

# Motor Cortex

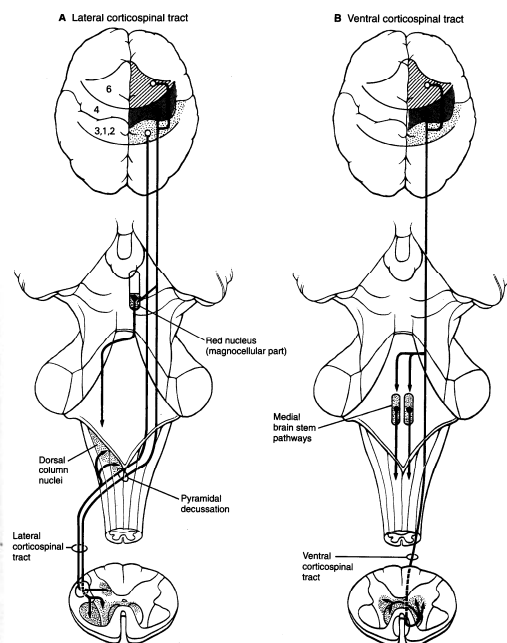
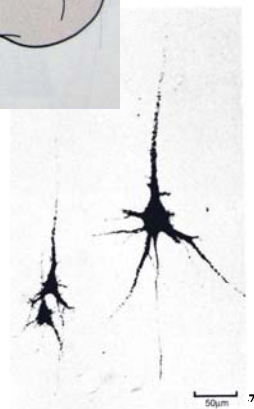
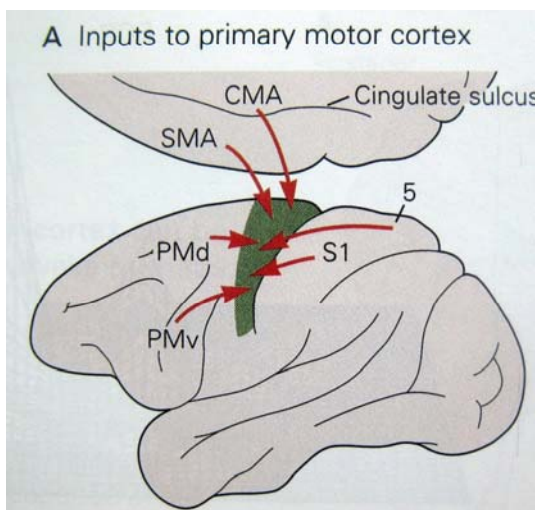
Emo Todorov

Applied Mathematics  
Computer Science and Engineering

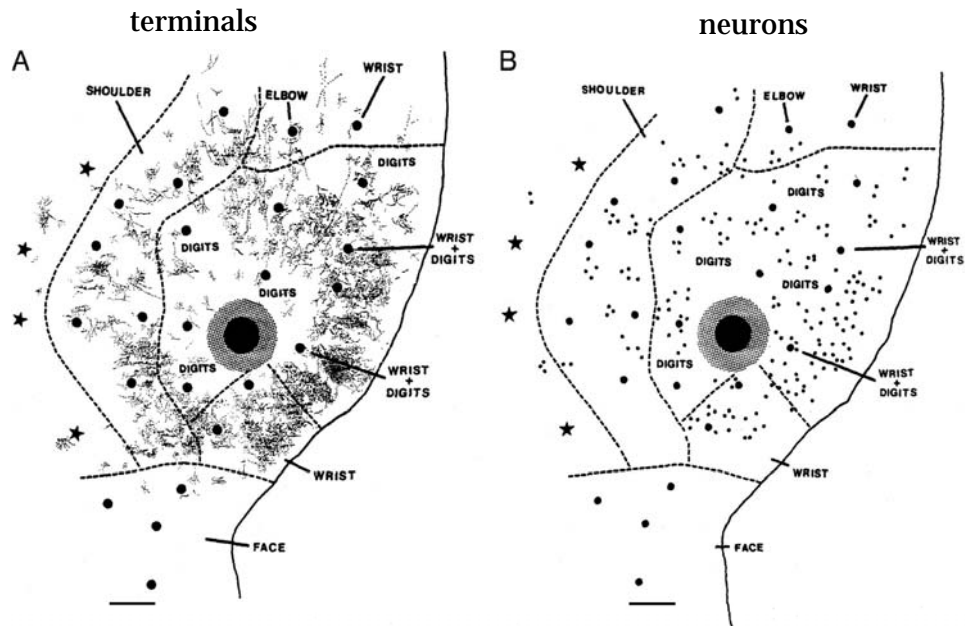
University of Washington

## Projections to and from M1

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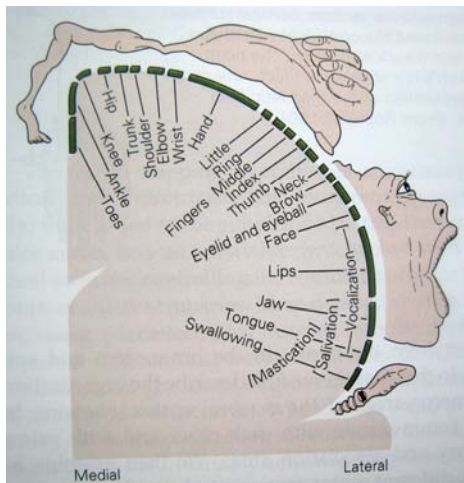


Labeling due to HRP injection

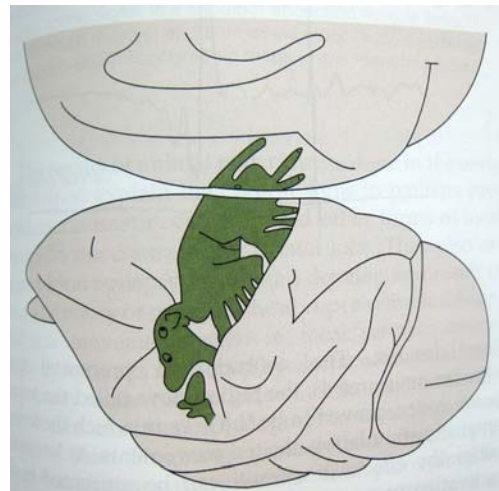


## Body maps: Reasonable

homunculus (Penfield)

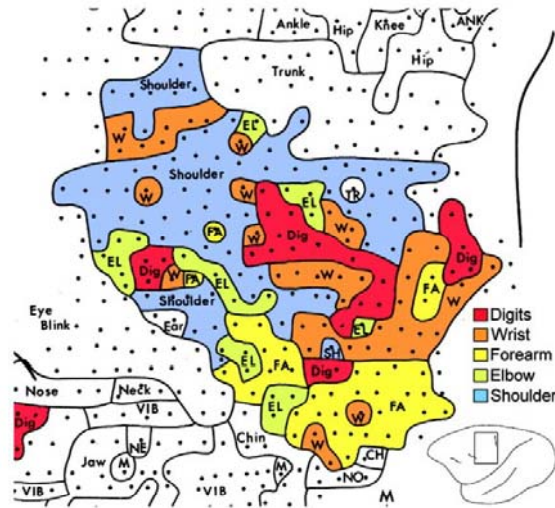
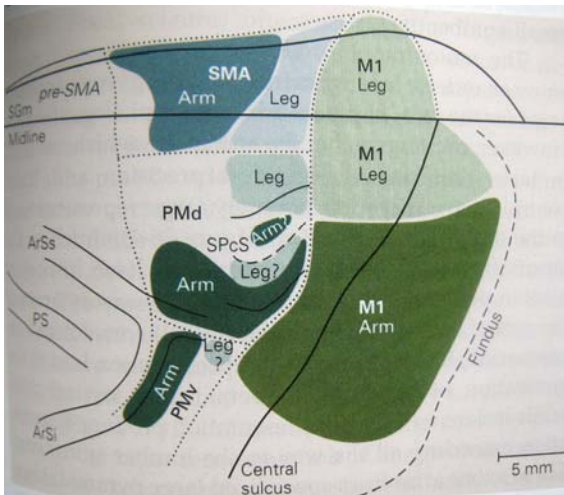


simiunculus (Woolsey)



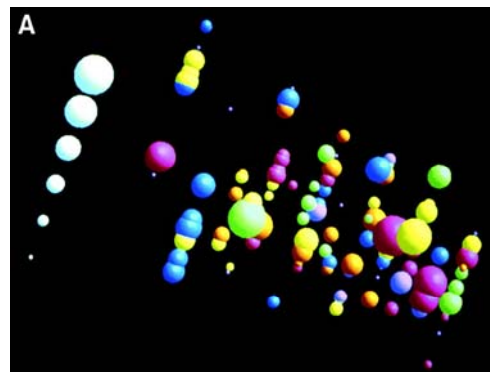
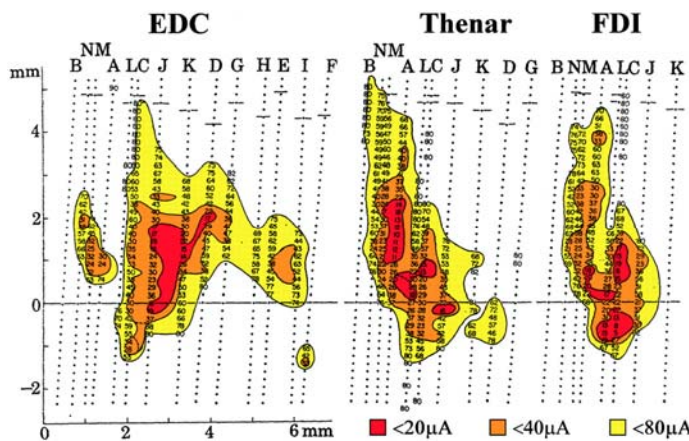
# More detailed maps: Repeated representations

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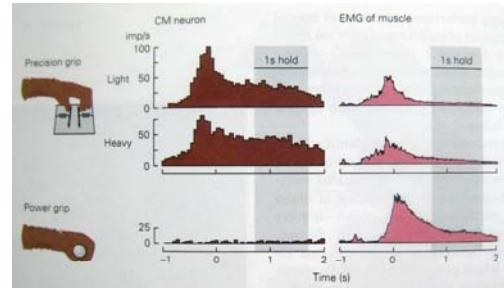
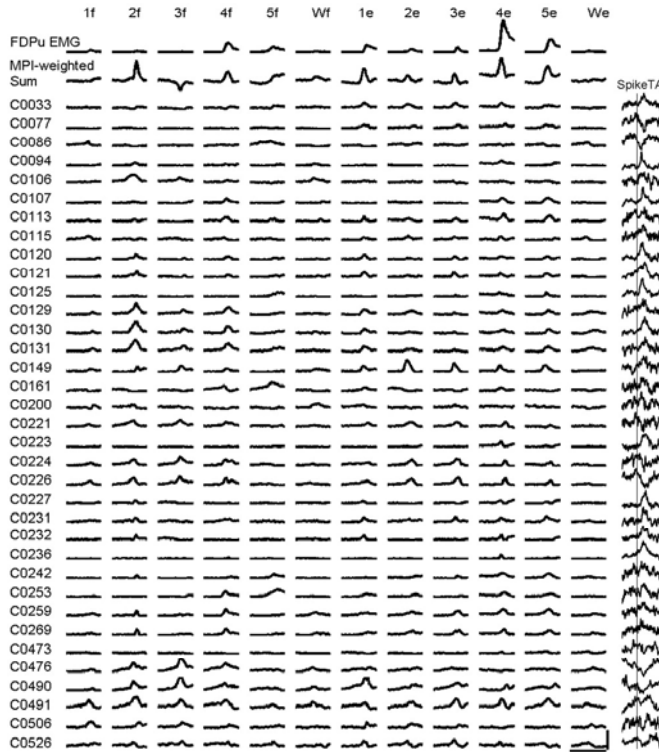
# Muscle and movement “maps”: Complete mess

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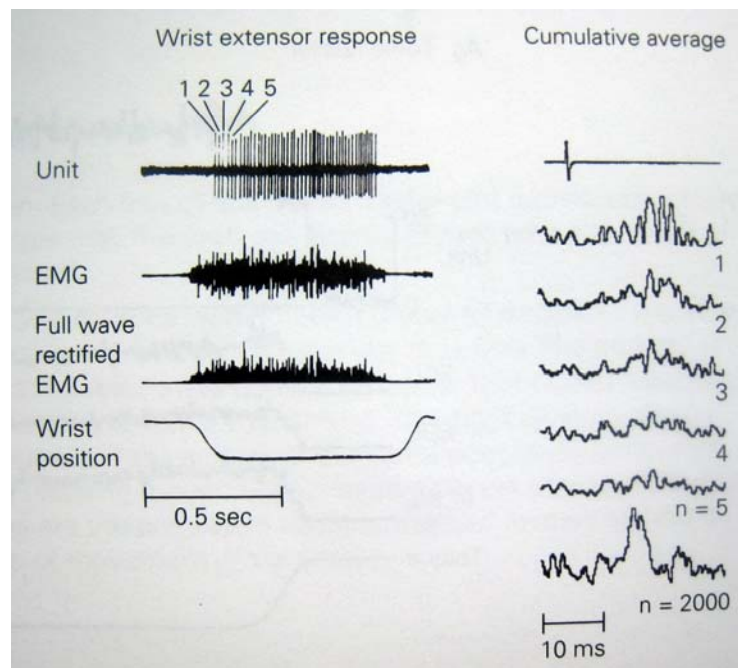
# M1 activity explains EMG, but not vice versa

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# Spike-triggered EMG averaging

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Early view (Everts)

**Force (muscle) control**

Later view (Georgopoulos)

Encoding of **hand kinematics**

(velocity, position) in 2D tasks

Even later (Kalaska, Scott)

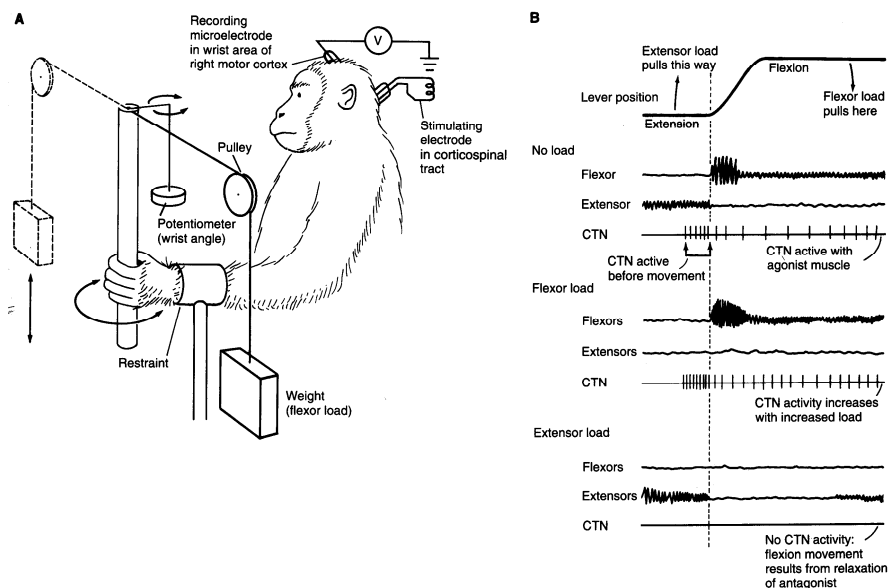
M1 also encodes **external loads**  
and **posture** in the same 2D tasks

M1 activity also correlates with:

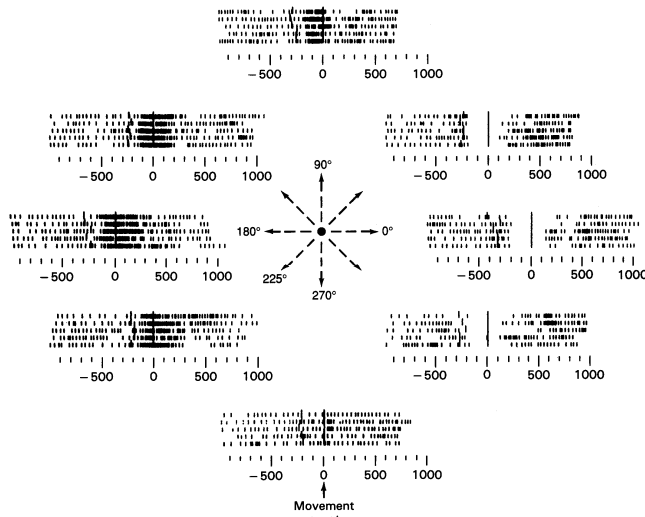
Position	Georgopoulos et al. 84, Kettner et al. 88
Joint configuration	Scott and Kalaska 95, Kakei et al. 99
Rate of change of force	Cheney and Fetz 80, Georgopoulos et al. 92
Acceleration	Bedingham et al. 85, Flament and Hore 88
Movement preparation	Thach 78
Target position	Alexander and Crutcher 90, Fu et al. 93
Distance to target	Fu et al. 93
Movement trajectory	Hocherman and Wise 91
Muscle coactivation	Humphrey and Reed 83
Serial order	Carpenter et al. 99
Visual target position	Georgopoulos et al. 89
Path curvature	Schwartz 94
Time from onset	Fu et al. 95

Individual neurons do bizarre things that lack a simple relation to any aspect of behavior (Churchland)

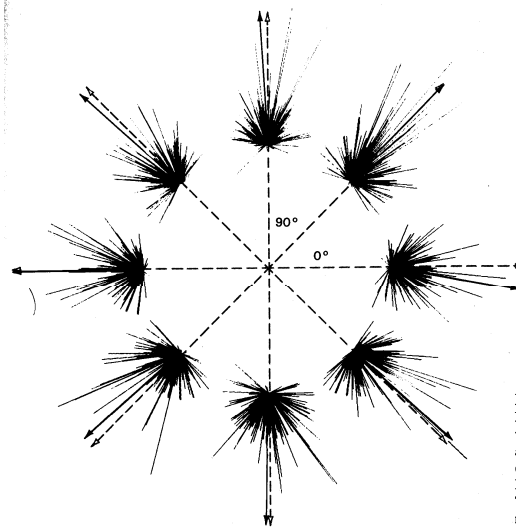
## Force encoding



## Broad directional tuning (cosine)



## Population vectors

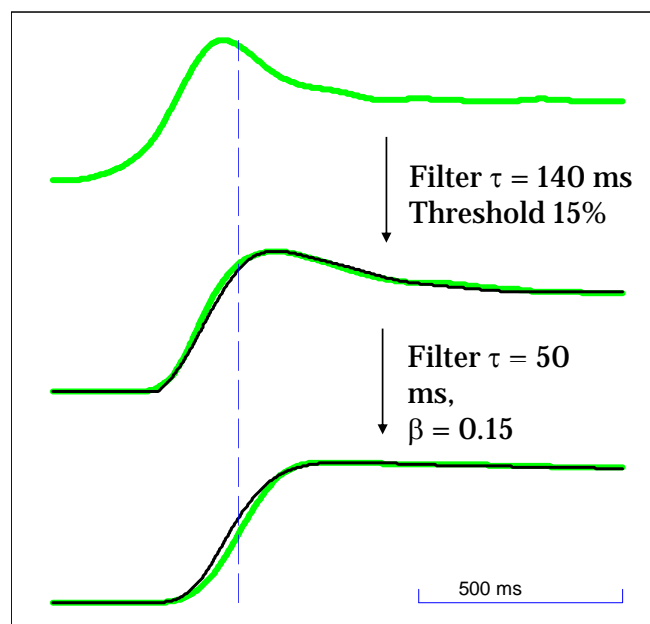


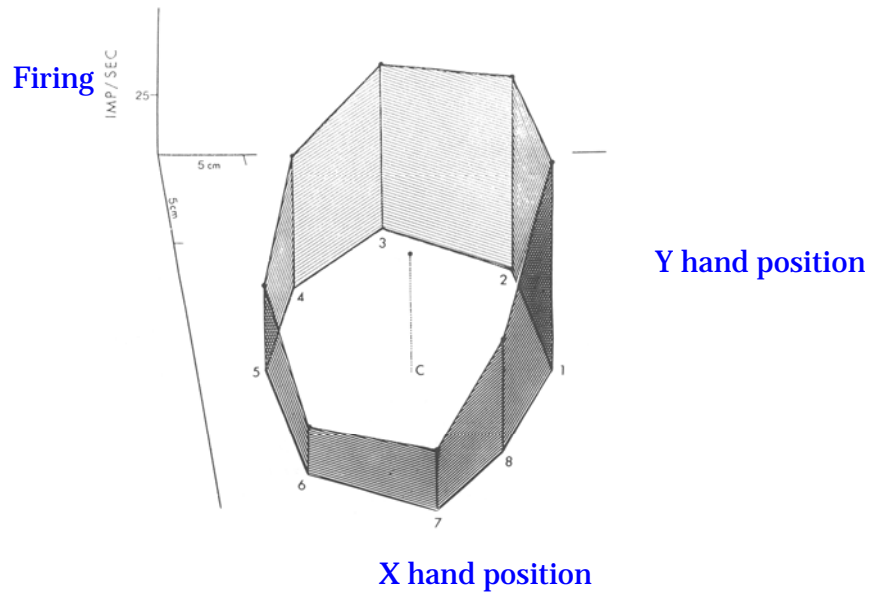
# Phasic activity at movement/force onset

Cortex

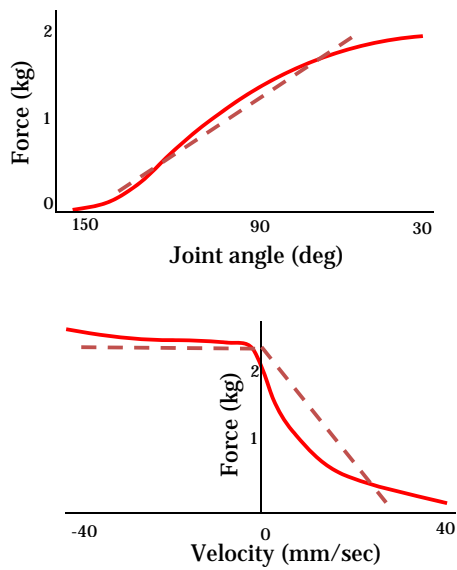
Muscle

Torque

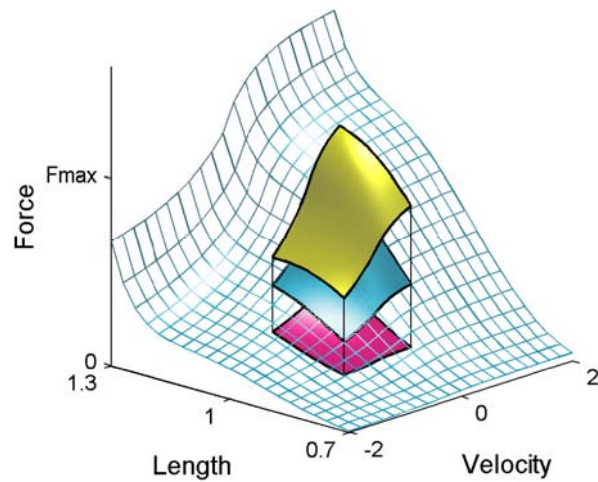




Joyce et al. 69



Brown et al. 99



# A mechanistic model

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(Todorov, Nat Neurosci 2000)

M1 cell firing:  $c_j(t)$

Muscle activity:  $a_i(t) = \sum_j w_{ij} c_j(t - \Delta)$

Muscle model:  $f(a, x, \dot{x}) = a - kx - [b\dot{x}]$

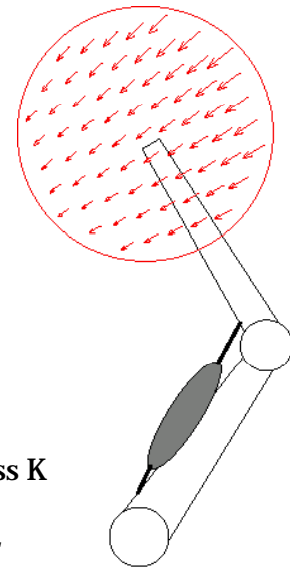
Force field:  $\mathbf{f}_i(a_i, \mathbf{x}, \dot{\mathbf{x}}) = (a_i - k_i \mathbf{x} \cdot \mathbf{p}_i - b_i [\dot{\mathbf{x}} \cdot \mathbf{p}_i]) \mathbf{p}_i$

Net force:  $PW\mathbf{c} - K\mathbf{x} - B\dot{\mathbf{x}} = M\ddot{\mathbf{x}} + \mathbf{f}_{ext}$

Arm model: asymmetric mass  $M$ , damping  $B$ , stiffness  $K$

Mechanics:  $PW = F_{2 \times 2} U_{2 \times \text{Cells}}, M = mF, B = bF, K = kF$

Parameters:  $m = 1 \text{Ns}^2/\text{m}, b = 10 \text{Ns}/\text{m}, k = 50 \text{N}/\text{m}, F_{asp} = 2:1$

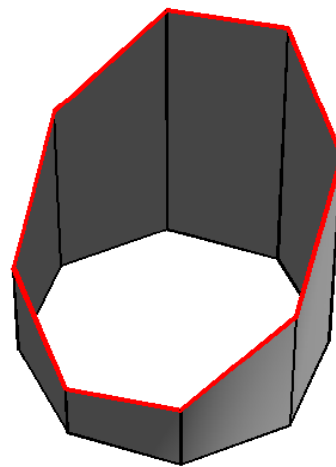
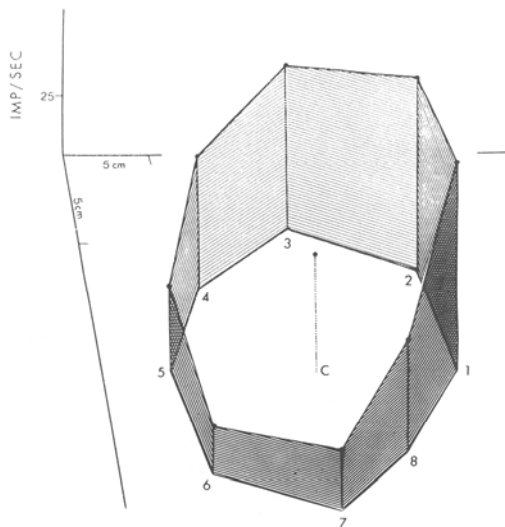


# Position encoding

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Georgopoulos and Massey 85

Model

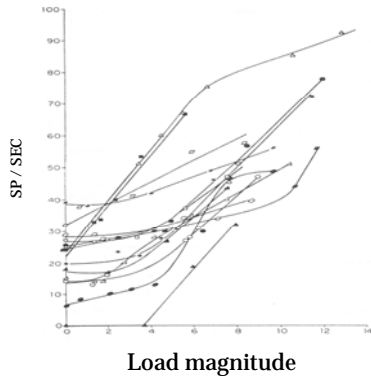




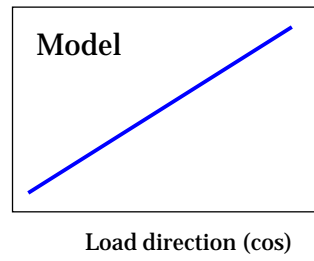
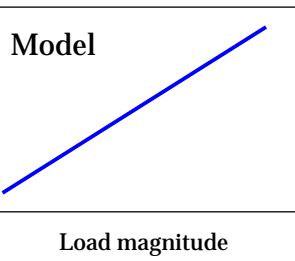
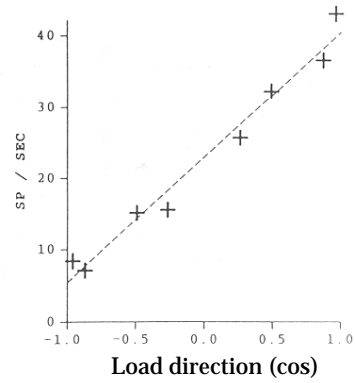
# Force encoding

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### Cheney and Fetz 80



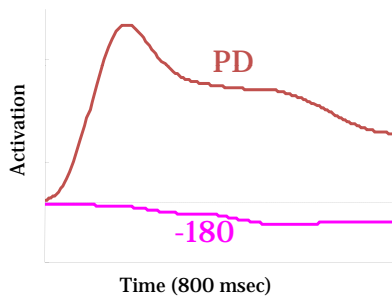
### Kalaska et al. 89



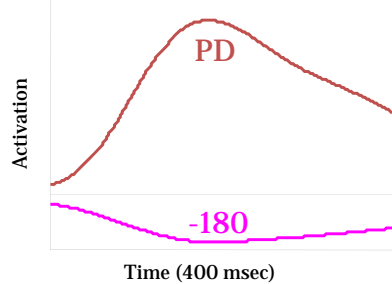
# Velocity encoding

18

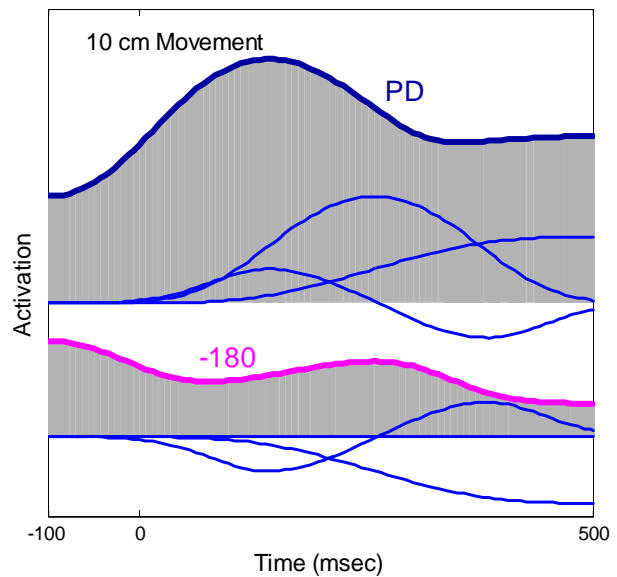
### Crammond and Kalaska 96



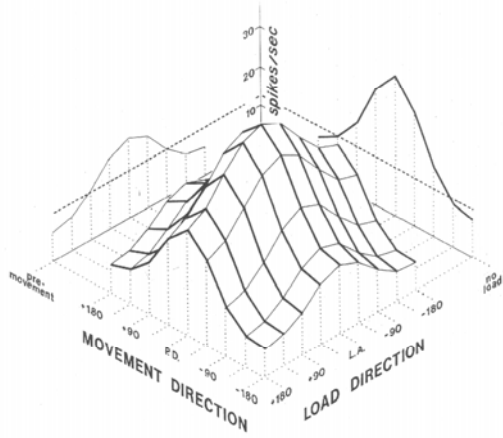
### Moran and Schwartz 99



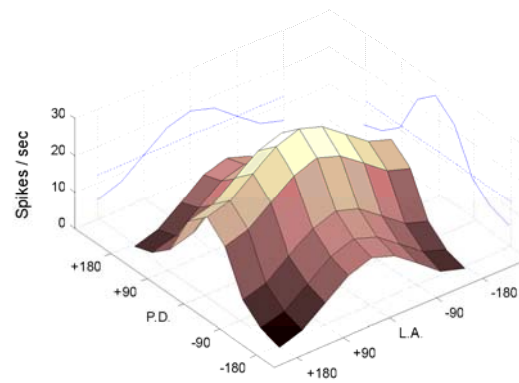
### Model



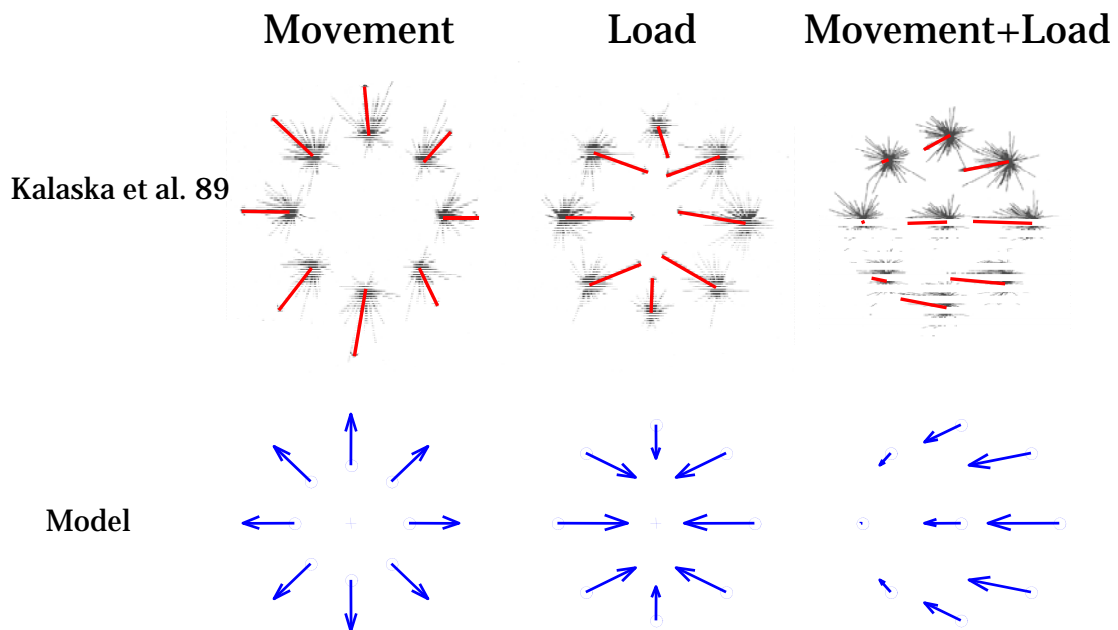
Kalaska et al. 89



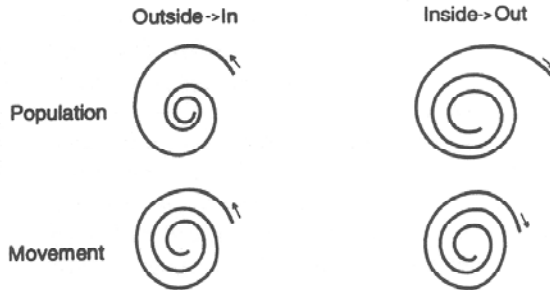
Model



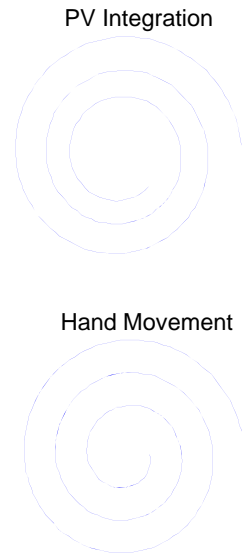
## Population vector distortions



## Schwartz 94

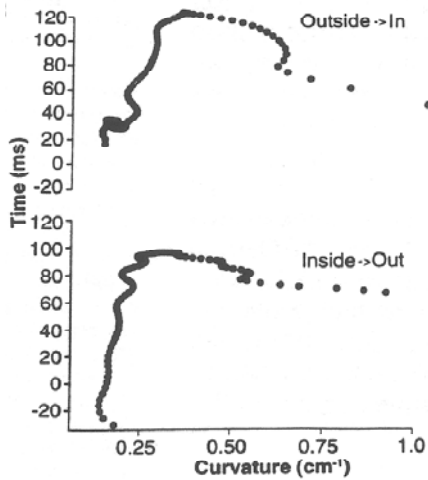


## Model

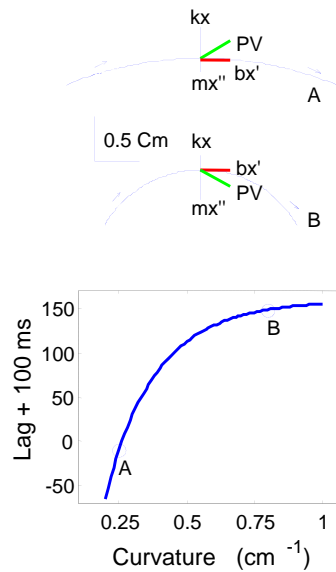


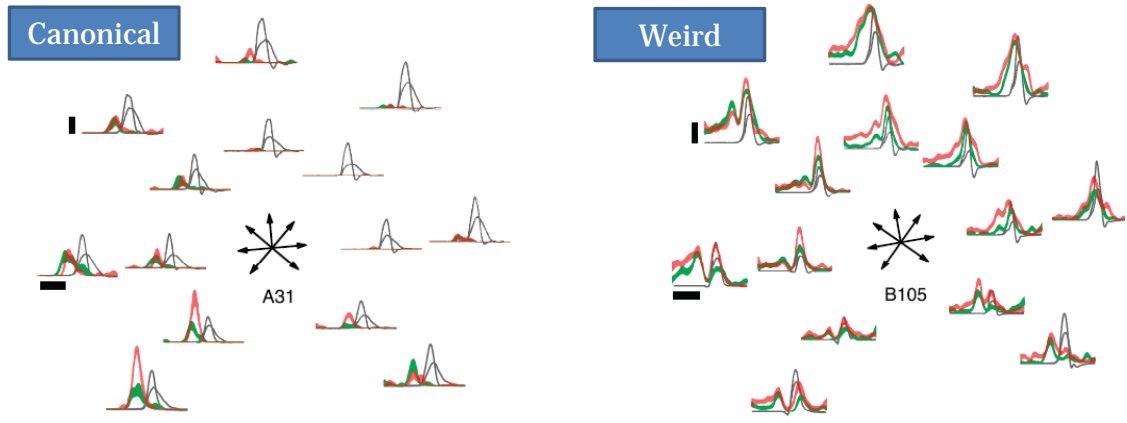
# Apparent changes in M1-movement latency

## Schwartz 94



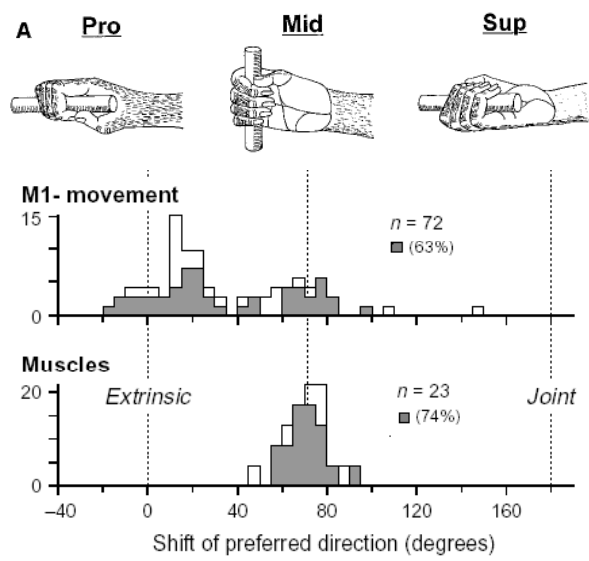
## Model



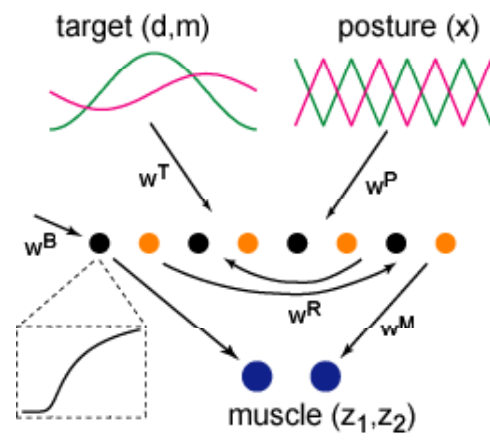


Churchland and Shenoy 2007

## Extrinsic and intrinsic signals in M1



Kakei, Hoffman and Strick (1999)

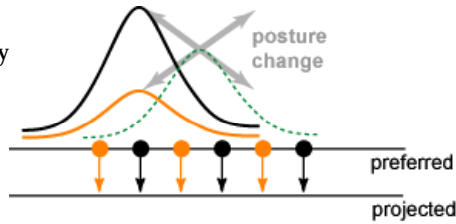


Poisson-like **noise** added to:

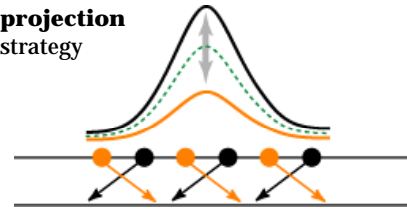
- input signals
- recurrent signals
- output signals

candidate “pure” strategies for postural compensation

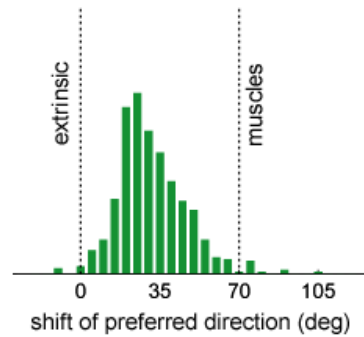
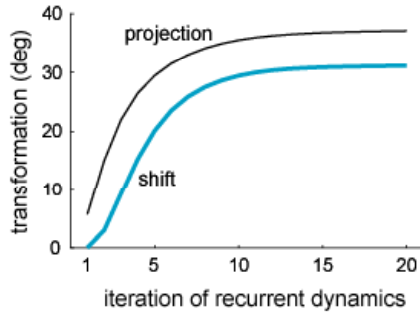
**shift**  
strategy



**projection**  
strategy

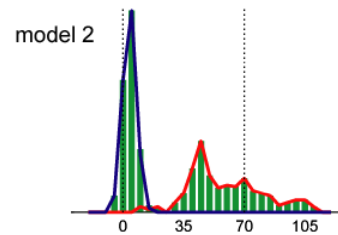
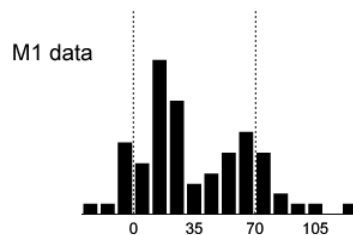
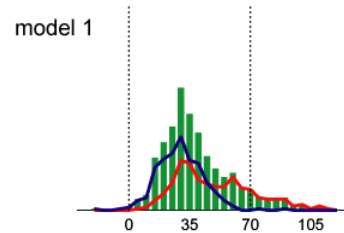
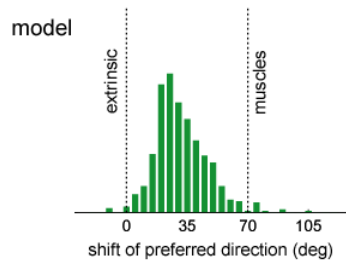


the trained network uses a mixed strategy

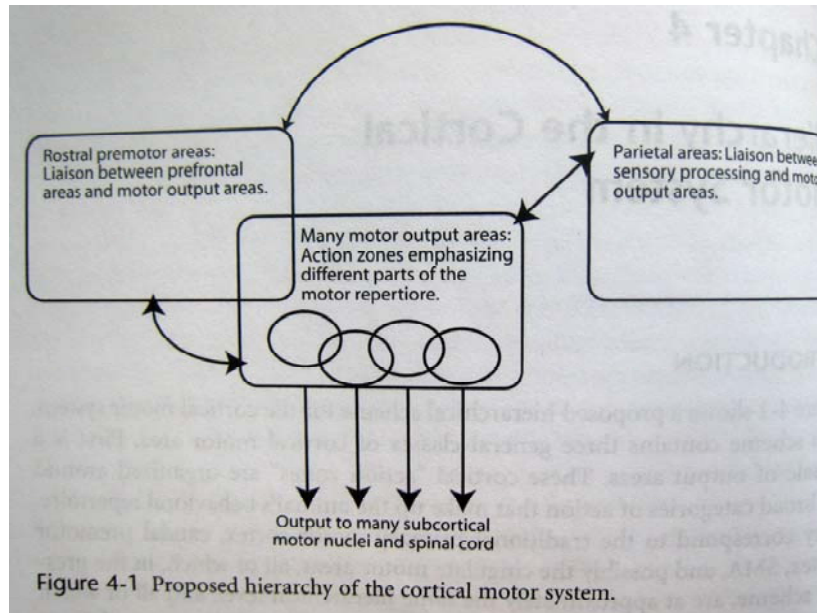


the key determinant of what strategy is optimal turns out to be **noise**:  
when any 2 out of the 3 noise terms are removed the preferred directions no longer shift

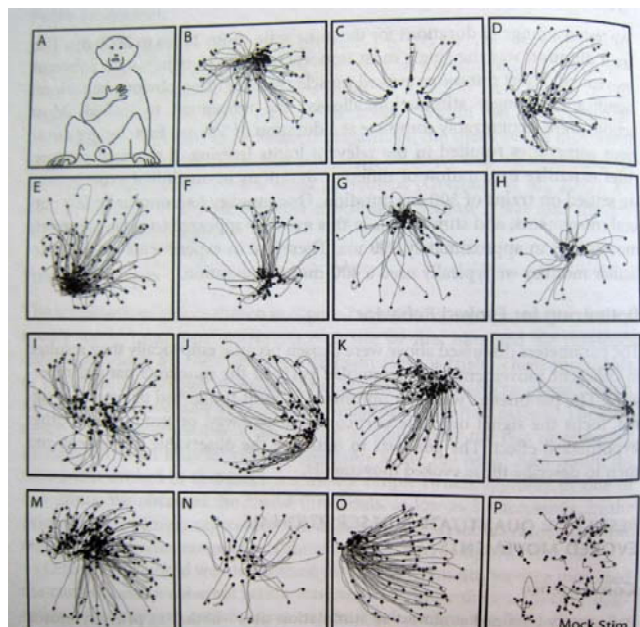
## Bi-modal distributions



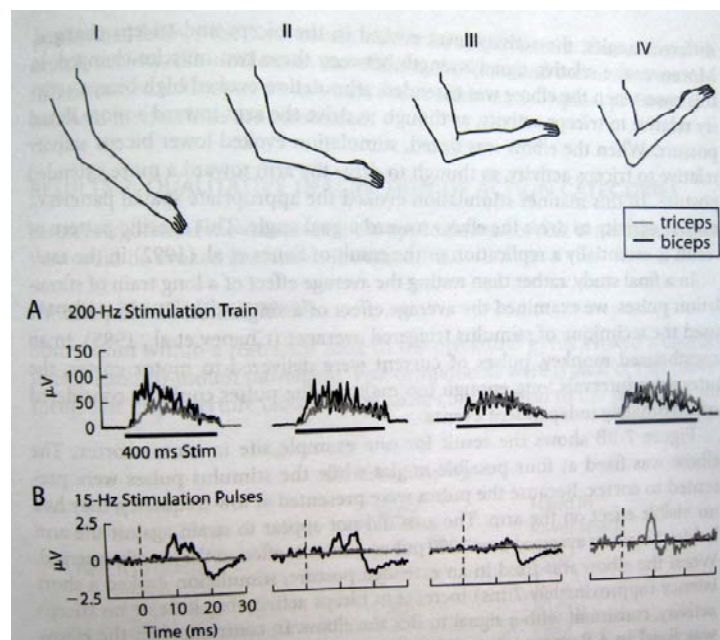
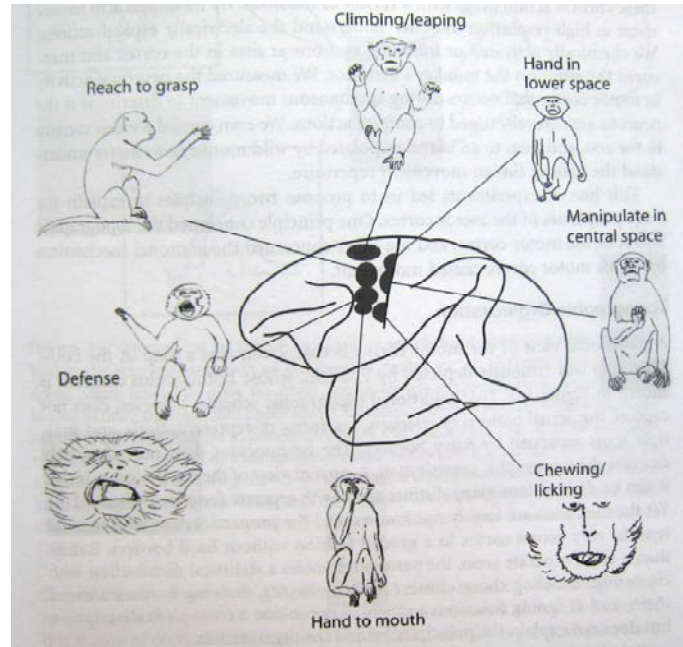
- model: all neurons are interconnected and project to the muscles
- model 1: half of the neurons (“interneurons”) do not project to the muscles
- model 2: the **output** neurons do not project to the **interneurons**

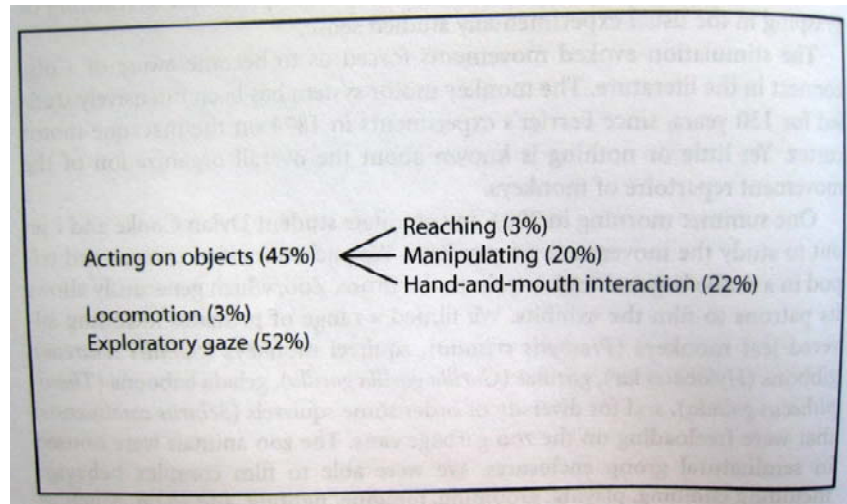


## Effects of macro-stimulation



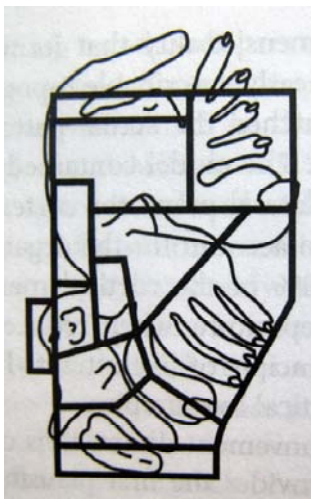






## Modeling of the topographic map

Initialization of the Kohonen map model



Results

