

# Relationship between Flash-Lag Effect and Delay Compensation in the Nervous System

*Cognoscenti Talk*

February 19, 2006

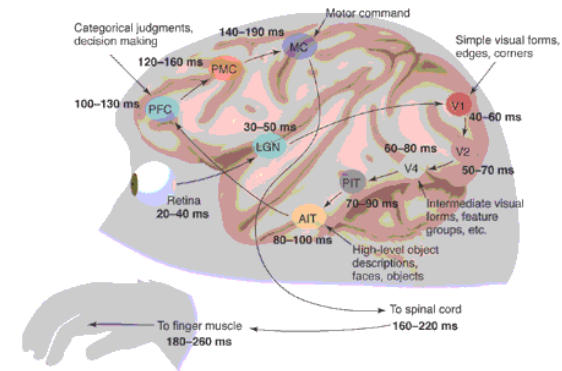
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1

## Whence Prediction?

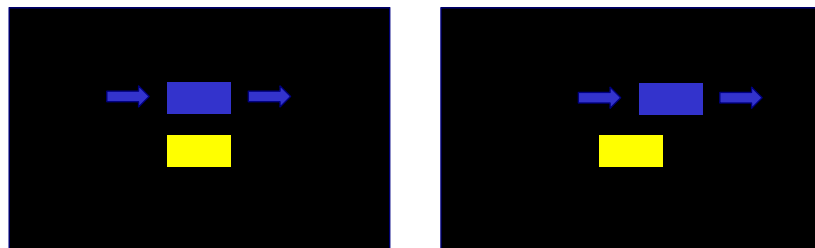


Thorpe and Fabre-Thorpe (2001)

- Due to **neural conduction delay** (couple of 100 ms), we cannot even seem to catch up with the present.
- At best, we will be predicting the **present**, based on the **past**.

2

## Strange Perceptual Illusion: Flash Lag Effect



Physical

Perceived

- Moving object seems to be ahead of an aligned, flashed object (Nijhawan 1994).
- Numerous variations: orientation, luminance, etc.

3

## Demo: Flash Lag Effect

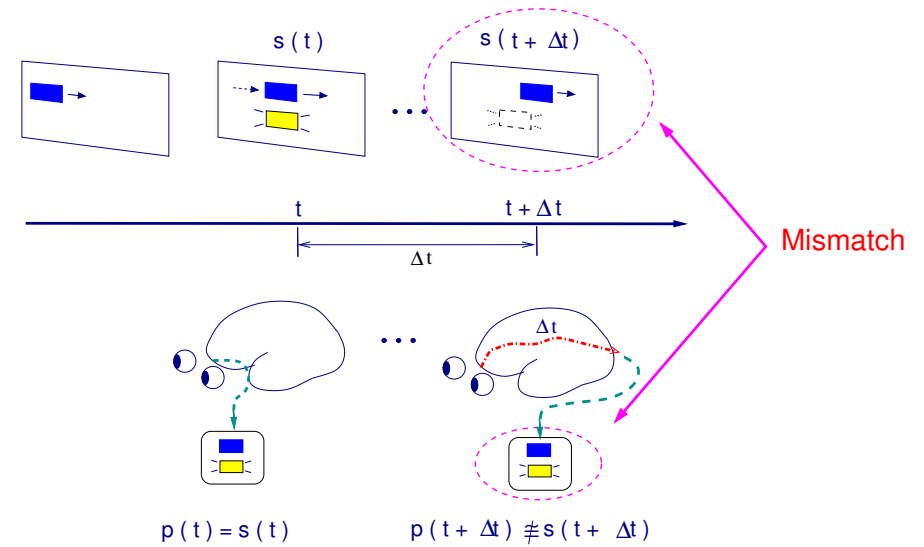
4

## Implications of FLE

- There may be mechanisms in the brain for **delay compensation** through **extrapolation**.
- The brain may **predict** the present, based on the past.
- Alternative hypotheses: differential latency (Whitney and Murakami 1998), postdiction (Eagleman and Sejnowski 2000), etc.

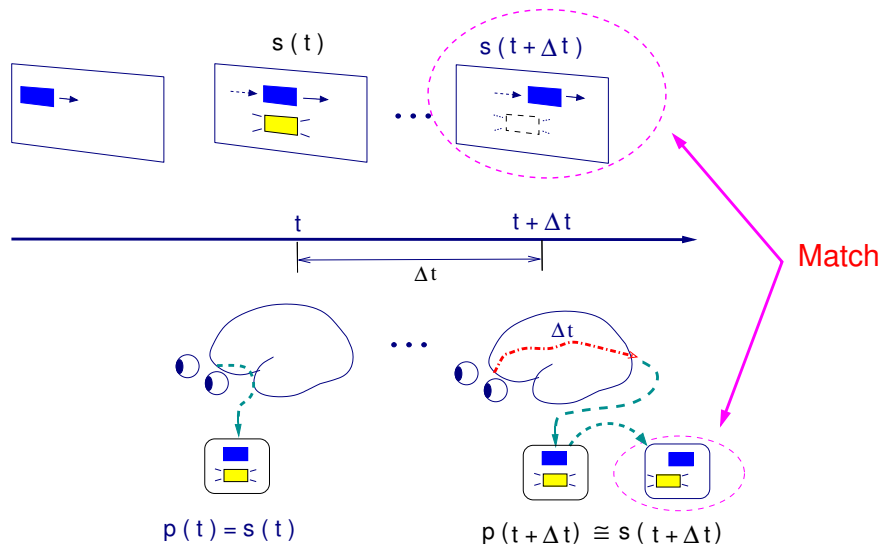
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## W/O Delay Compensation: No FLE



6

## With Delay Compensation: FLE



7

## Research Questions

- How can the nervous system compensate for internal delay?
- Are there single-neuron-level mechanisms for that?

8

## Potential Answers

**Extrapolation** can be used to compensate for delay:

- That can happen at a single-neuron level.
- Facilitatory neural dynamics may be the underlying mechanism.
- FLE may be a side-effect of such a compensatory process.

9

## Dynamic Synapses

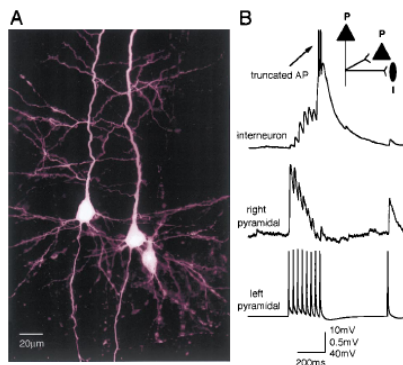


FIG. 2. Differential synaptic facilitation and depression via the same axon innervating two different targets. (A) A light microscopic pseudocolor image of three biocytin-filled neurons. The pyramidal neuron on the left innervated the pyramidal neuron on the right and the bipolar interneuron on the right. (B) Single trial responses (30 Hz) to same AP train. Failure rate for first EPSP: interneurons, 24%; pyramidal neuron, 0% (60 sweeps). Coefficient of variation (CV; as in ref. 15) for first EPSP: interneuron, 1.12; pyramidal neuron, 0.15. CV for 6th EPSP: interneuron, 0.32; pyramidal neuron, 0.68.

(Markram et al. 1998)

11

## Approach

Integrate insights from:

1. Psychophysics: Flash-lag effect
2. Neurophysiology: Dynamic synapses
3. Computational theory: Extrapolation

And, potential link to neurology (autism and dyslexia).

10

## Dynamic Synapses

The effect of synaptic transmission changes dynamically.

- Dynamic increase: Facilitating synapse.
- Dynamic decrease: Depressing synapse.
- Time scale: several hundred milliseconds from the onset (Liaw and Berger 1999; Fortune and Rose 2001; Markram 2002)

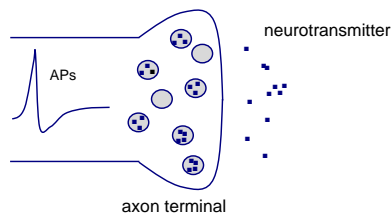
12

## Alternative Role of Dynamic Synapses

- Previous: **memory** (sensitization and habituation) (Zucker 1989; Fisher et al. 1997).
- Previous: **temporal information processing** (Fuhrmann et al. 2002; Markram et al. 1998; Fortune and Rose 2001).
- Proposed: **extrapolation** (facilitating synapses).

13

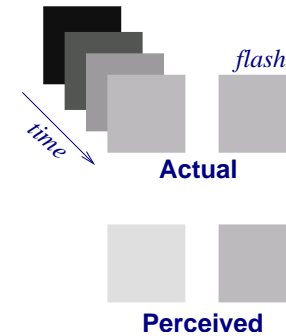
## Available Resource ( $R$ ) and Synaptic Efficacy ( $U$ )



- $R$ : Fraction of recovered neurotransmitters.
- $U$ : Probability of neurotransmitter release.
- Postsynaptic response is dependent on  $R$  and  $U$ .

15

## Target Experiment: Luminance FLE



Sheth et al. (2000)

- Works in both directions: increasing or decreasing.
- A single neuron can model the phenomenon.
  - Firing rate represents the perceived luminance.

14

## Model: Dynamic Synapse

- Synaptic efficacy  $U$  (Markram et al. 1998; Fuhrmann et al. 2002):

$$\frac{dU}{dt} = -\frac{U}{\tau_f} + C(1 - U)\delta(t - t_s), \quad (1)$$

where  $\tau_f$ : time constant for the decay of  $U$ ;  $C$  a constant determining the increase in  $U$  due to spikes at  $t_s$ ; and  $\delta(\cdot)$  the Dirac delta function.

- To model extrapolation in the decreasing direction:

$$C = \text{sign}(I(n-1) - I(n)) \left( \frac{I(n-1)}{I(n)} \right) r, \quad (2)$$

where  $I(n)$  is the inter-spike interval.

16

## Model: Membrane Potential

- Postsynaptic current  $P(t)$ :

$$P(t) = Ee^{-\frac{t}{\tau_p}}, \quad (3)$$

$$E = AU, \quad (4)$$

- Membrane potential  $V_m(t)$ :

$$V_m(t) = V_m(t-1)e^{-\frac{t}{\tau_m}} + P(t)(1 - e^{-\frac{t}{\tau_m}}). \quad (5)$$

- Once  $V_m$  exceeds the spike threshold  $\theta$ , a spike is generated, followed by an absolute refractory period of  $\tau_{\text{refrac}}$ .

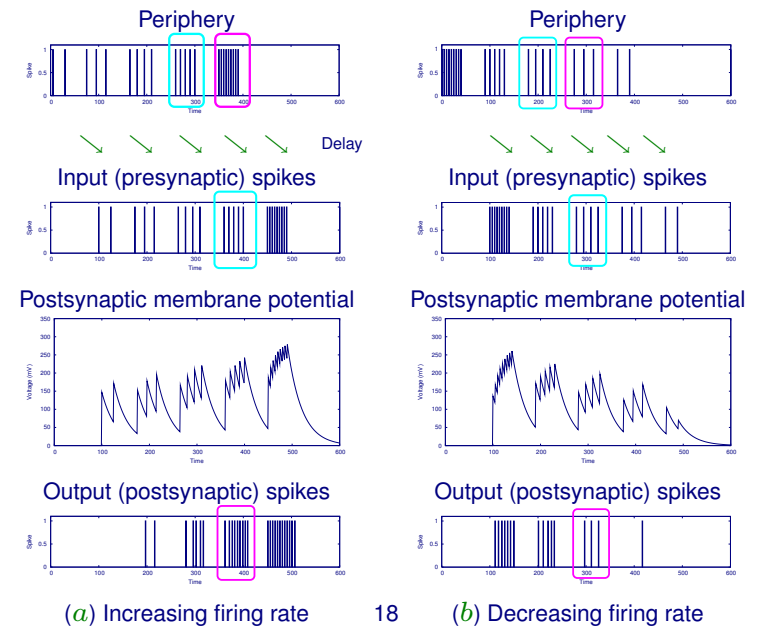
17

## Luminance FLE: Summary

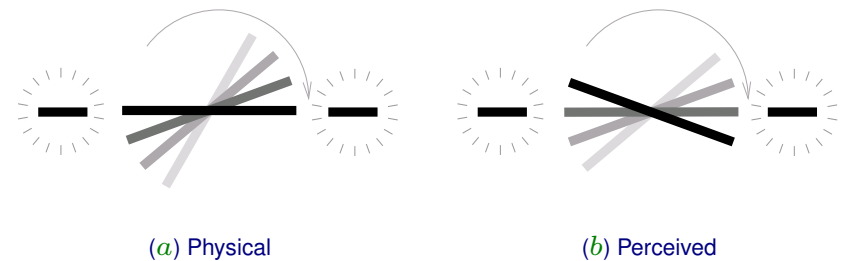
- FLE can be due to delay compensation mechanism.
- Facilitating synapses may be the neural basis of delay compensation.
- Limitations:
  - Cannot explain cross-neuronal facilitation such as orientation FLE

19

## Results



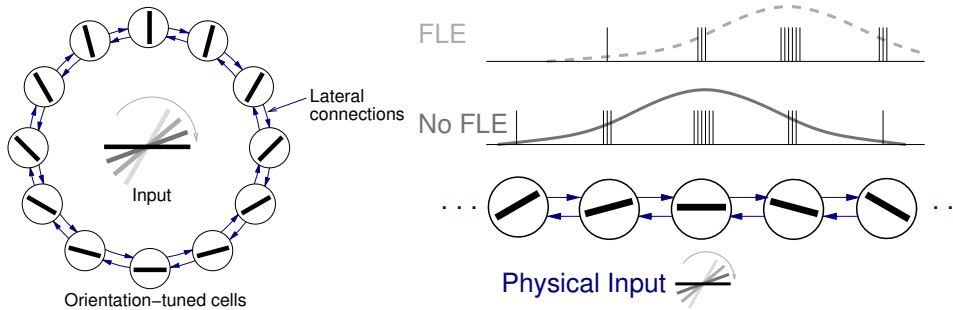
## Target Experiment: Orientation FLE



- Cannot model with single neuron.
  - V1 orientation-tuned cells have narrow tuning.
- Need network of neurons, with directionally biased weights.

20

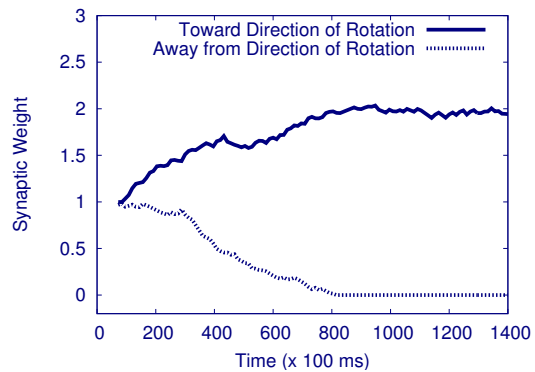
## Model: A Ring of Orientation Cells



- Shift in firing rate distribution when FLE occurs.
- Needed:
  - Directionally biased connection weights.
  - Facilitating dynamics.

21

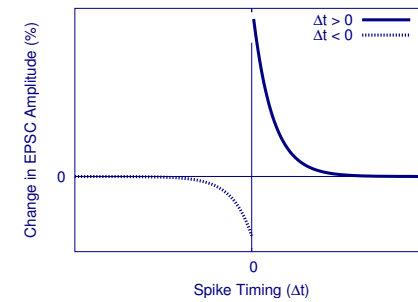
## Results: Learned Weights



- Weight in the direction of rotation increases.
- Weight in the opposite direction of rotation decreases.

23

## Model: STDP and Facil. Synapses



(a) STDP ( $\Delta t = t_{\text{post}} - t_{\text{pre}}$ )

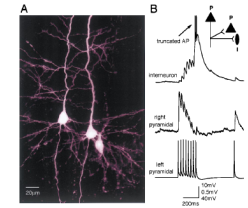


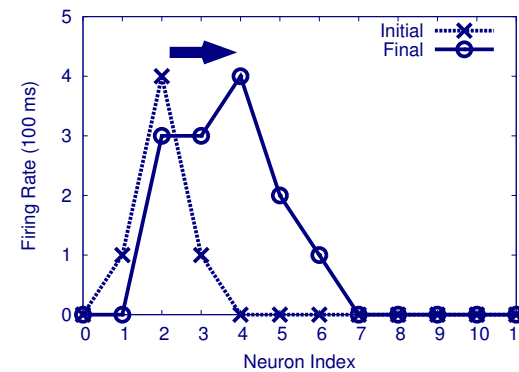
Fig. 2. Differential synaptic facilitation and depression via the same axon innervating two different targets. (A) A light microscopic pseudocolor image of three biocytin-filled neurons. The pyramidal neuron on the left innervated the pyramidal neuron on the right and the bistratified neuron on the right. (B) Single trial responses (S1-S10) to same AP train. (a) baseline for first EPSP; interneuron, 24%; pyramidal neuron, 5%. (b) sweeps. Coefficient of variation (CV, as in ref. 25) for first EPSP: interneuron, 1.22; pyramidal neuron, 0.15; CV for 6th EPSP: interneuron, 0.32; pyramidal neuron, 0.68.

(b) Facil. Synapses

- Spike Timing Dependent Plasticity (Bi and Poo 1998): Set up directionally biased weights.
- Facilitating Synapses: Extrapolation across connections.

22

## Results

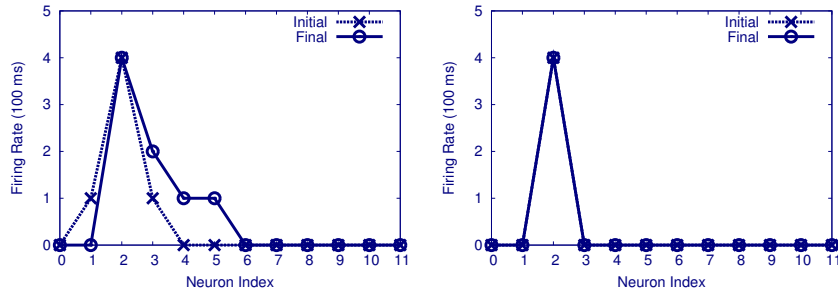


- Peak firing neuron shifts in the direction of rotation.

24

## Results: STDP or Facil. Synapse

### Alone



- STDP or facilitating synapses alone was insufficient.

25

## Orientation FLE: Summary

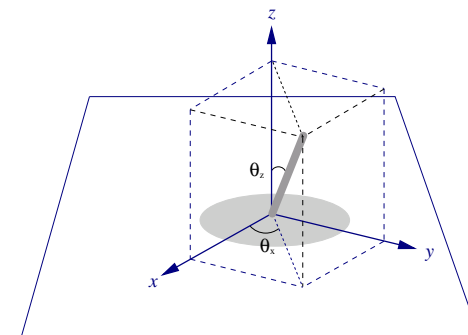
For cross-neuronal facilitation, both

- STDP
- Facilitating synapses

are needed.

26

## Application: Pole Balancing

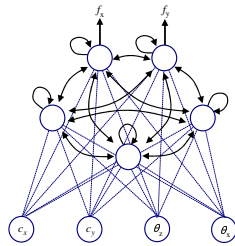


- 2D pole balancing problem.
- **Delay introduced** in input (position and pole angle).

27

28

# Neuroevolution of Recurrent Neural Network Controller



- Fully recurrent neural network controller.
- Trained through neuroevolution (ESP by Gomez and Miikkulainen 1998, 1999; Gomez 2003).

29

# ESP Activation

- Neuron state is determined by **instantaneous** weighted sum of activity:

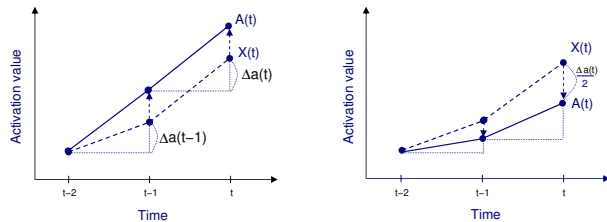
$$X_i(t) = g\left(\sum_{j \in N_i} w_{ij} X_j(t)\right),$$

where  $g(\cdot)$  is a nonlinear activation function,  $N_i$  the set of neurons sending activation to neuron  $i$ , and  $w_{ij}$  the connection weight from neuron  $j$  to neuron  $i$ .

30

# Approach: Add Dynamics to Neuron

## Activation



- Facilitatory activity (left):

$$A(t) = X(t) + (X(t) - A(t - 1))r,$$

$A(t)$ : facilitated activation level at  $t$ ;  $X(t)$ : instantaneous activation;  $r$ : facilitation rate ( $0 \leq r \leq 1$ ).

- Decaying activity (right):  $A(t) = A(t - 1)r + X(t)(1 - r)$ .

31

# Encoding $r$

- ESP was modified to use the facilitating or decaying dynamics.
- The rate parameter  $r$  was encoded in the chromosome so that it can evolve.

32



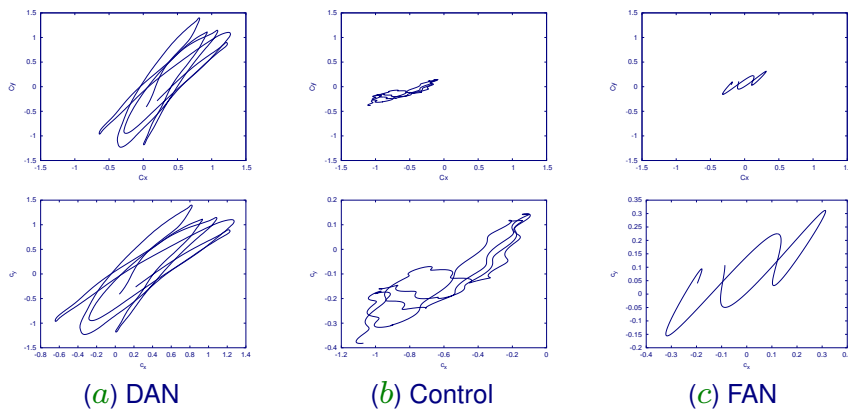
# Experiment

Compare task performance under three types of dynamics:

- Control: Basic ESP implementation.
- FAN: Facilitatory Activation Network.
- DAN: Decaying Activation Network.

33

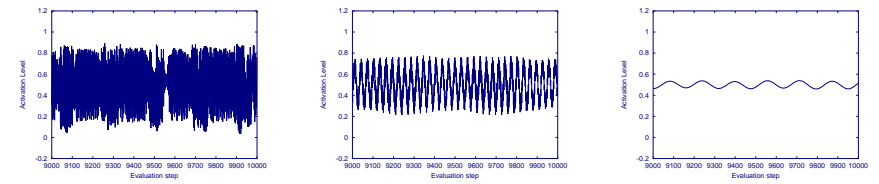
## Results: Cart Trajectory



- Last 1000 steps in successful balancing trials.
- 1-step delay, from iteration 50 to 150.
- FAN shows a smooth trajectory with a much smaller footprint.

35

# Results: Activation Pattern

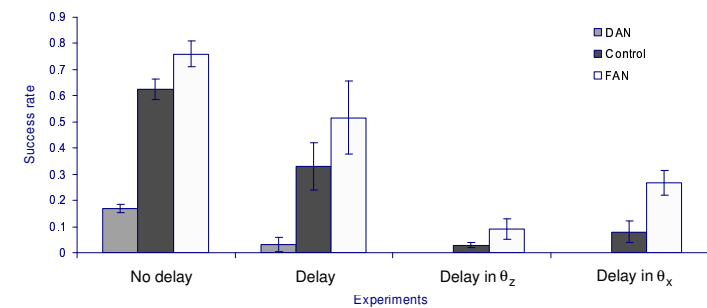


(a) DAN                      (b) Control                      (c) FAN

- Last 1000 steps in successful balancing trials.
- 1-step delay, from iteration 50 to 150.
- FAN shows smoother, low-amplitude oscillation.

34

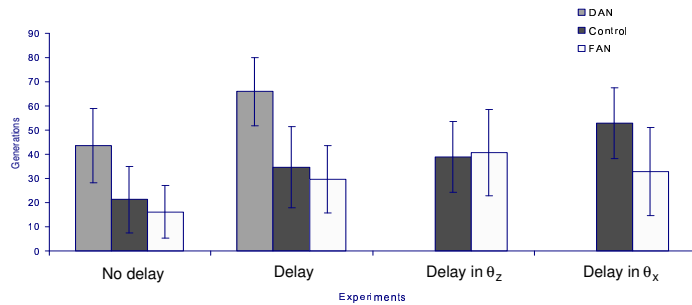
## Results: Success Rate



- Different delay conditions were tested.
- FAN showed best performance under all conditions (t-test,  $p < 0.005$ ,  $n = 250$ ).

36

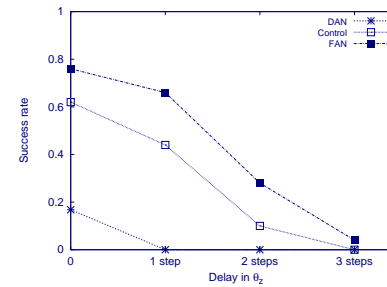
## Results: Speed of Learning



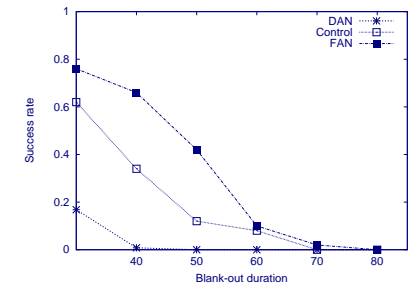
- Different delay conditions were tested (same as above).
- FAN showed best performance under all conditions (t-test,  $p < 0.0002$ ,  $n = 250$ ), except for the  $\theta_z$ -delay case ( $p = 0.84$ , i.e., no difference).

37

## Results: Effect of Increased Delay



(a) Increased delay

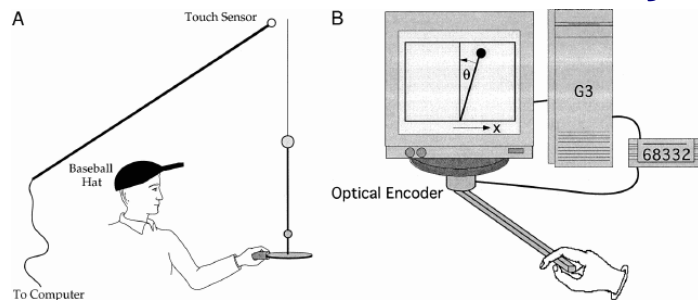


(b) Increased blank-out duration

- Performance under increased delay and input blank-out period.
- In all conditions, FAN performed the best.

38

## Blank-Out as External Delay

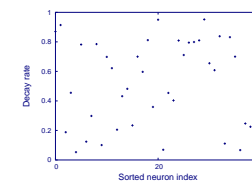


Mehta and Schaal (2002)

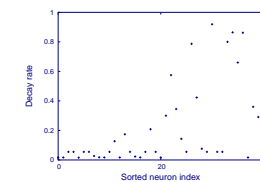
- Input feed cut off for  $40 \sim 500$  ms while balancing a virtual pole.
- Humans are good at dealing with input blank-out.
- FAM shows similar robustness.

39

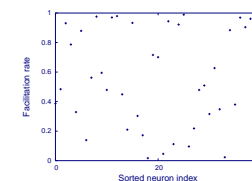
## Analysis: Evolution of $r$



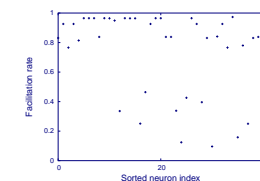
(a) DAN: Initial state



(b) DAN: Final state



(c) FAN: Initial state



(d) FAN: Final state

- FAN: best neurons had high  $r$
- DAN: best neurons had low  $r$

40

## Summary: Pole Balancing

- Facilitatory dynamics help combat debilitating effects of noise in the input.
- Facilitatory dynamics can help in delay in **external** environment as well (potential for real prediction?).
- Decaying dynamics make things worse.

41

## Future Directions

### Autism:

- Problem in coherent motion detection (Milne et al. 2002).
- Problem with processing moderately rapid motion (Gepner et al. 2001; Gepner 2002).

### Dyslexia:

- Difficulty with processing rapidly changing stimulus (Hari and Renvall 2001)

### Predictions:

- Autistics and dyslexics may not perceive FLE.
- Abnormal growth in brain size may outgrow built-in delay compensation mechanisms.

43

## Discussion

- New role for facilitating synapses: extrapolation.
- Facilitation should happen both in the increasing and the decreasing directions.
- Novel prediction regarding facilitating synapses: equation 2.
- Ability to predict future arising from the need to predict the present?

42

## Conclusions

- Facilitatory (extrapolatory) dynamics at a single-neuron level can help compensate for neural delay.
- Facilitatory synapses may be implementing such a function: They are not just for memory!
- There may be possible connections to predictive mechanisms in the brain.

44

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44-1

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44-2