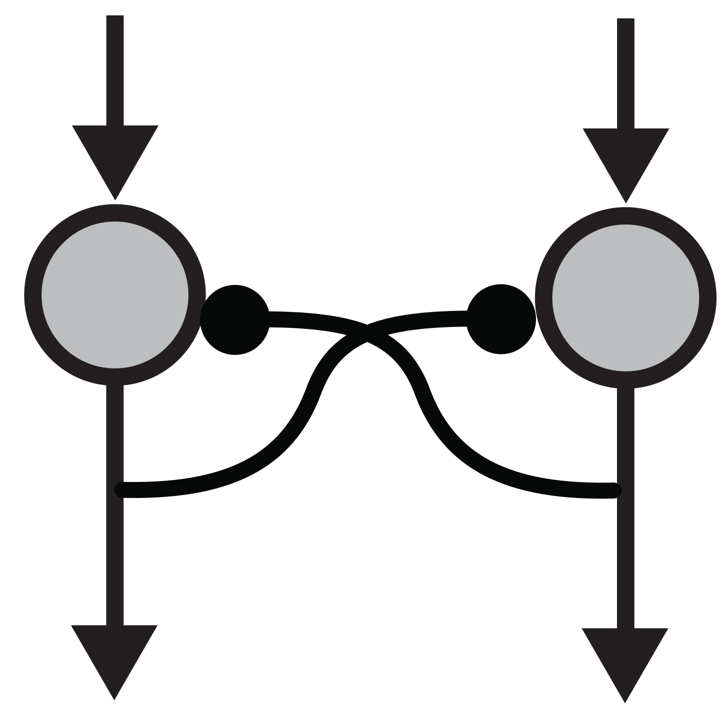


$$\tau \dot{u}(t) = -u(t) + h + \text{ inputs(t)}$$

Neural Dynamics

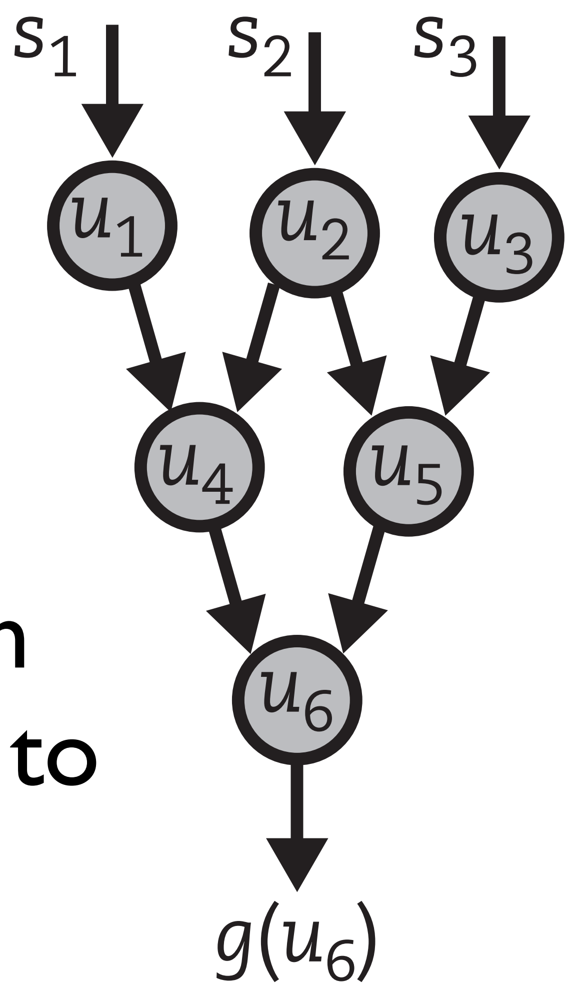
- dynamic neural "networks" consisting of one or two neurons





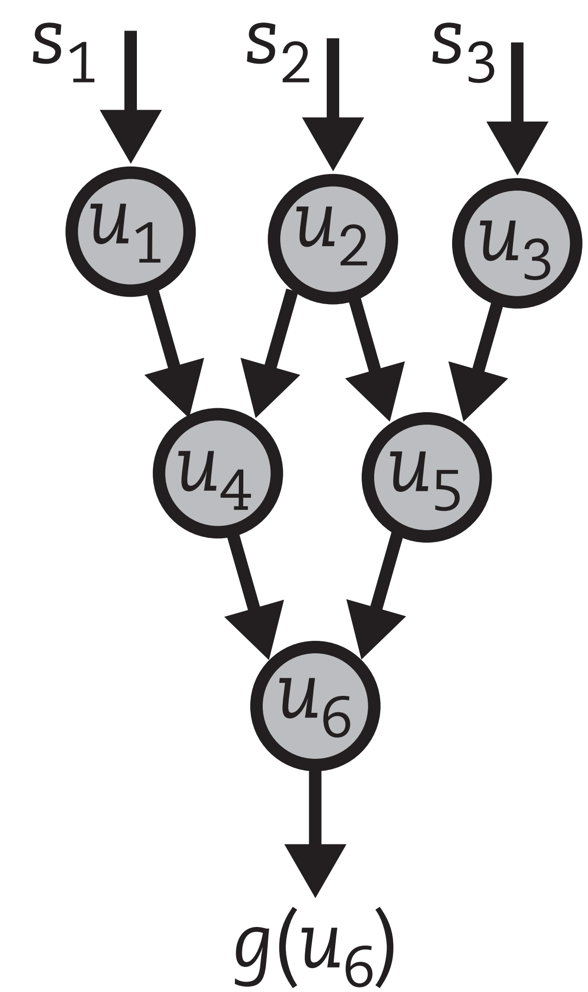
… toward fields

- 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



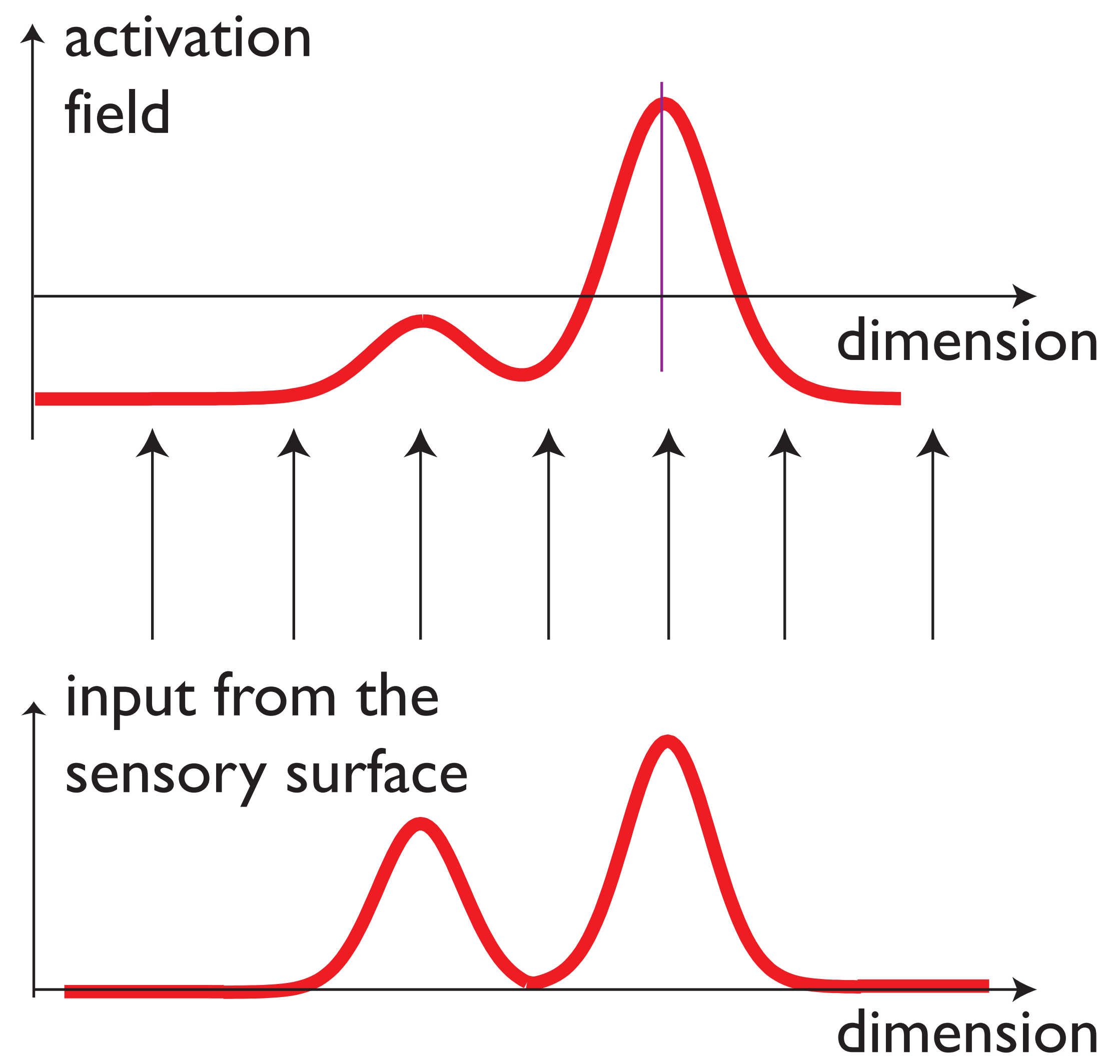
… toward fields

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



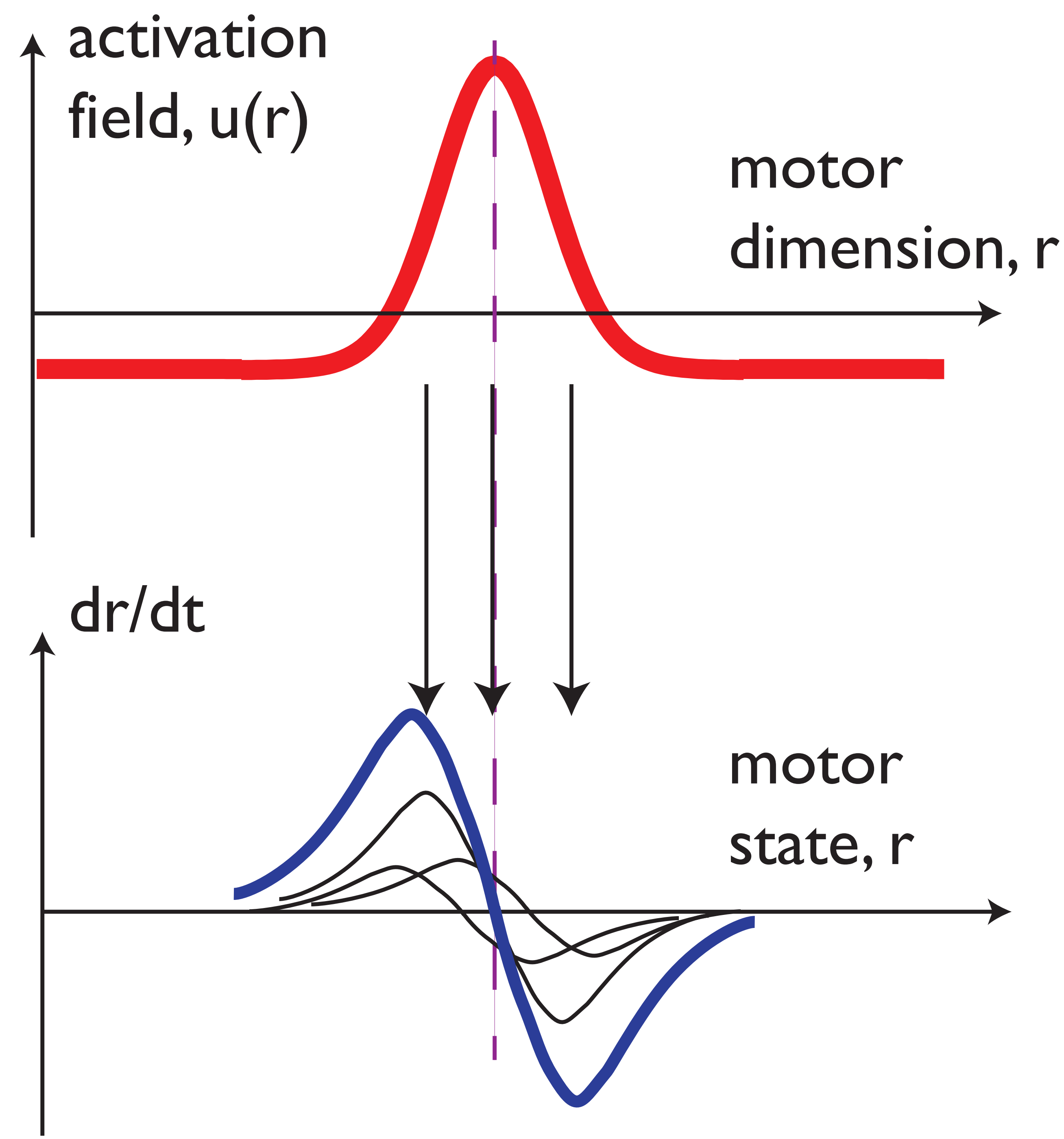
… toward fields

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

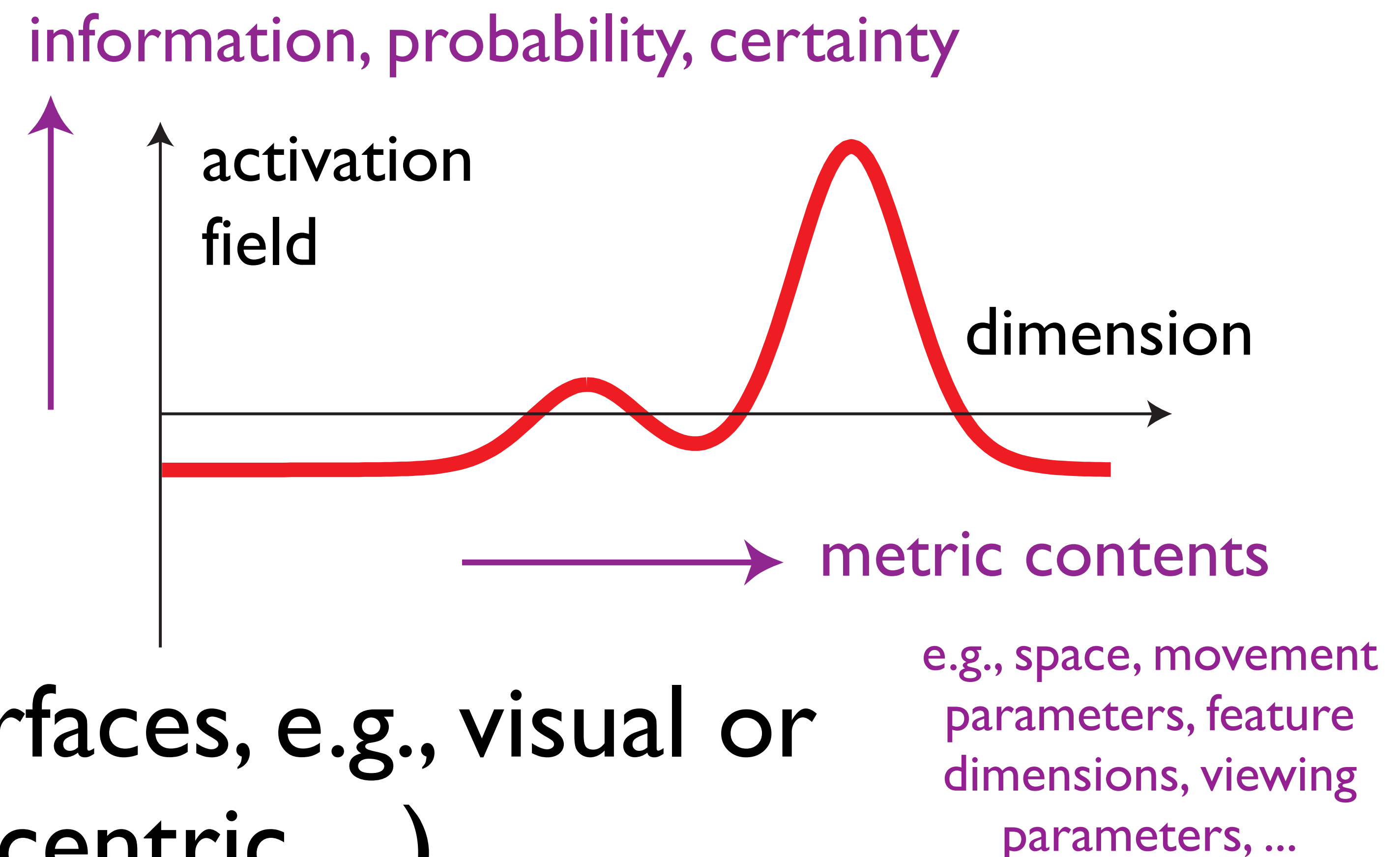


… toward fields

- or by forward projections onto motor surfaces…
- => behavioral dynamics
- e.g., through peripheral reflex loops

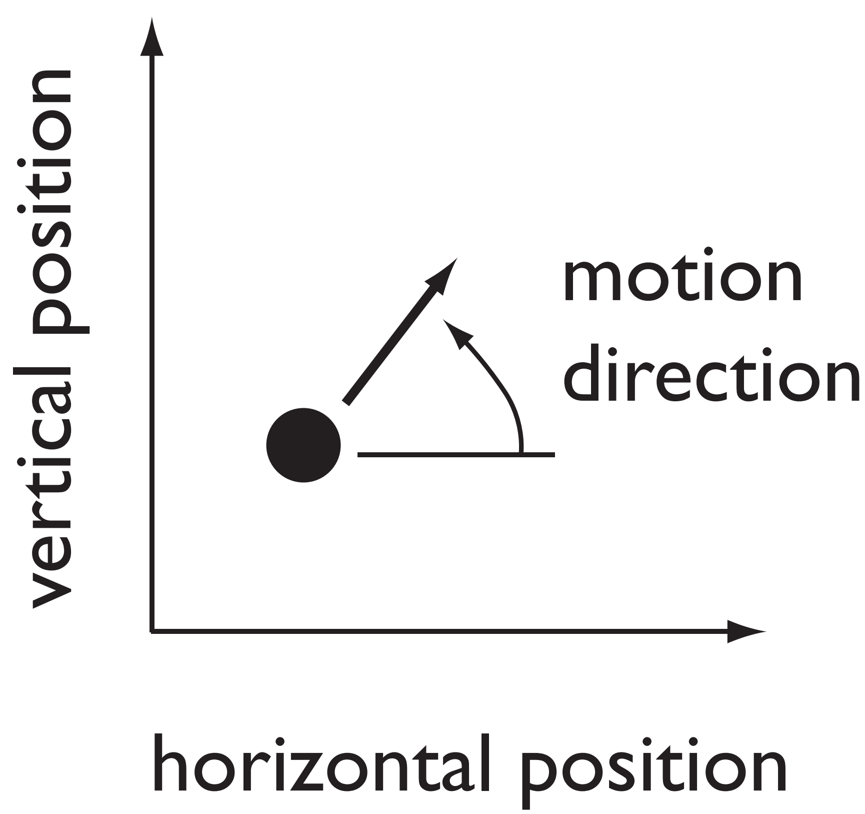


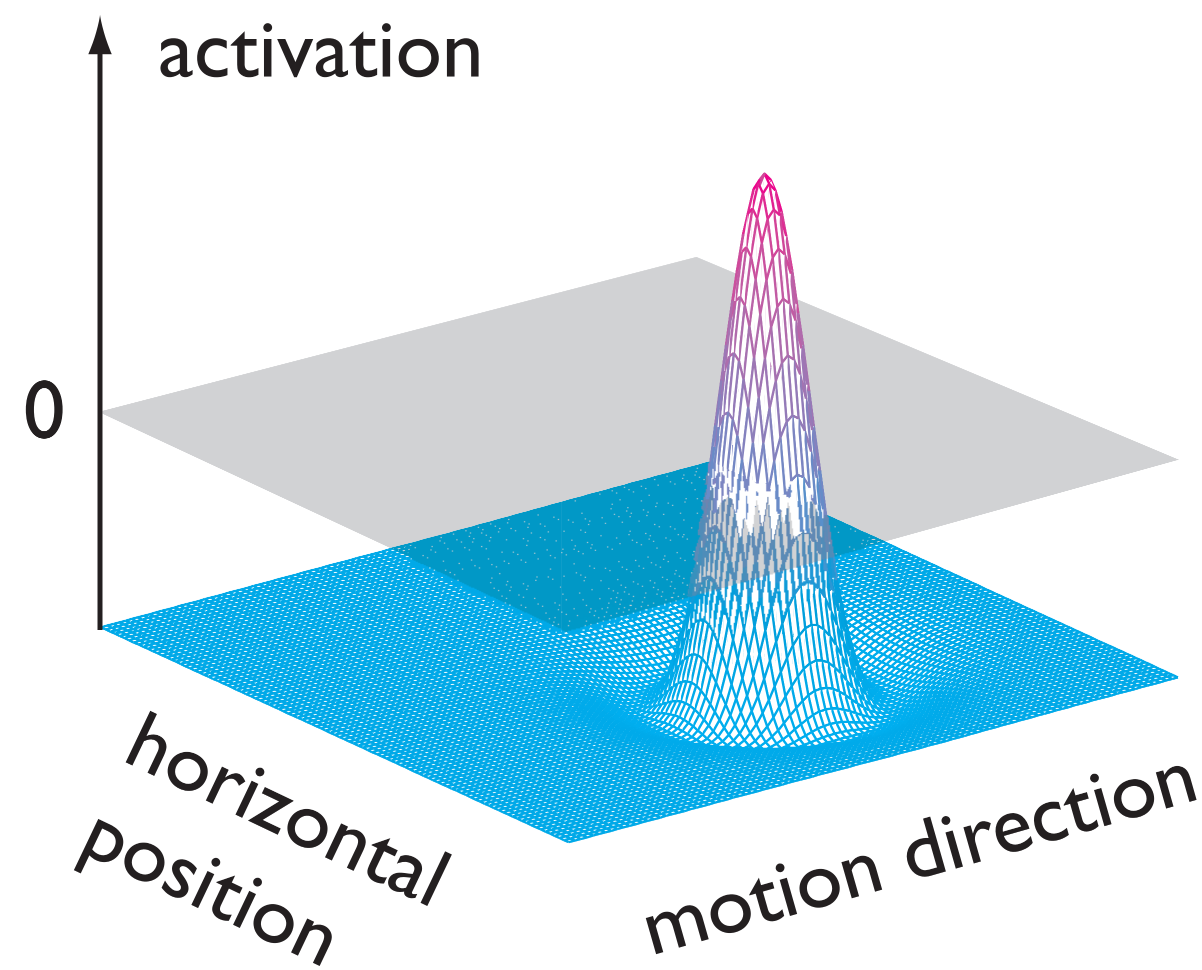
fields defined over continuous spaces



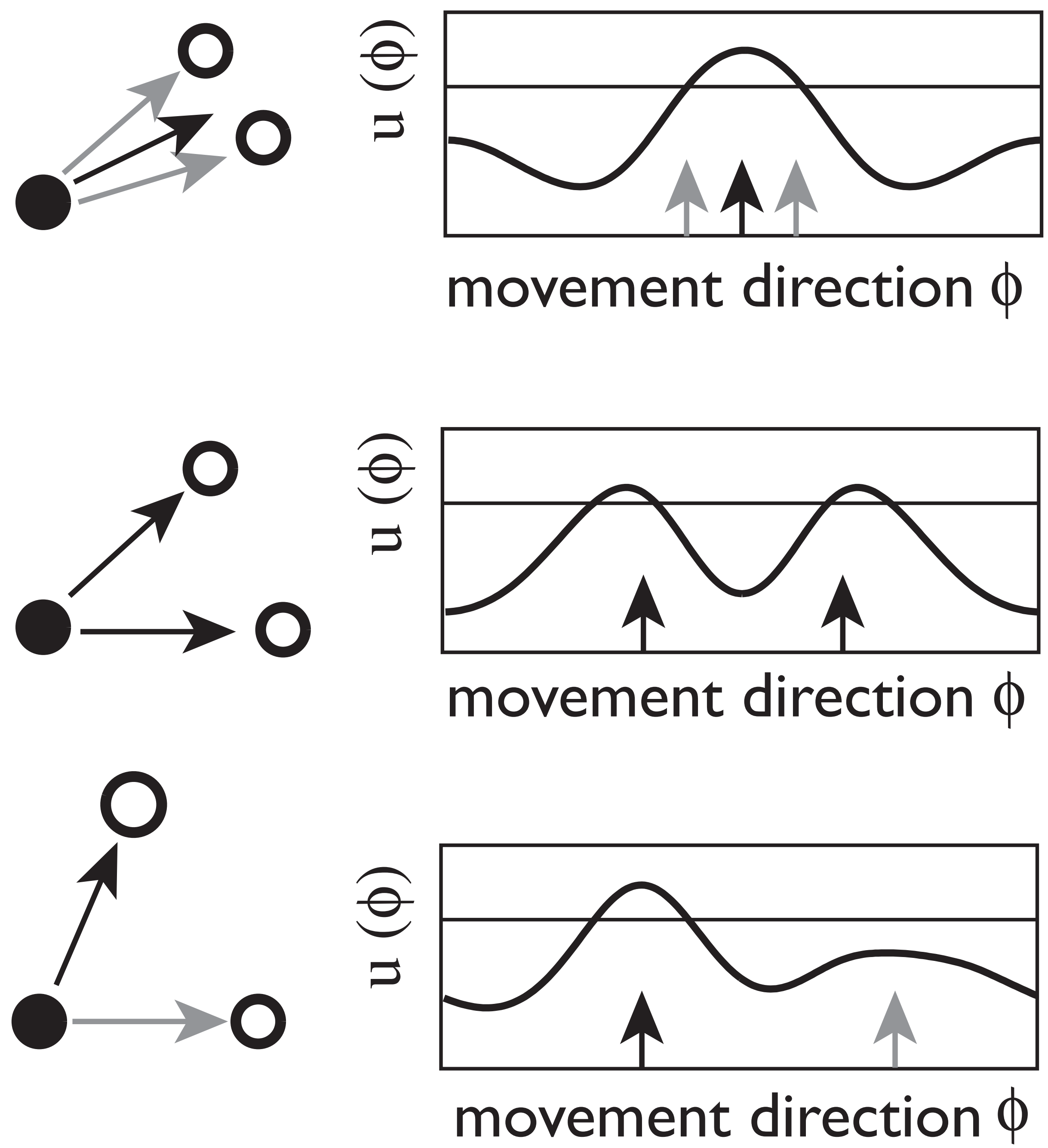
- homologous to sensory surfaces, e.g., visual or auditory space (retinal, allocentric, ...)
- homologous to motor surfaces, e.g., saccadic end-points or direction of movement of the end-effector in outer space
- feature spaces, e.g., localized visual orientations, color, impedance, ...
- abstract spaces,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

Example motion perception: space of possible percepts

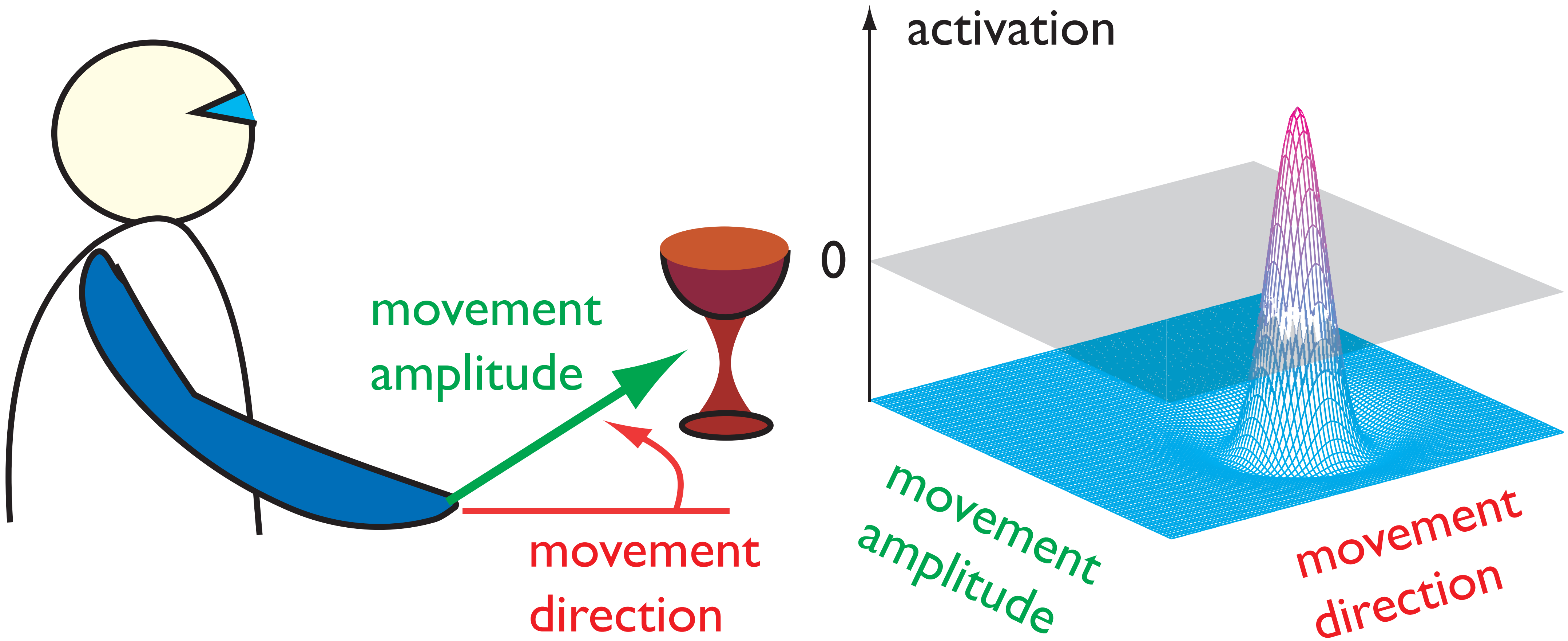




Activation patterns representing different percepts

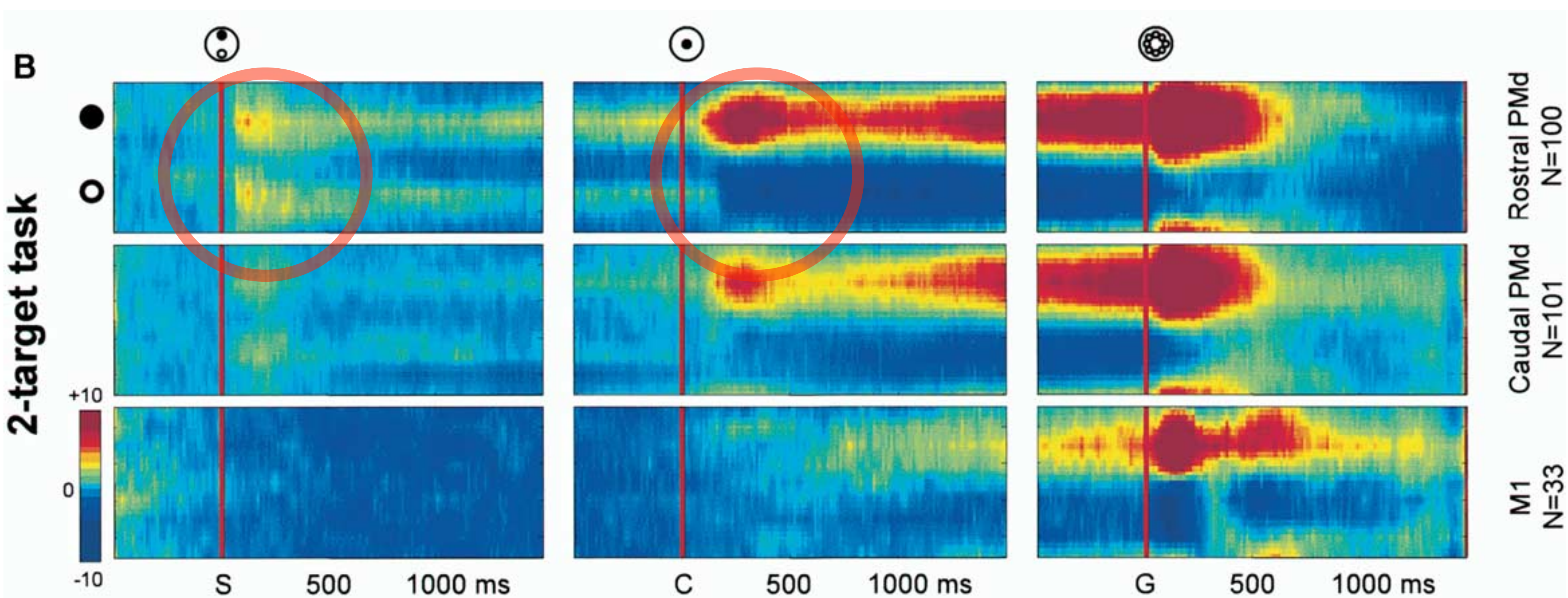


Example: movement planning: space of possible actions



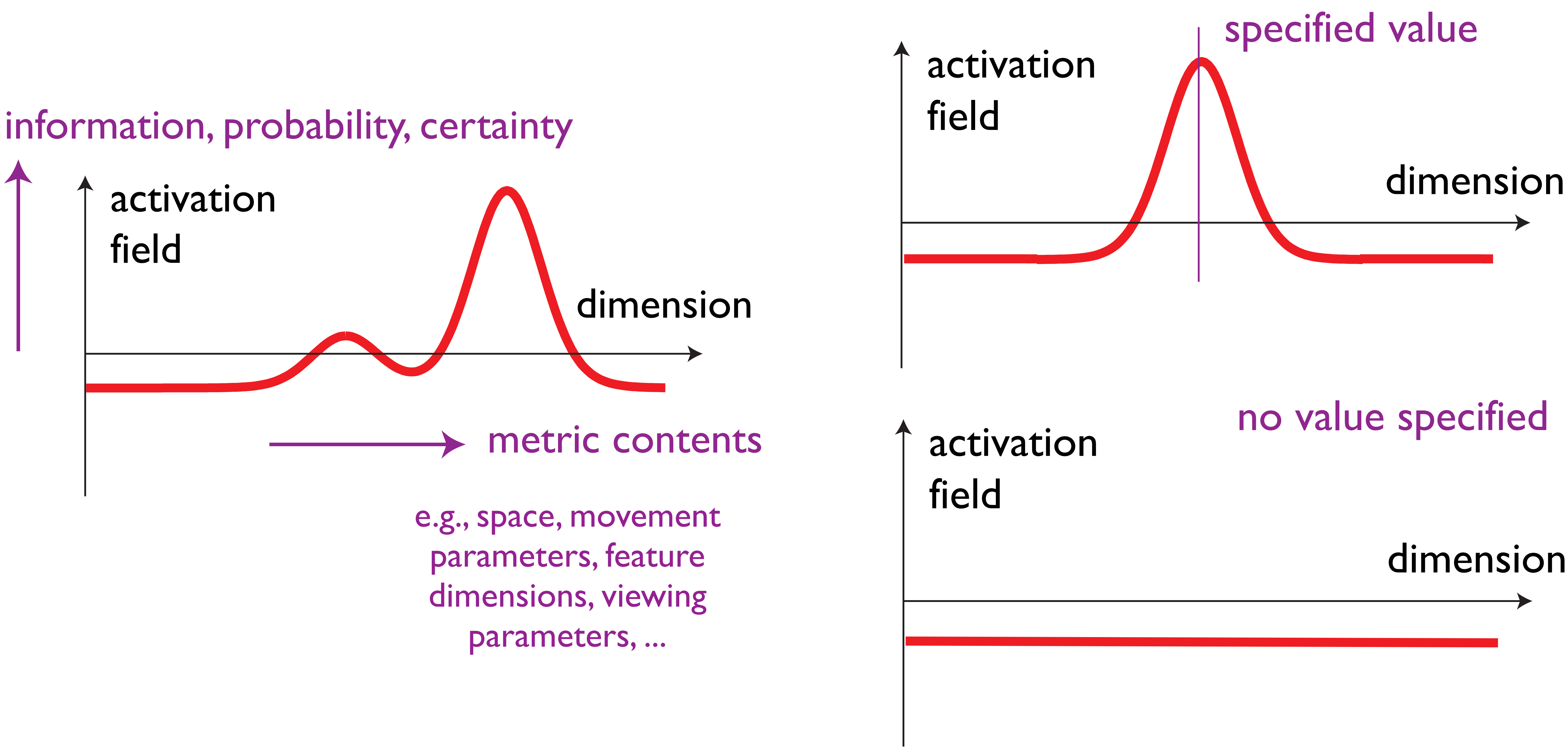
Activation patterns representing states of motor decision making

- 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



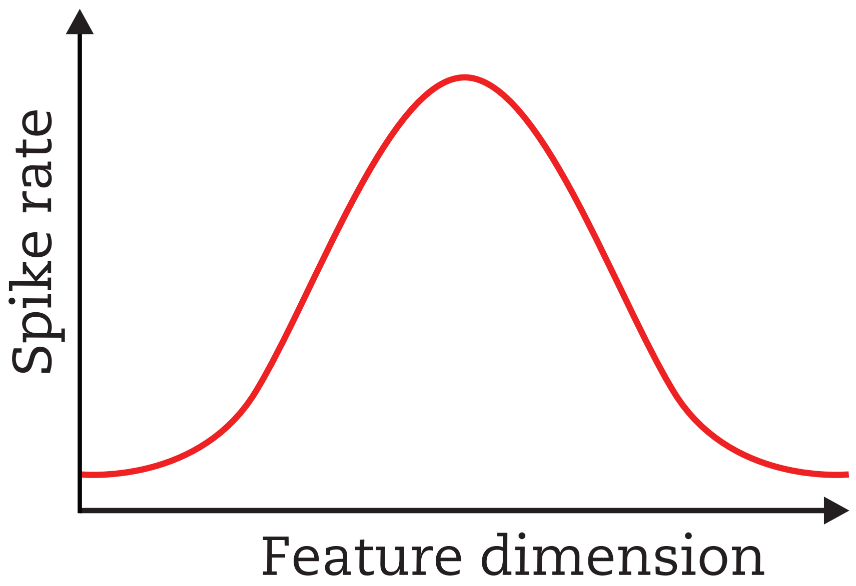
[Cisek, Kalaska: Neuron 2005]

Activation fields… peaks as units of representation

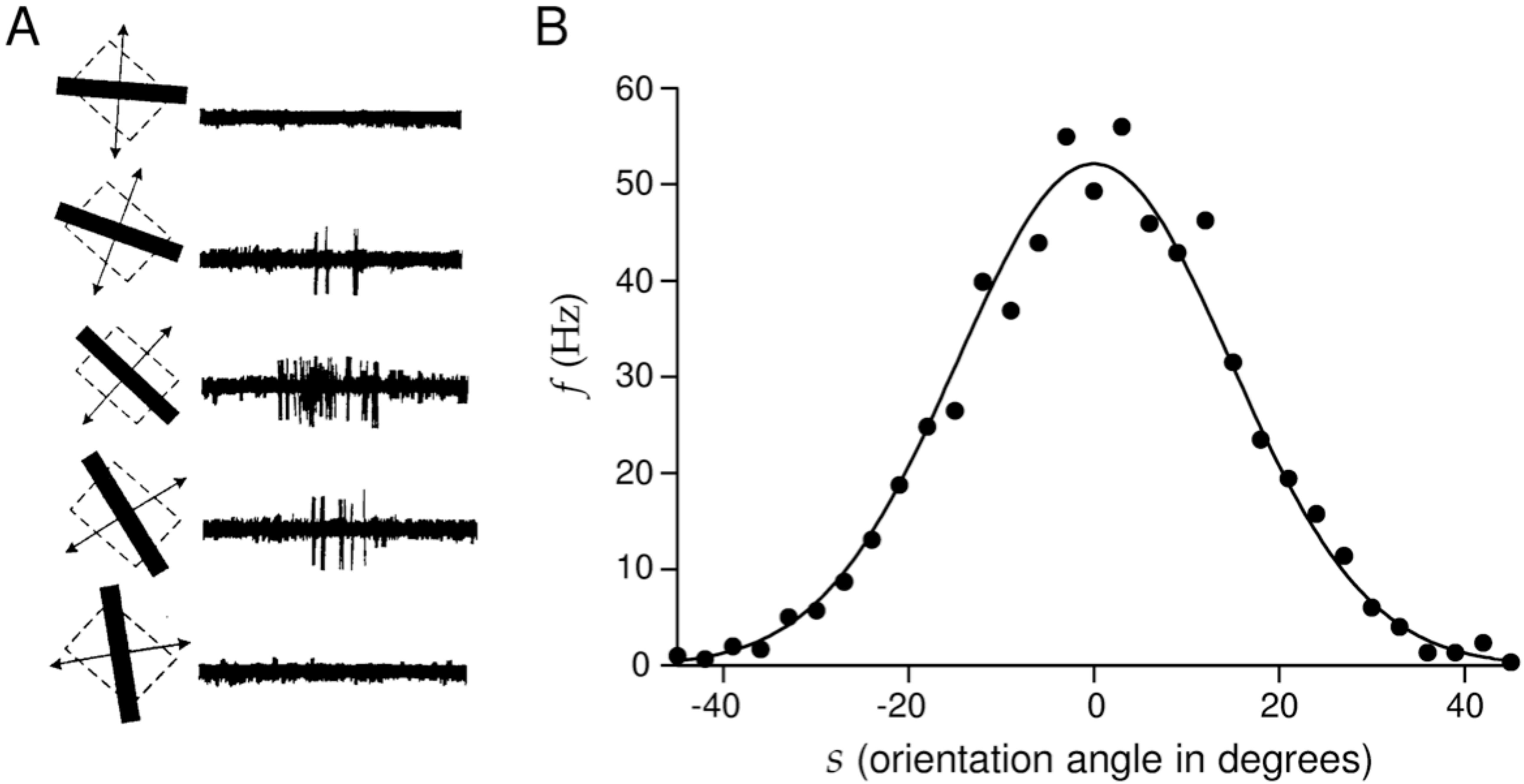


Formalizing the link between DFT and neurophysiology

- 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

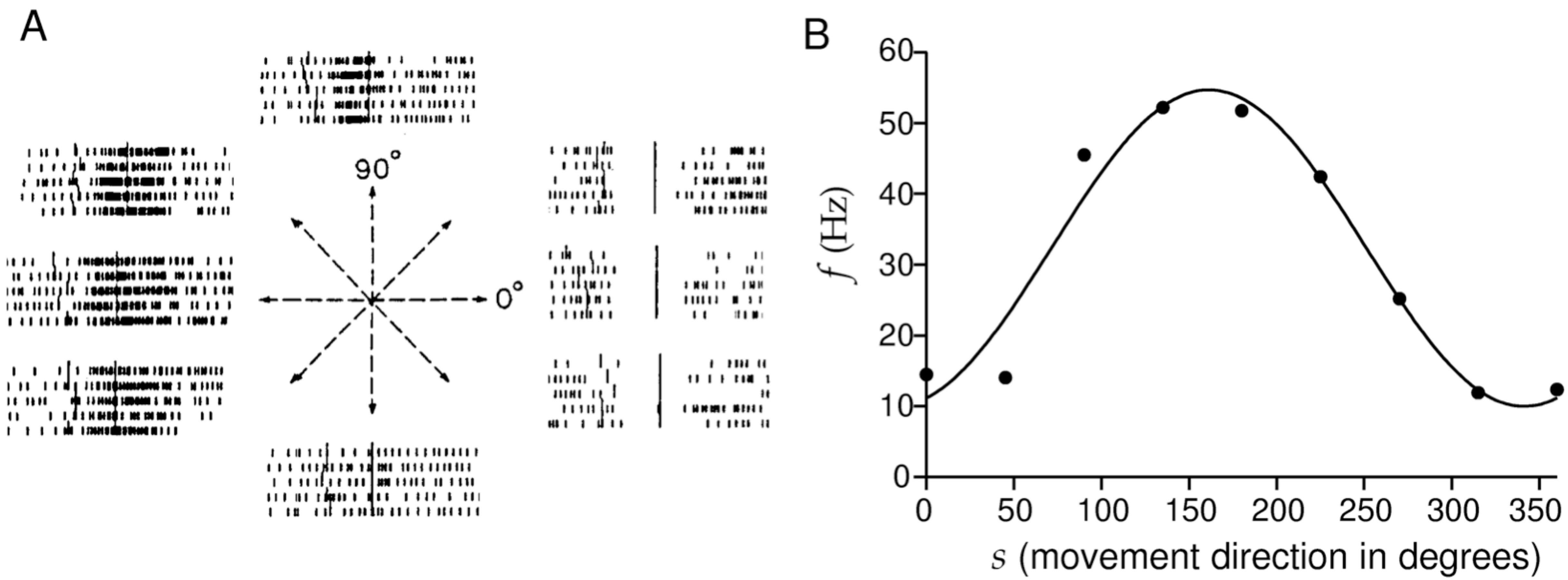


Example tuning curve in primary visual cortex (monkey)



[Hubel, Wiesel, 1962]

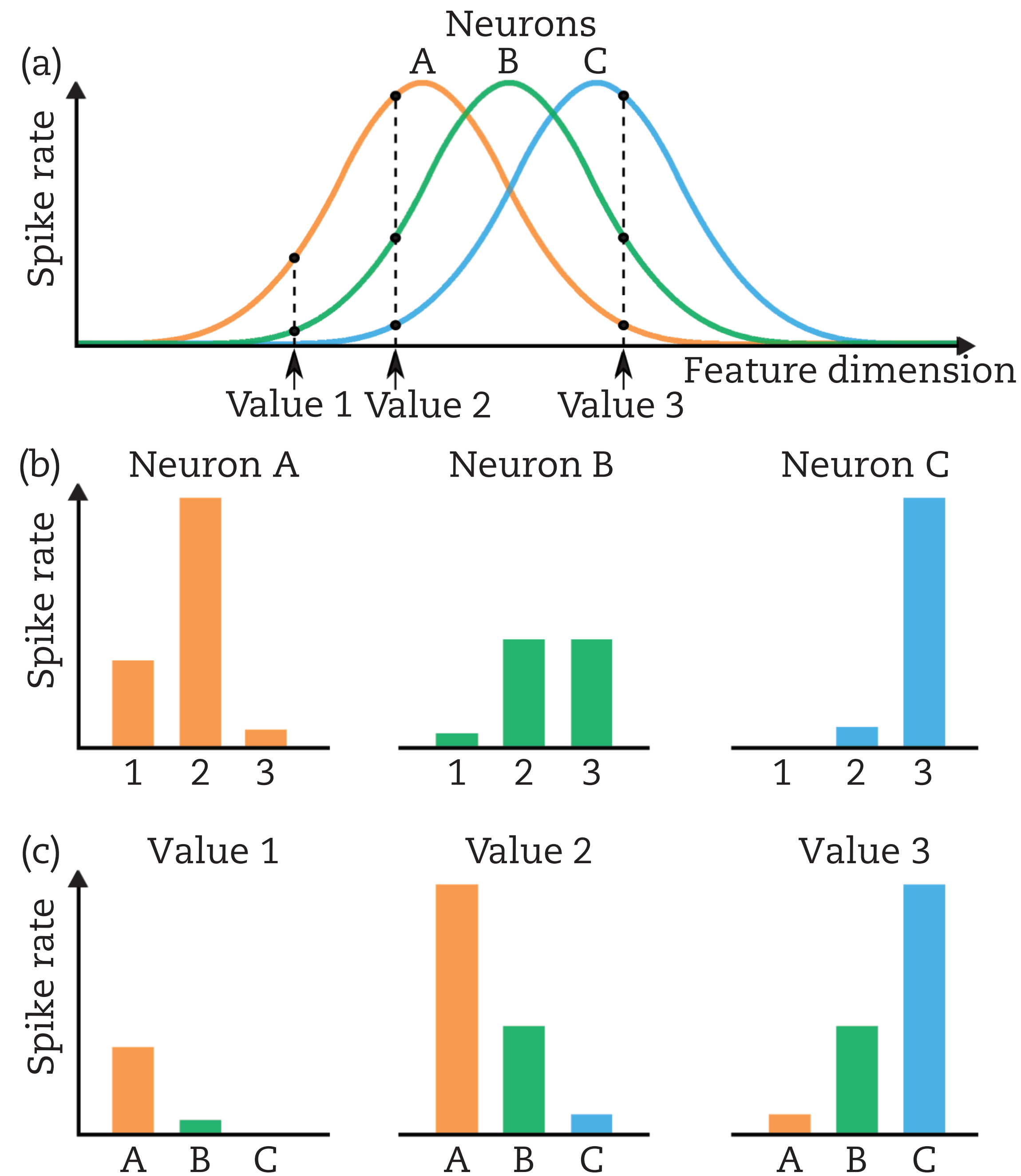
Example: tuning curve in primary motor cortex (monkey)



[Georgopoulos, Schwartz, Kalaska, 1986]

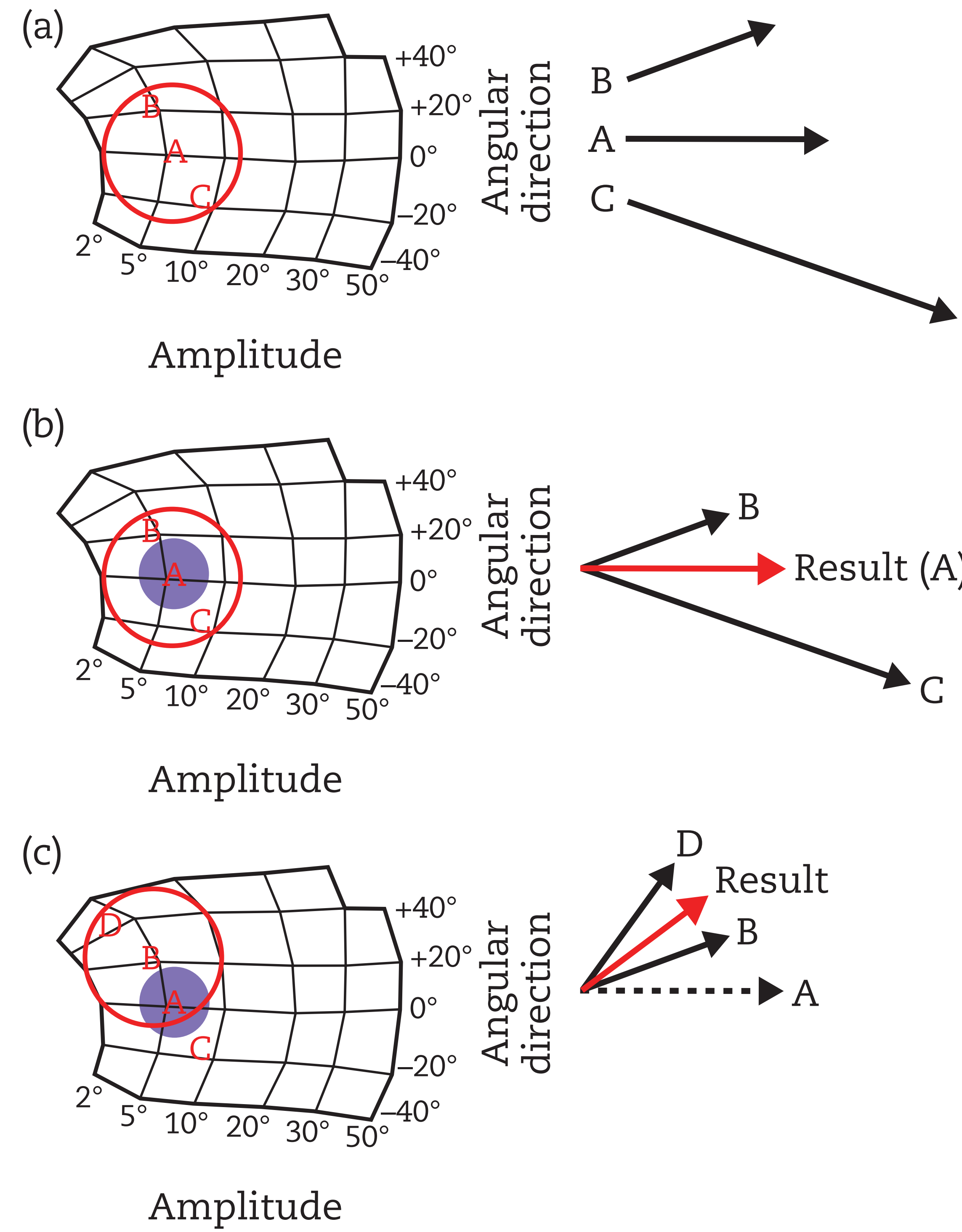
What do populations of neurons represent?

- 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

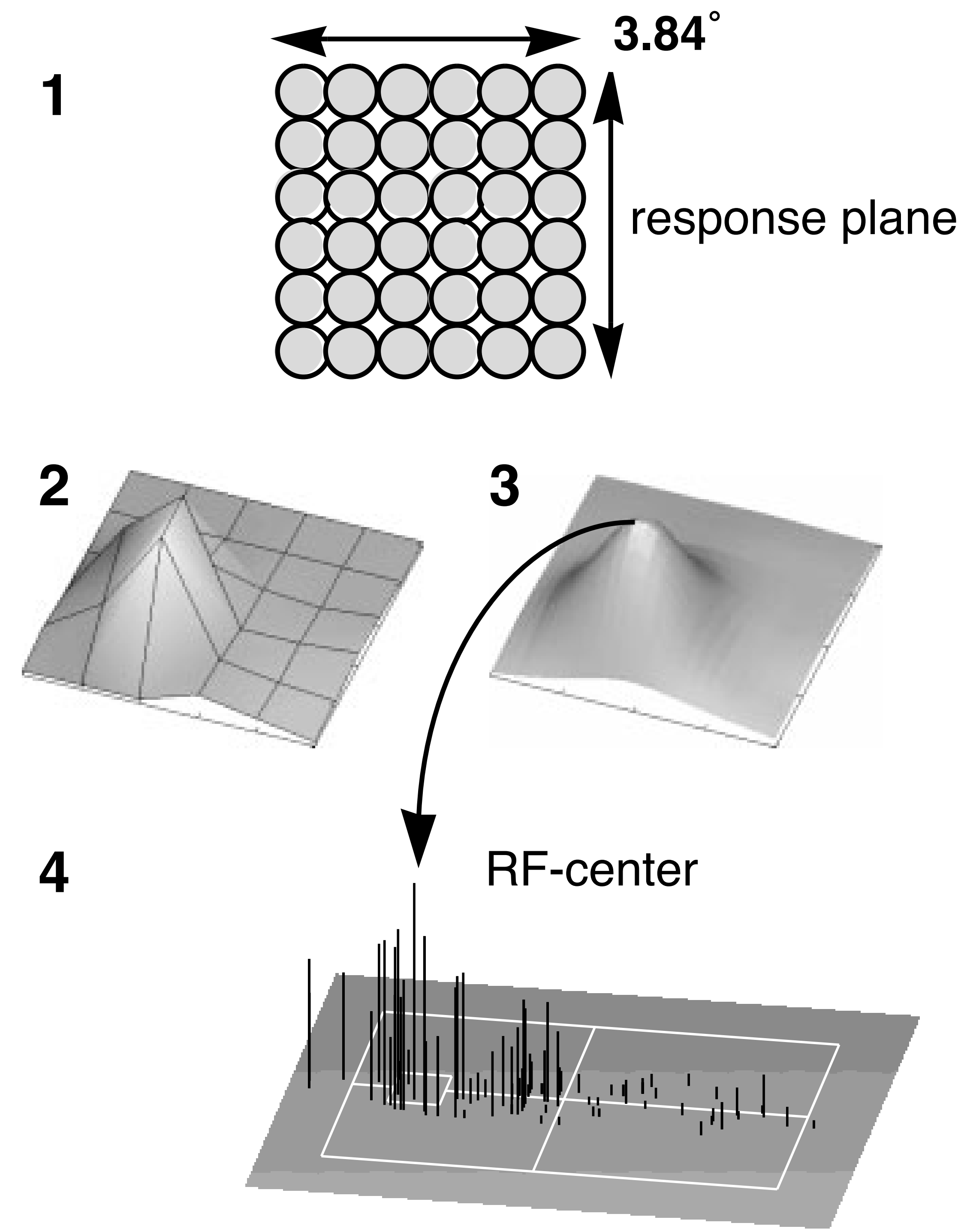
- similar work in MT
  - Purushothaman, G., & Bradley, Da. C. (2005). Neural population code for fine perceptual decisions in area MT. Nature Neuroscience, 8(1), 99–106.
- consensus, that localized populations of neurons best correlated with behavior
  - there are subtle issues of noise and correlation 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

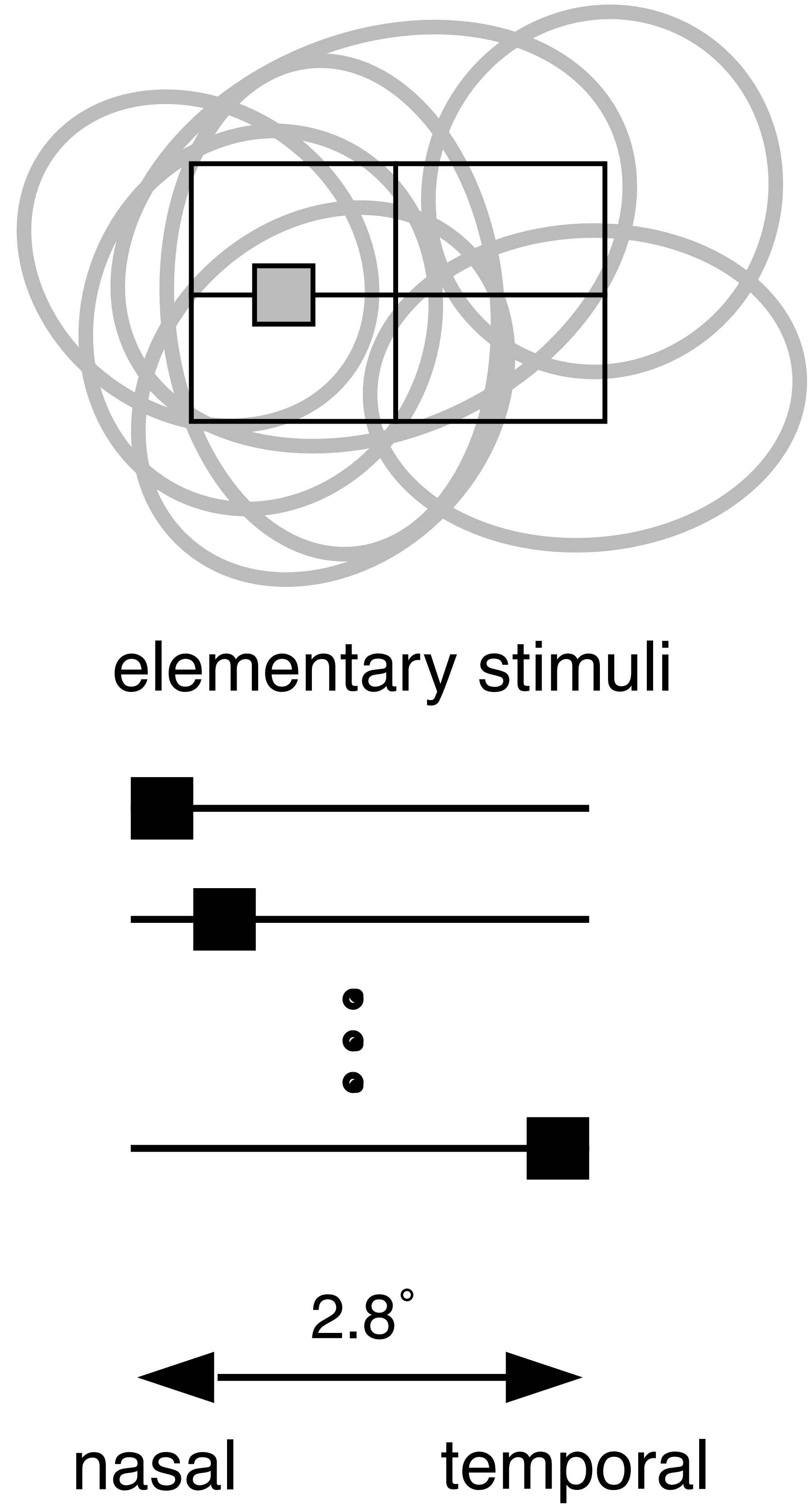
- Example 1: primary visual cortex A17 in the cat, population representation of retinal location

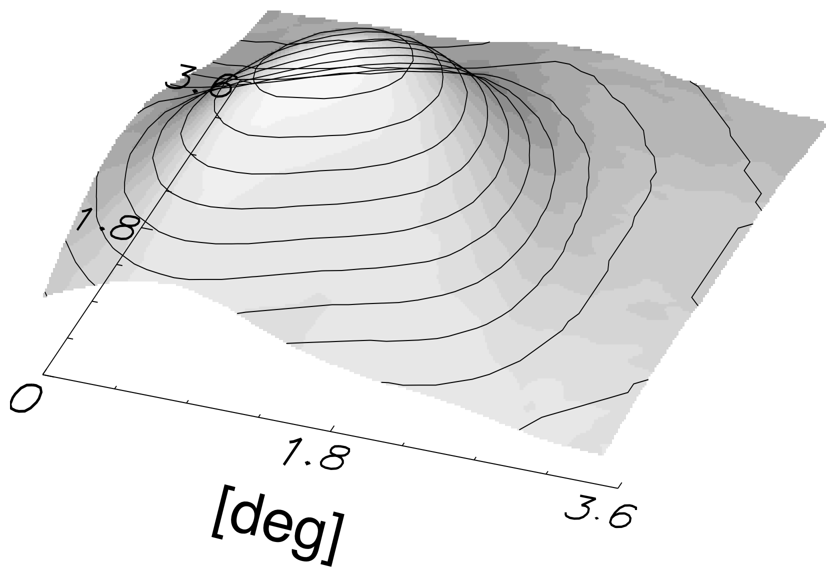
Jancke, Erlhagen, Dinse, Akhavan, Giese, Steinhage, Schöner JNsci 19:9016 (99)

- 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

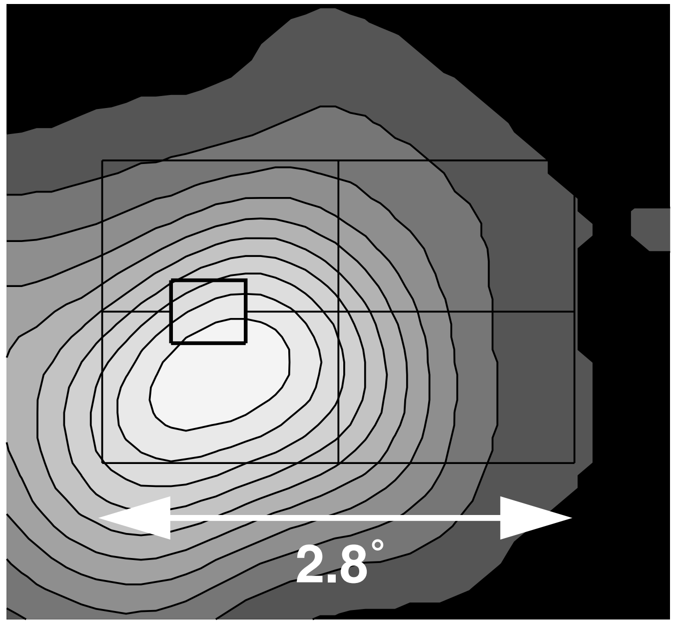


- The current response refers to a stimulus experienced by all neurons
- Reference condition: localized points of light





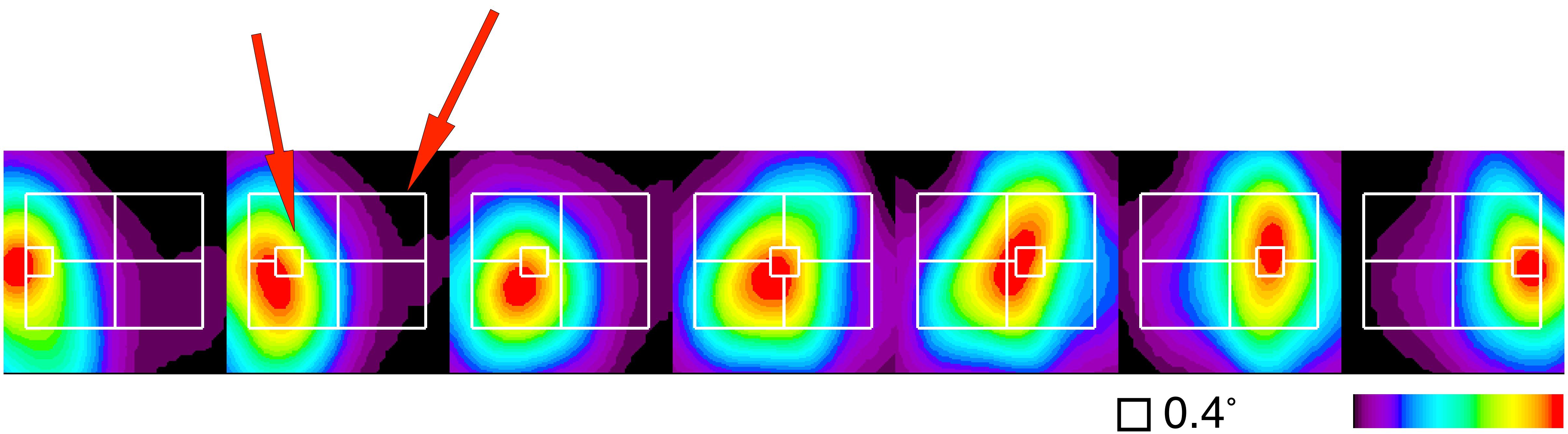
- result: population distribution of activation defined over retinal space = representation of visual location



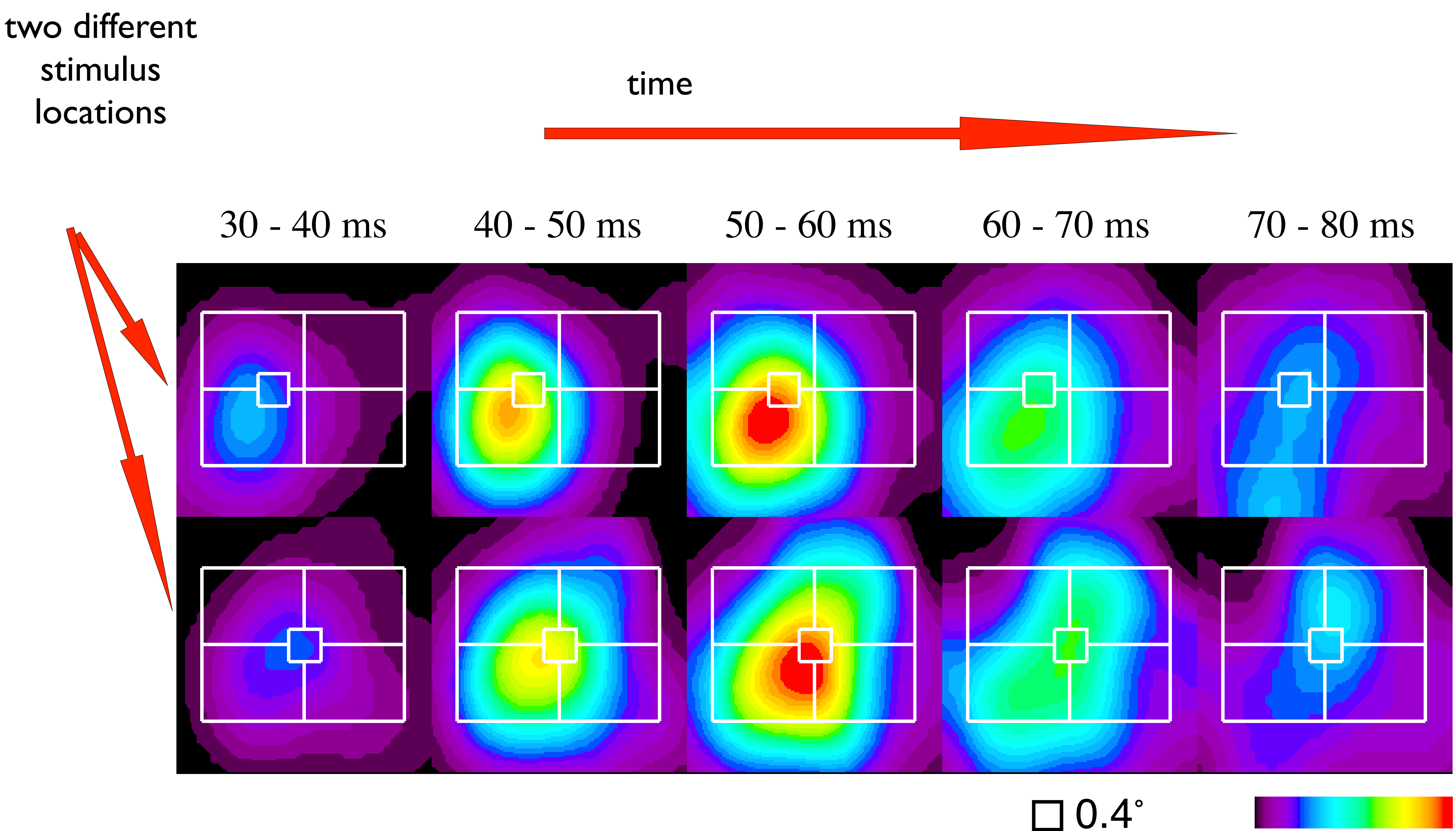
=> does a decent job estimating retinal position

current stimulus:
square of light

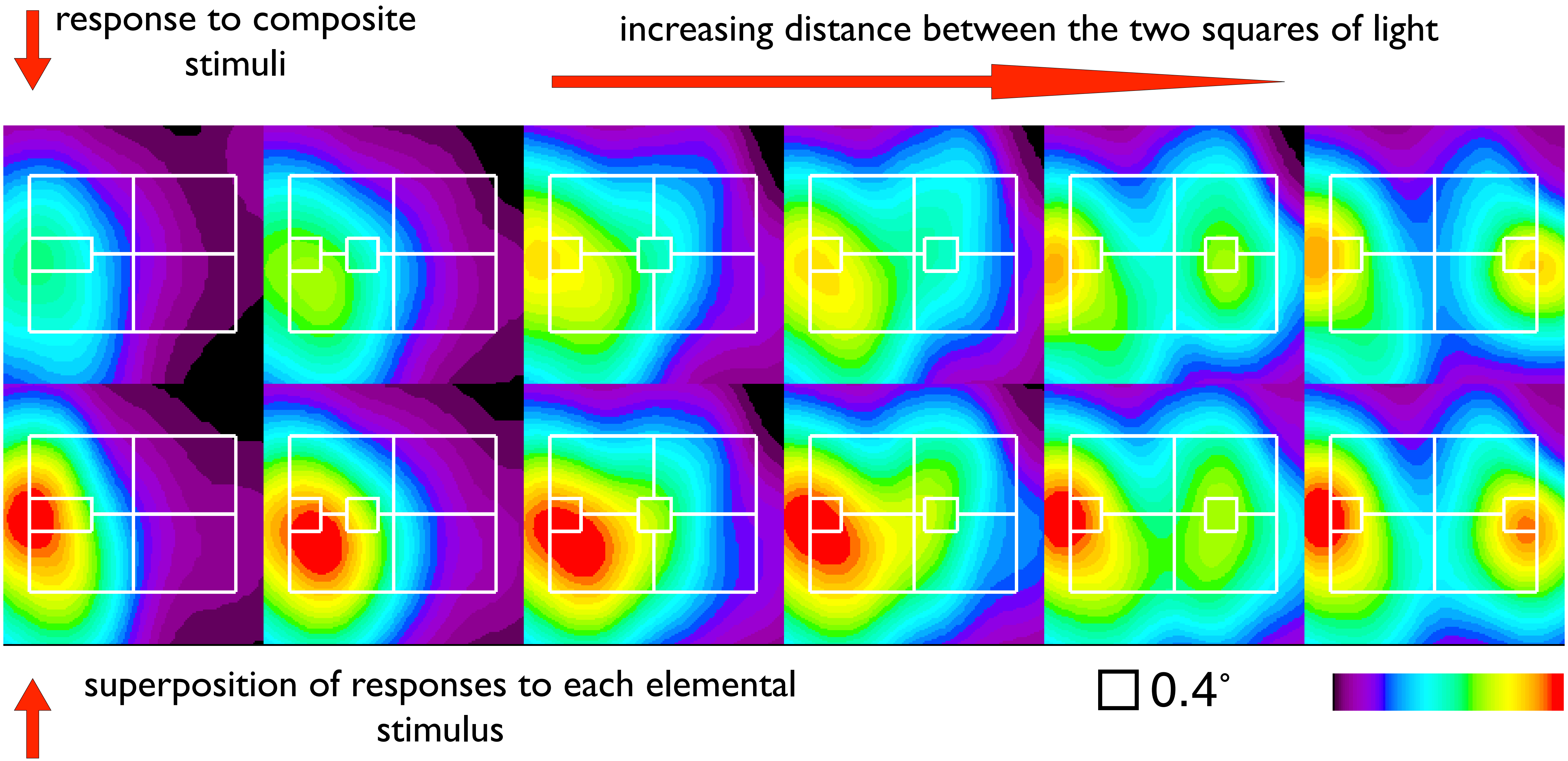
range of retinal field
sampled by neurons



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

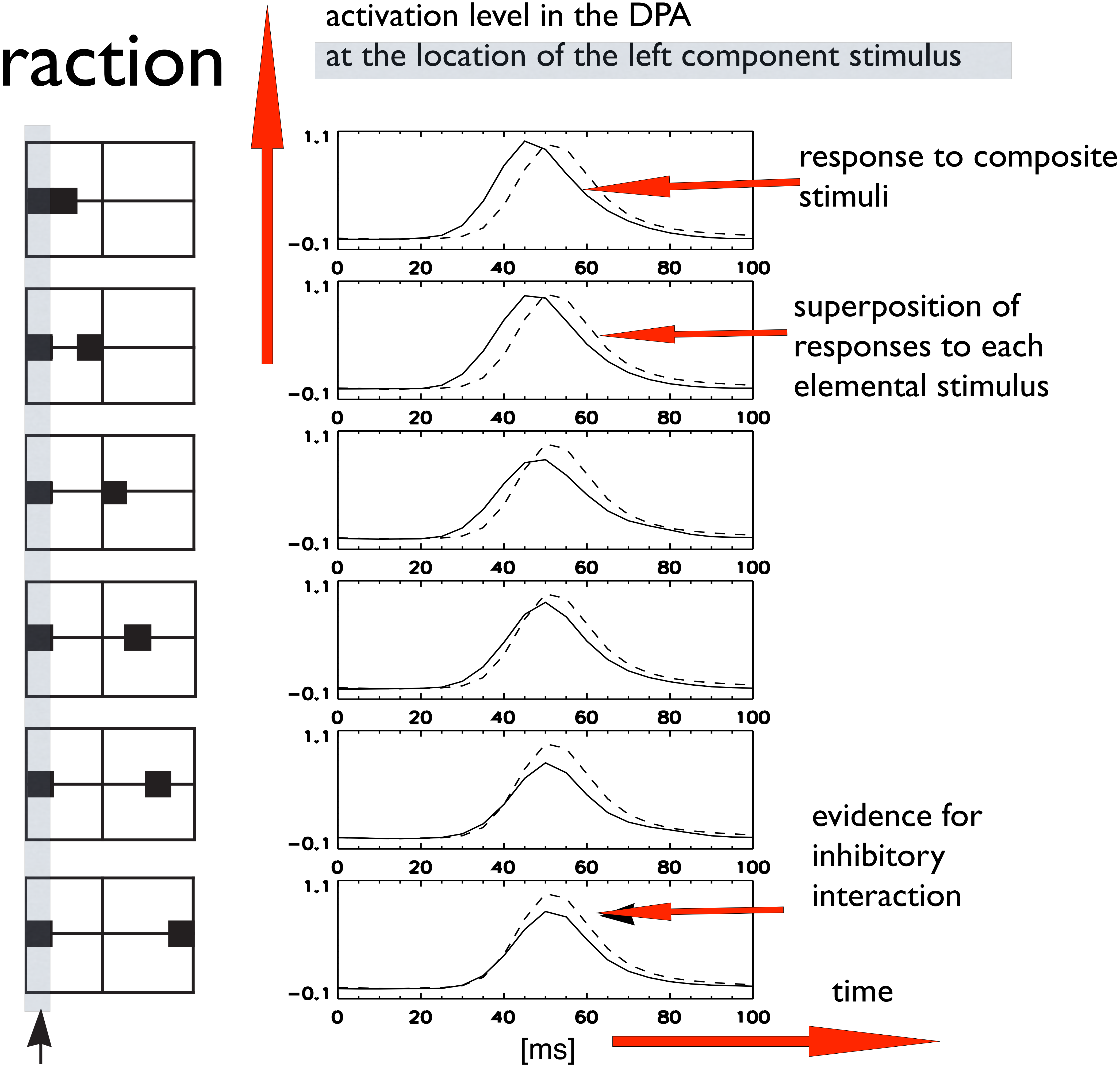


- or when complex stimuli are presented (here: two spots of light)

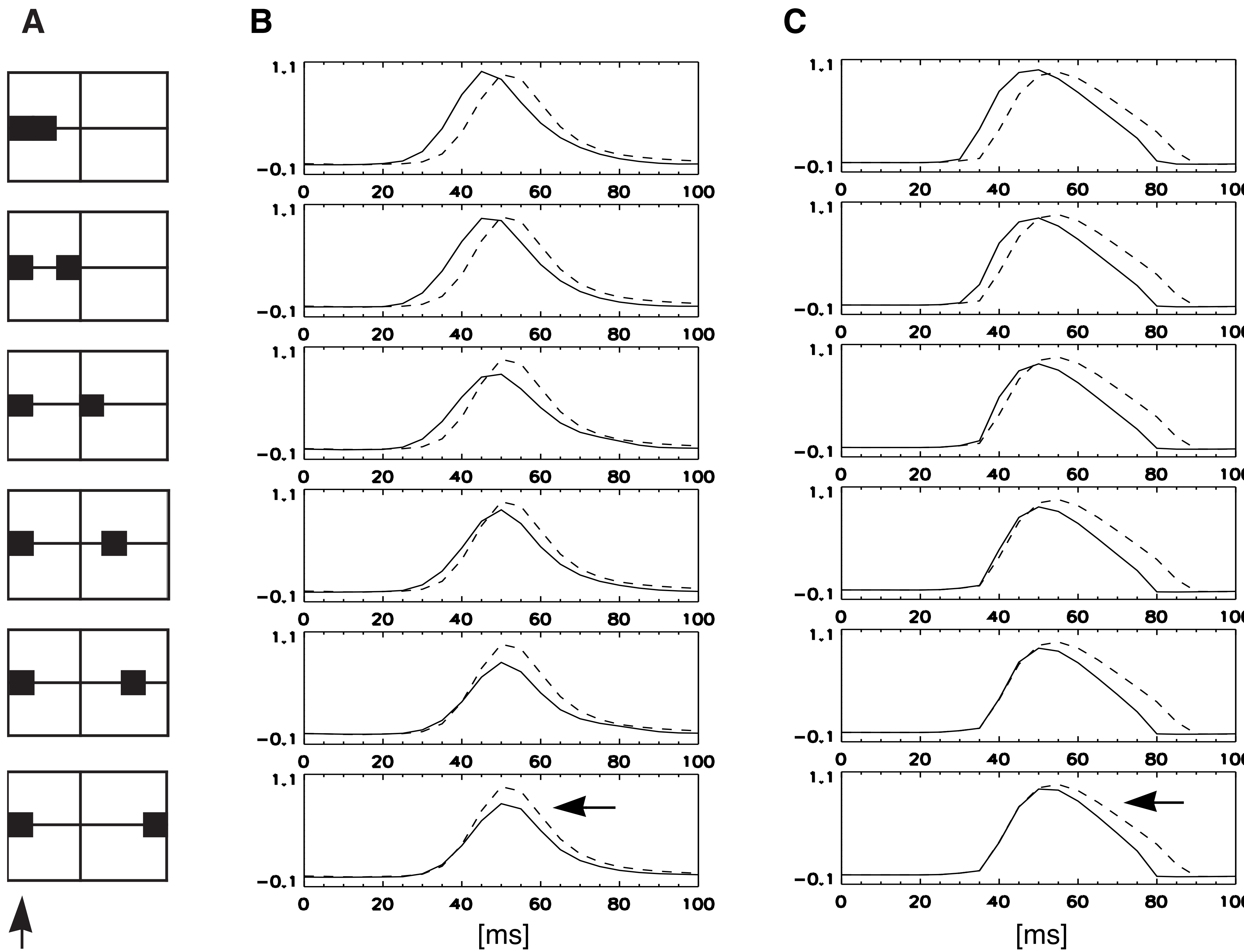


- by comparing DPA of composite stimuli to superposition of DPAs of the two elementary stimuil obtain evidence for interaction
  - early excitation
  - late inhibition

DPA: interaction



model by dynamic field:



stimulus   experiment   DFT model

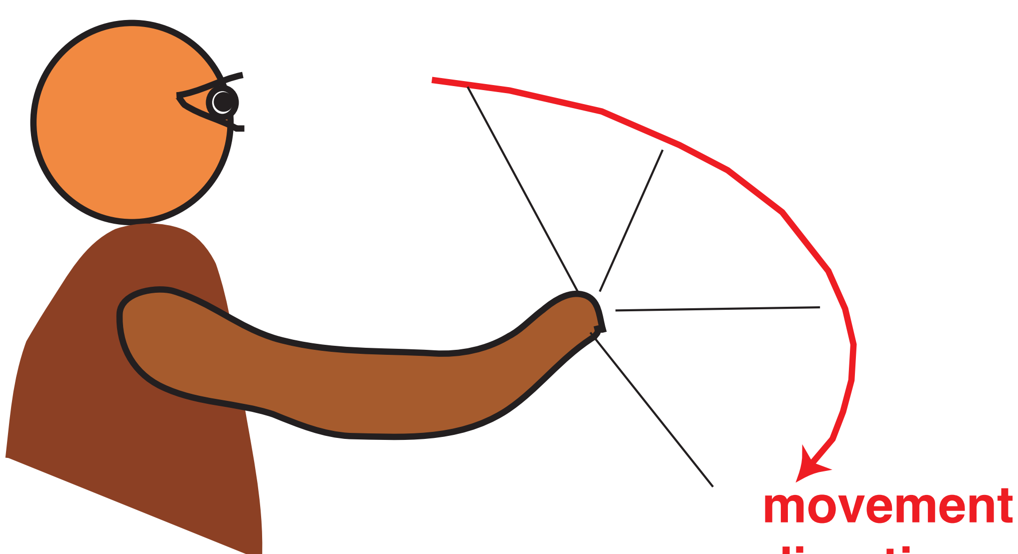
Neurophysiological grounding of DFT

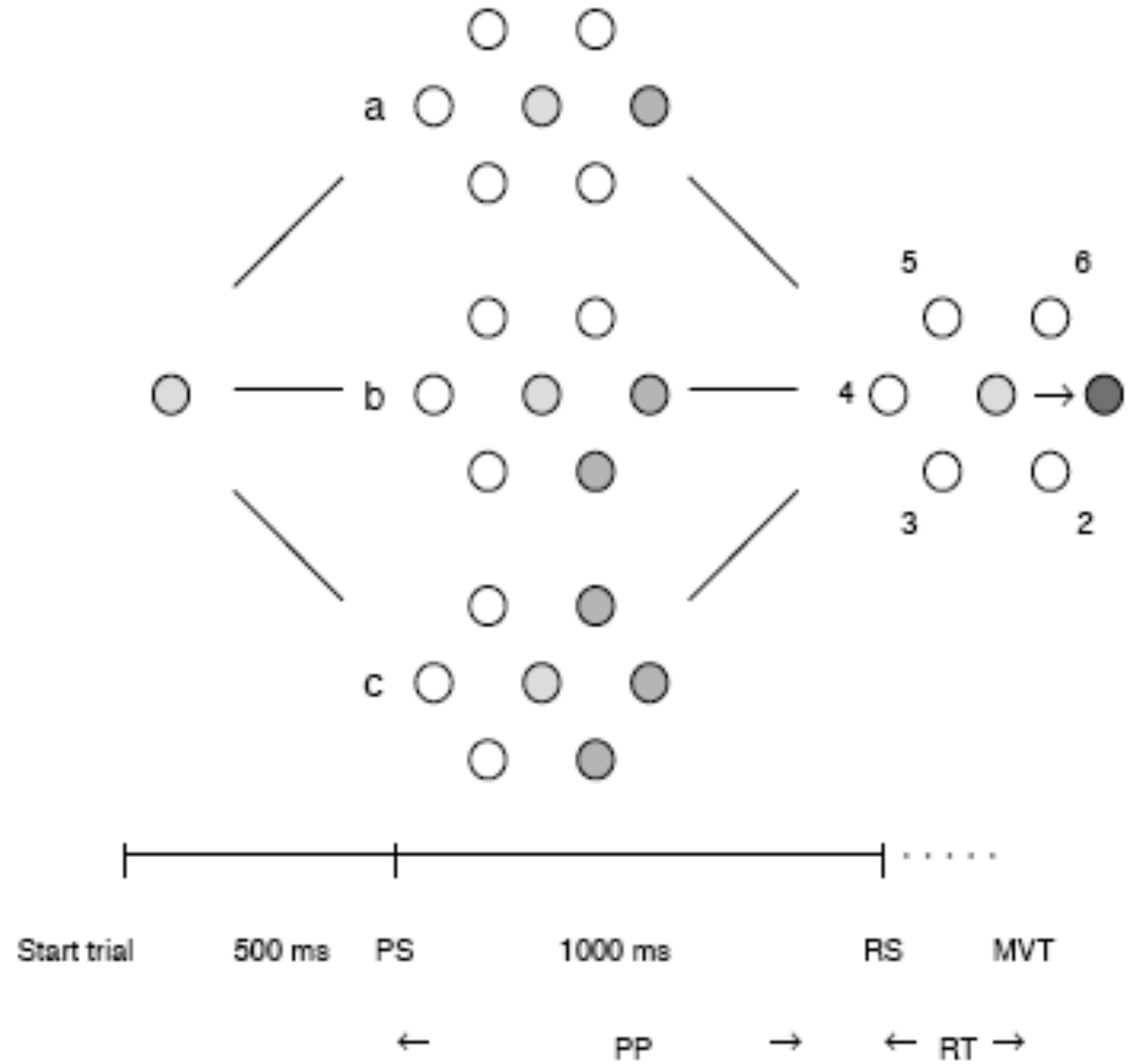
- Example 2: primary motor cortex (M1), population representation of movement direction of the hand

Bastian, Riehle, Schöner, 2003

Task

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

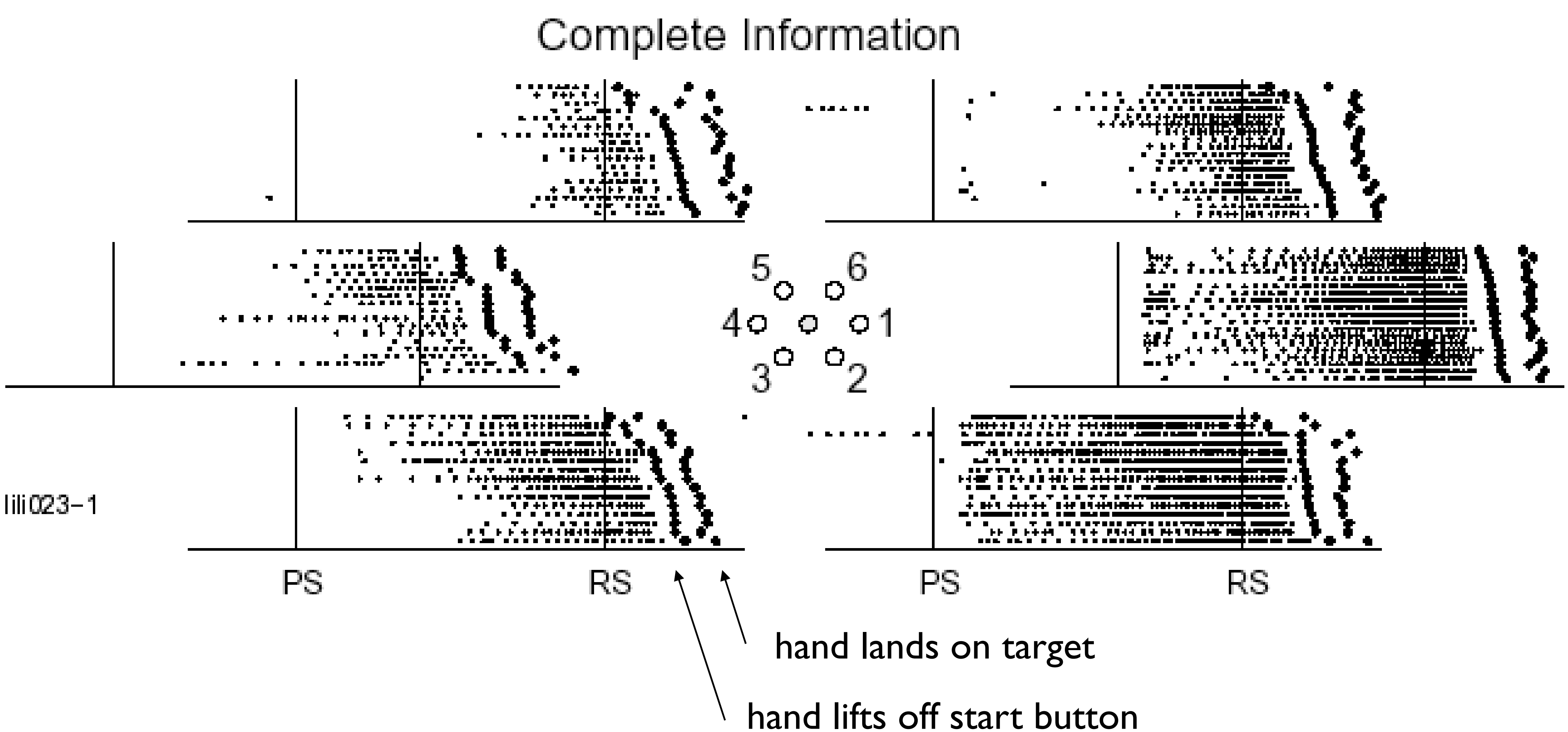




Bastian, Riehle, Schöner, 2003

Tuning of neurons in MI to movement direction

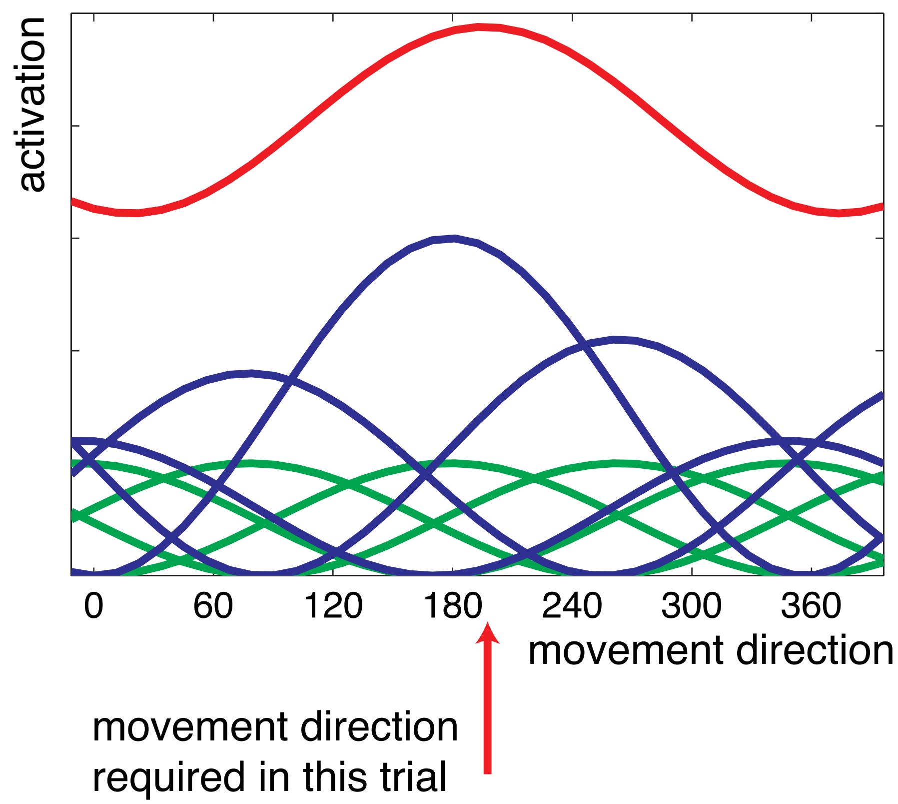
- trials aligned by go signals, ordered by reaction time

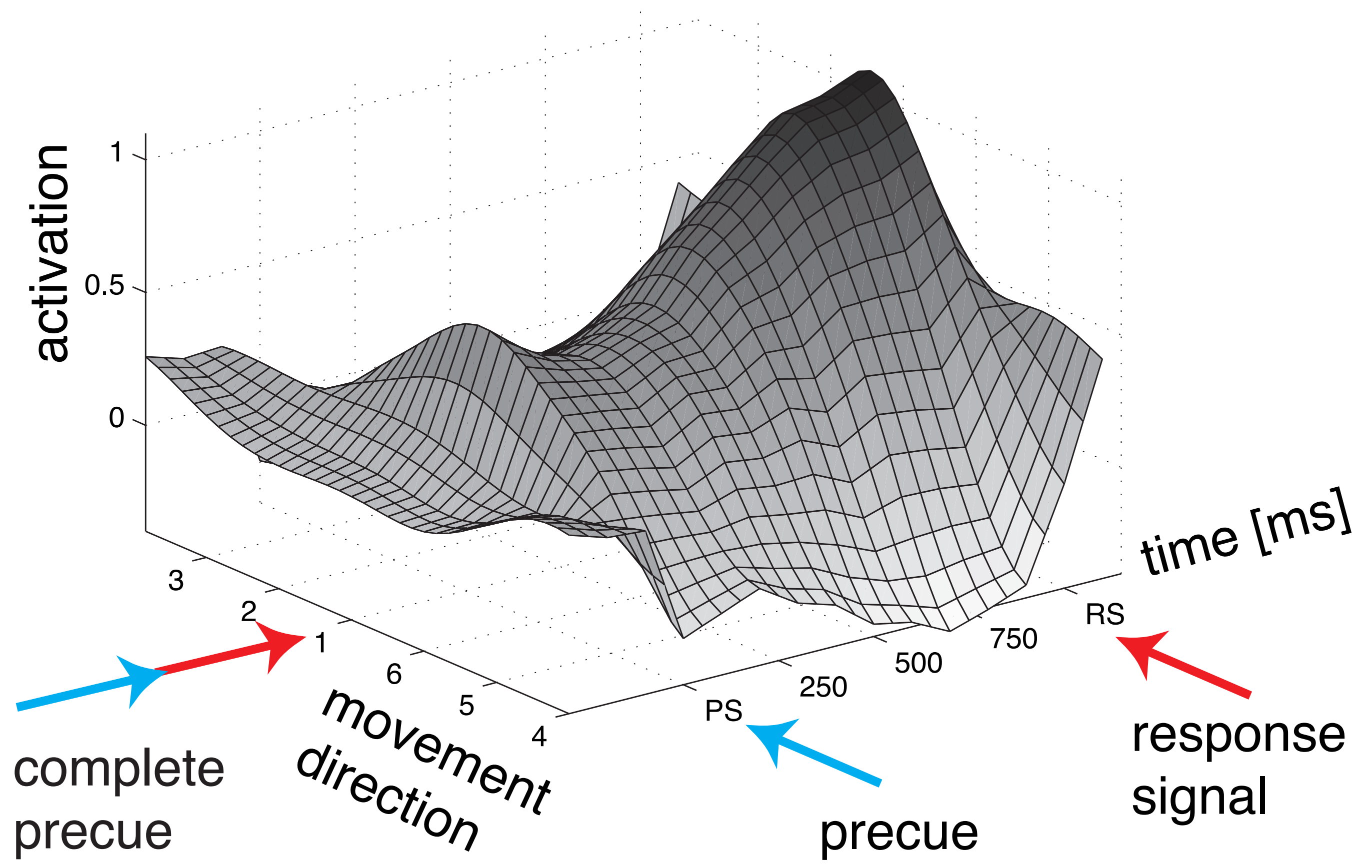


Distribution of Population Activation (DPA)

Distribution of population activation =

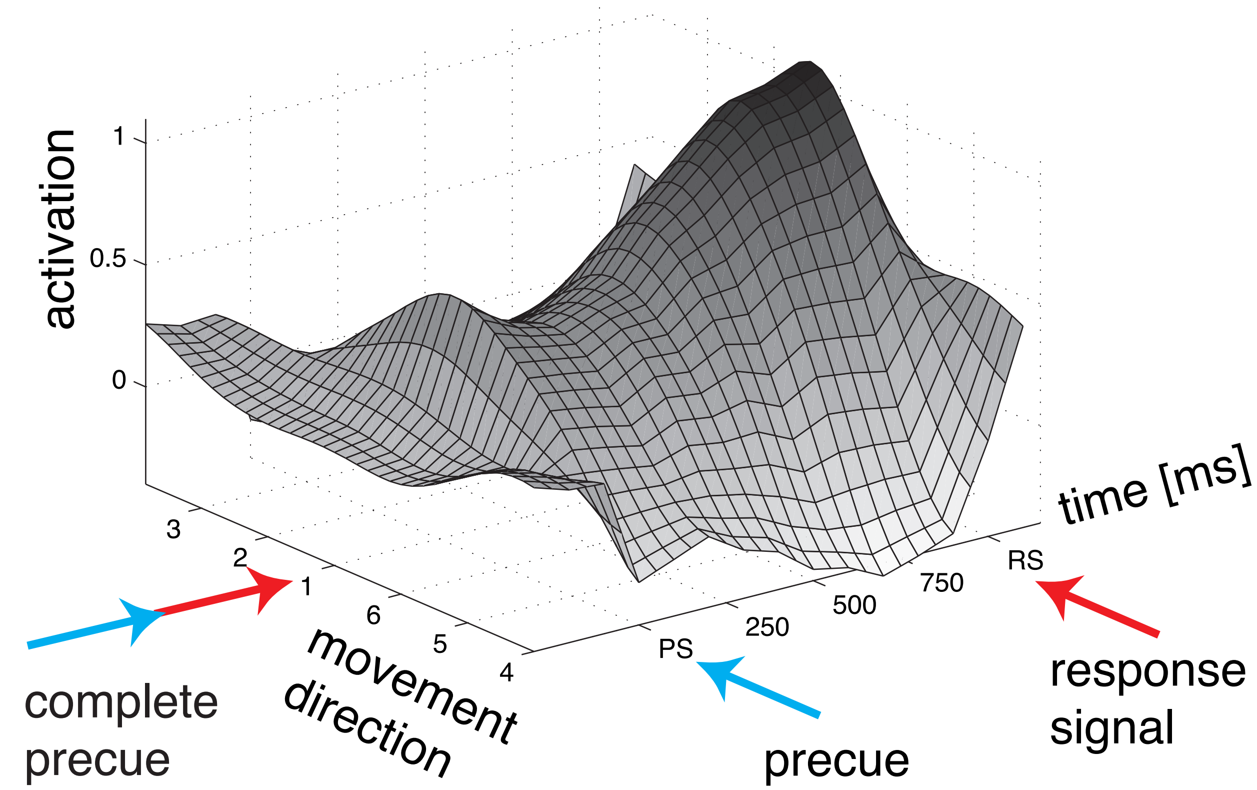
$\sum_{\text{neurons}}$ tuning curve * current firing rate

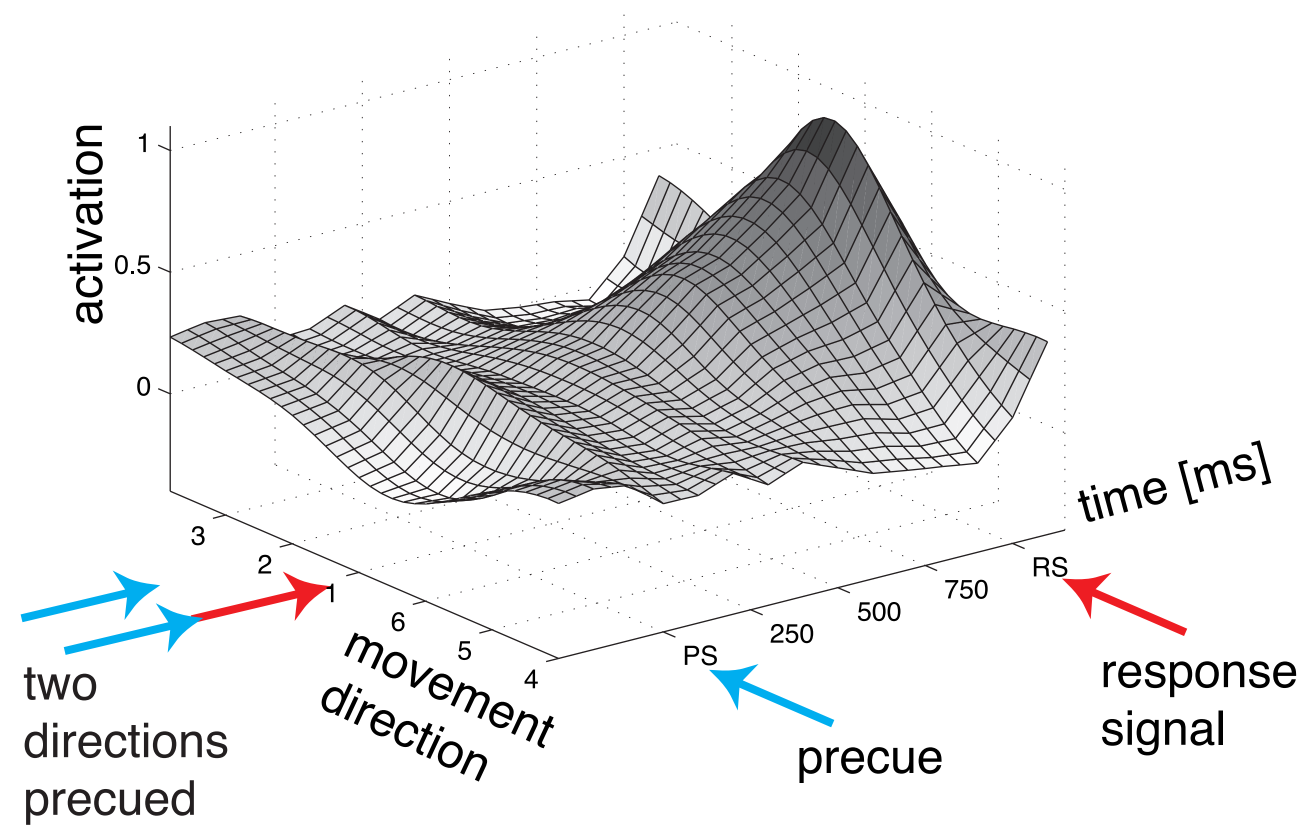




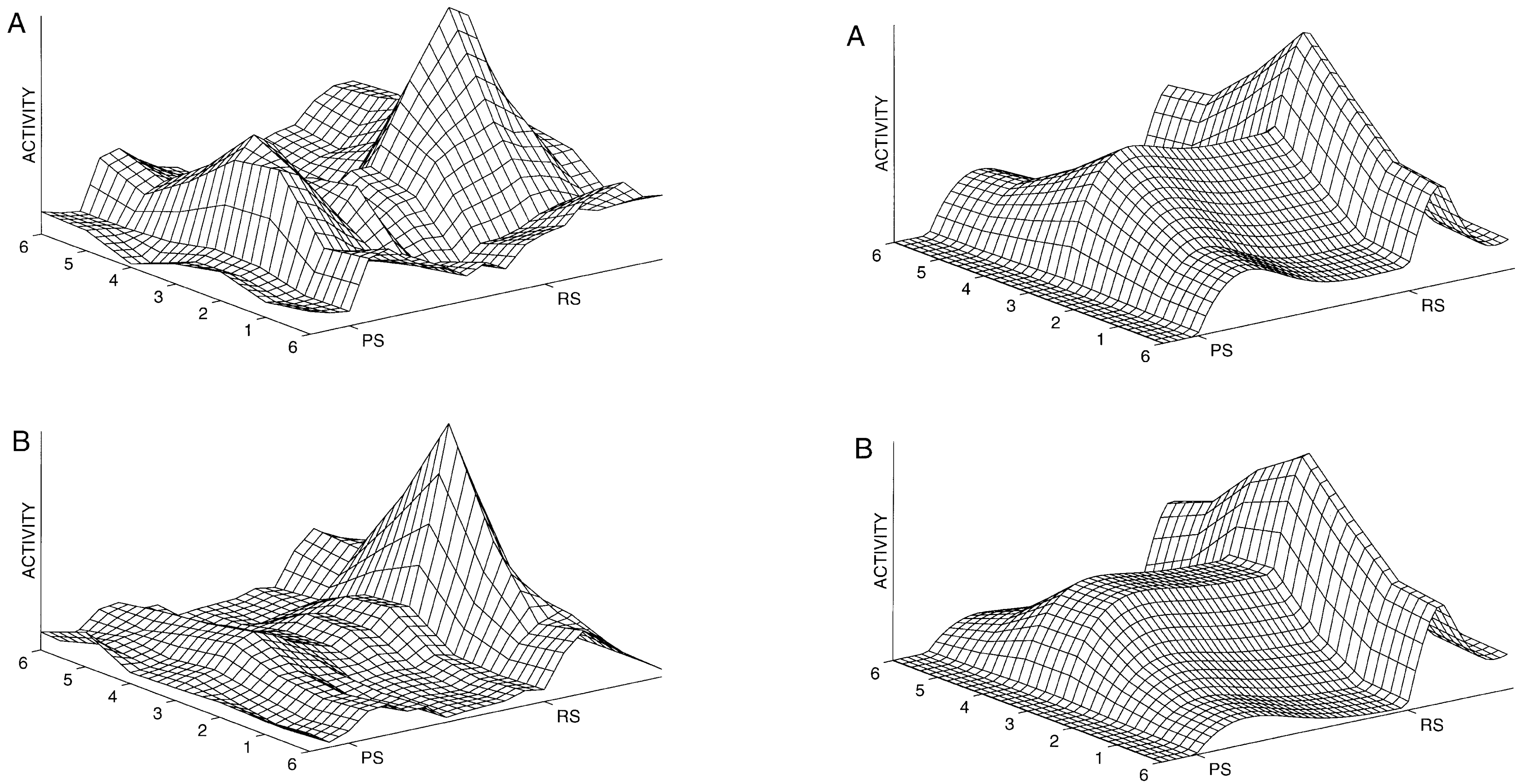
[Bastian, Riehle, Schöner, 2003]

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





Theory-Experiment

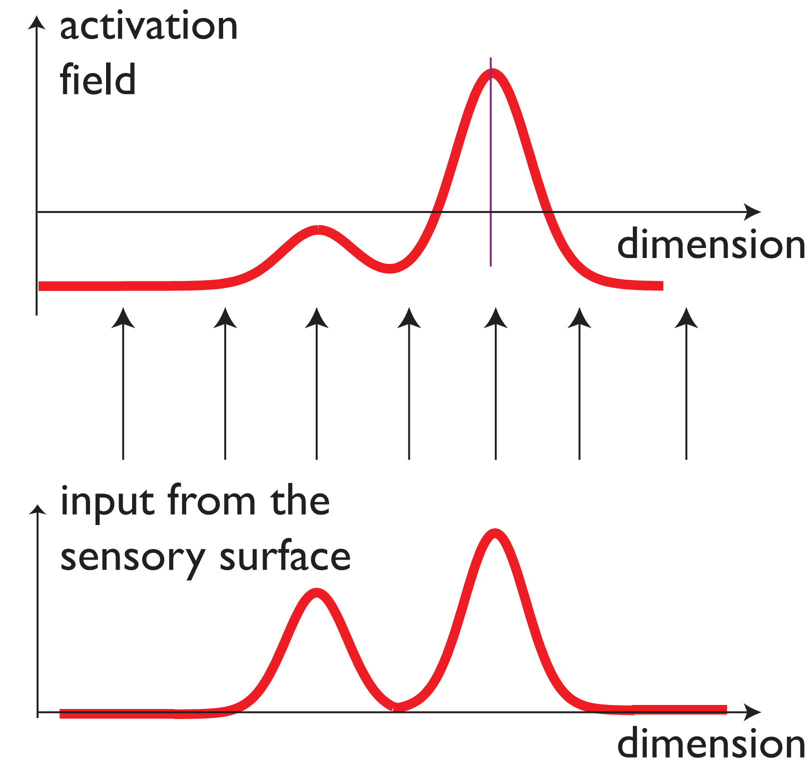


[Bastian, Riehle, Erlhagen, Schöner, 98]

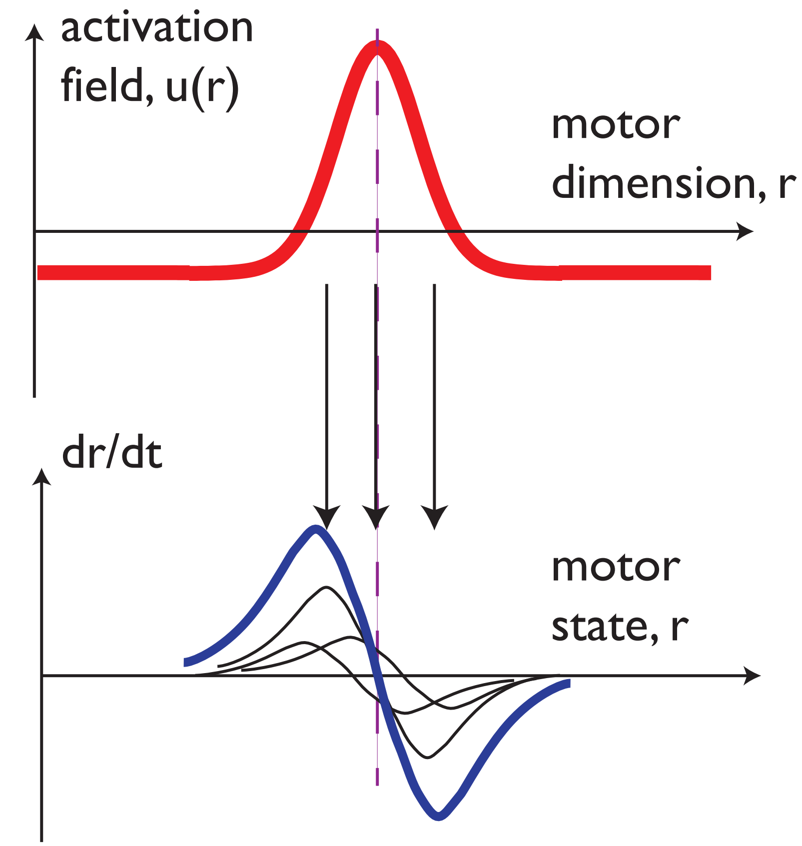
Distributions of Population Activation are abstract

- 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

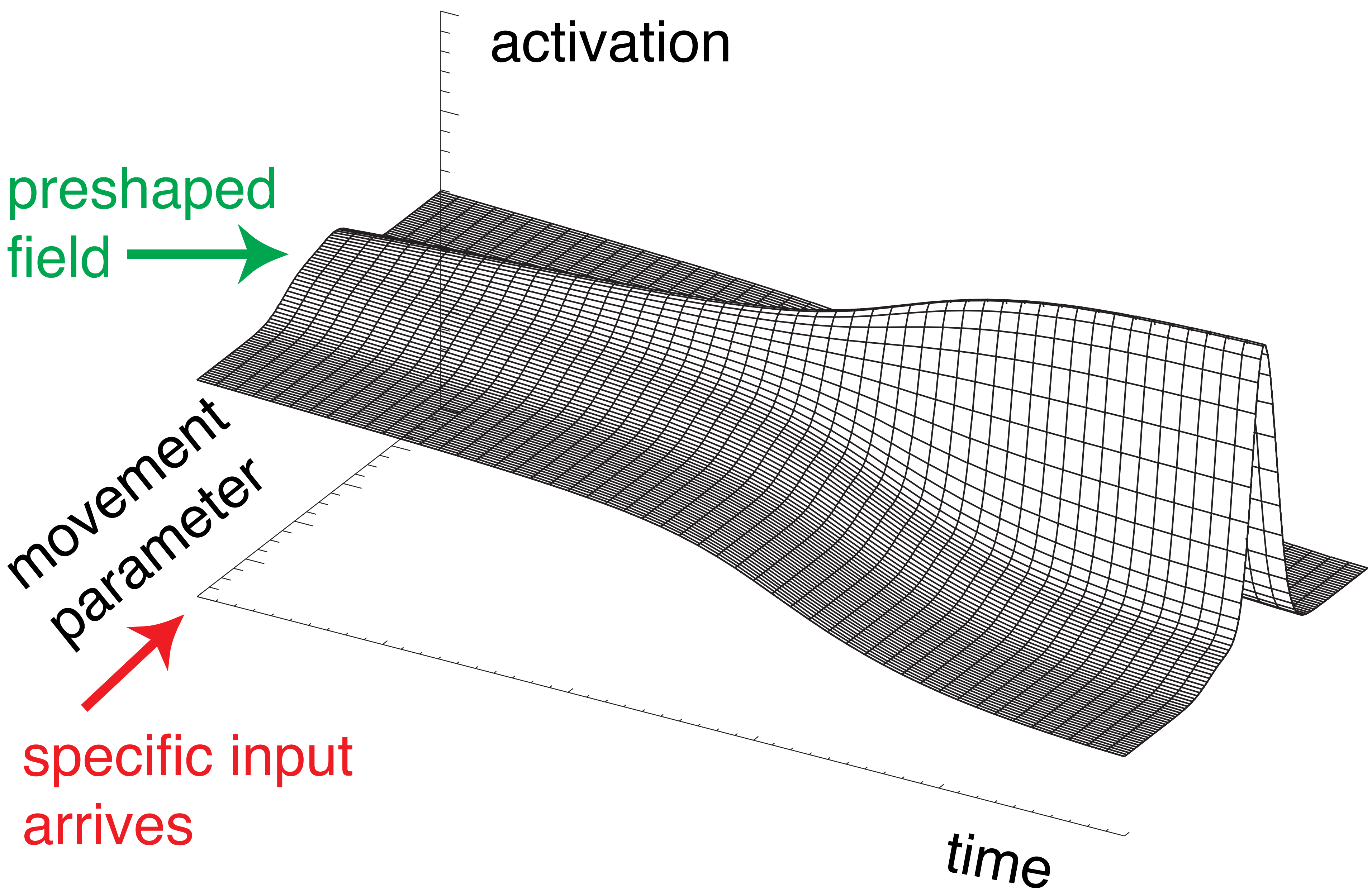
… back to the activation fields



- 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

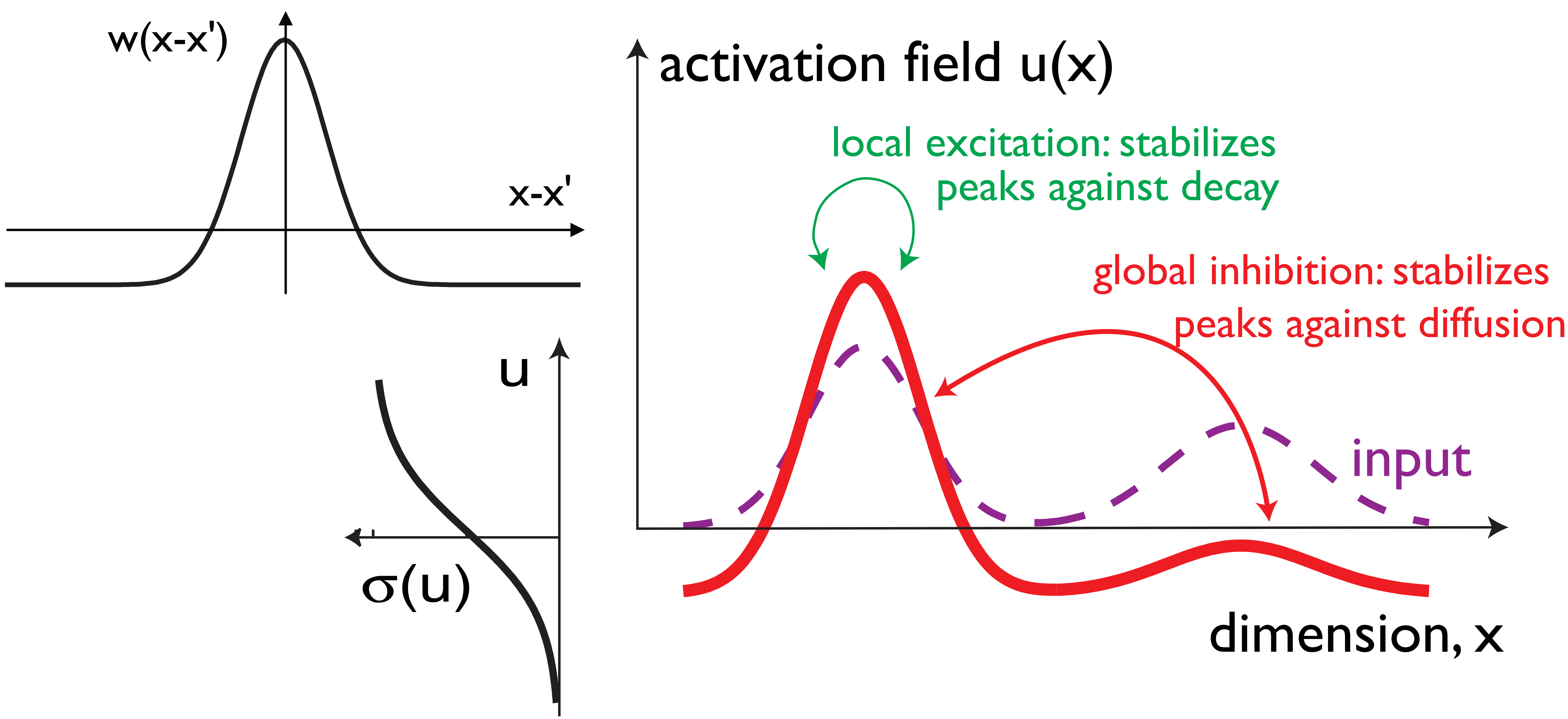


Neural dynamics of activation fields

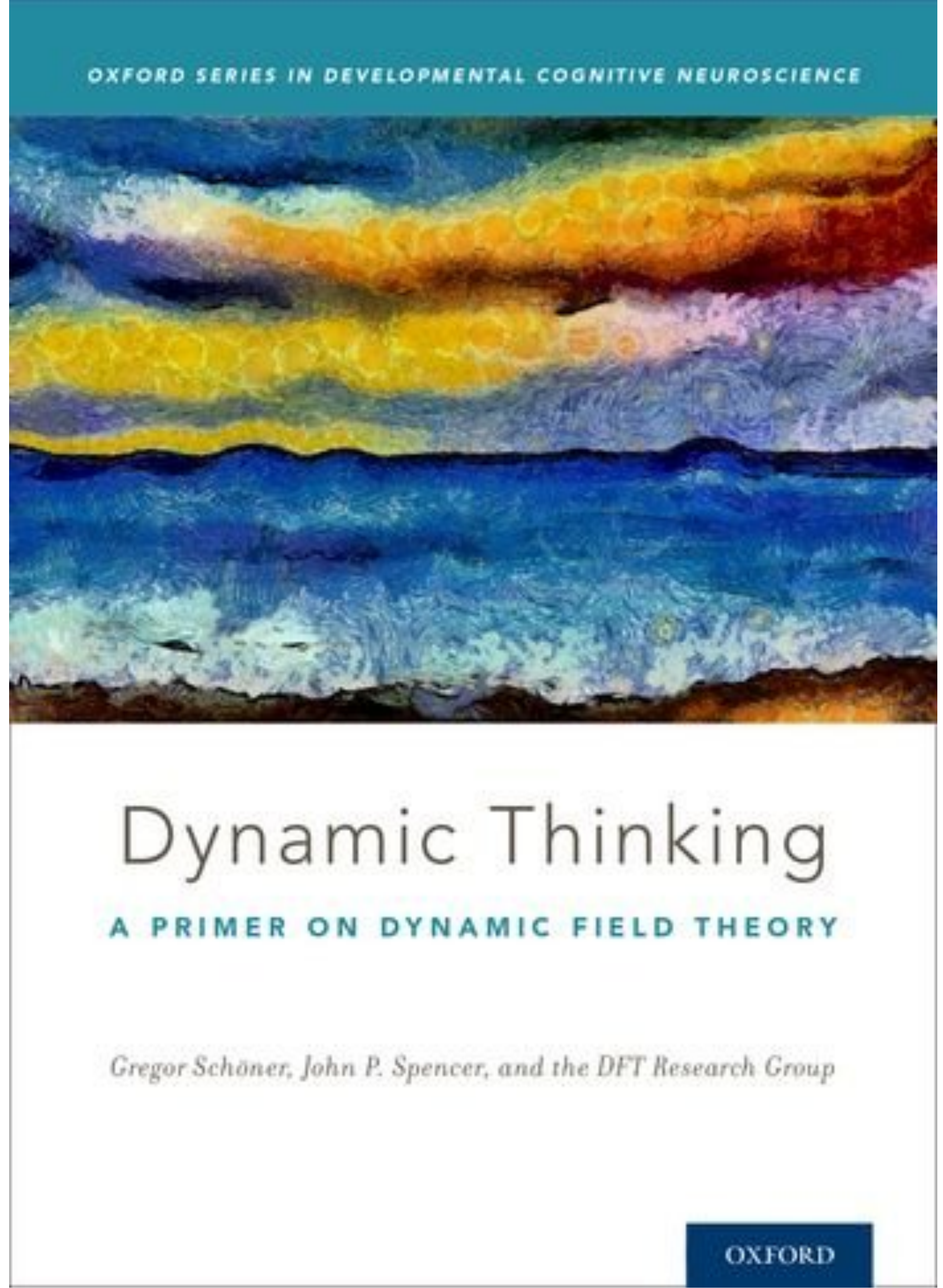


Neural dynamics of fields

- Peaks as stable states from intra-field interaction
- = local excitation/global inhibition



- dynamicfieldtheory.org



=> simulation

Attractors and their instabilities

- input driven solution (sub-threshold)
- self-stabilized solution (peak, supra-threshold)
- selection / selection instability
- working memory / memory instability
- boost-driven detection instability

detection instability

reverse detection instability

Noise is critical near instabilities

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

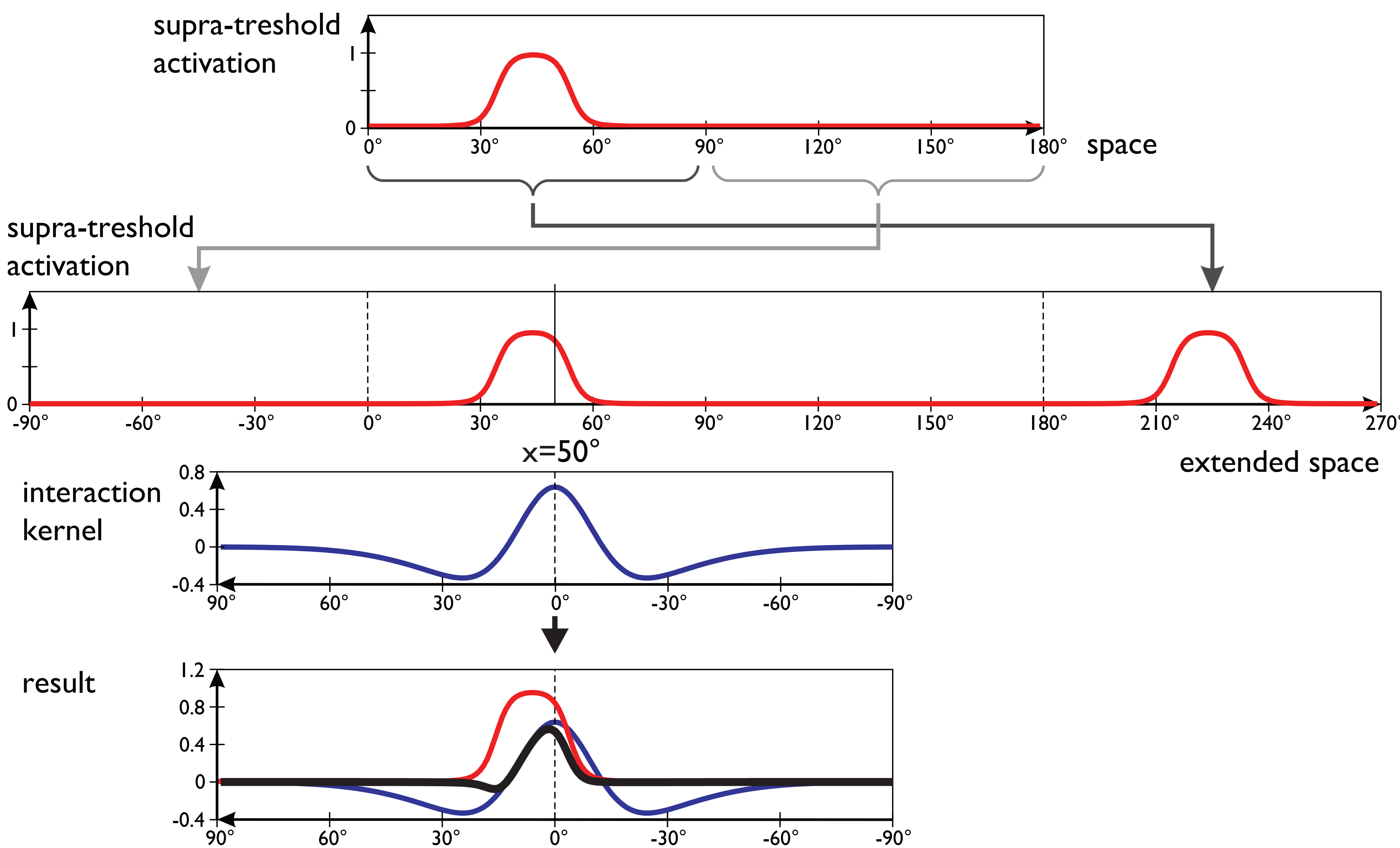
- time scale is τ
- resting level is $h < 0$
- input is $S(x,t)$
- interaction kernel is

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

- sigmoidal nonlinearity is

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

Interaction: convolution



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

Relationship to the dynamics of discrete activation variables