Prediction, a Prerequisite to Goal-directed Behavior, and Its Possible Origin in Delay Compensation

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Origin of Goal-Directed Behavior: Recasting the Question

• What is a goal?
  – It is something in the future.
  – To form a goal, one needs to see into the future.
  – That is, prediction is necessary.

• How does prediction arise in the nervous system and how does it affect behavior?

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.

Flash Lag Effect: Evidence of Prediction in the Brain?

Thorpe and Fabre-Thorpe (2001)

• Flash-Lag Effect (Nijhawan 1994) suggests that the brain may be performing extrapolation to compensate for delay.
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.

W/O Delay Compensation: No FLE

\[ p(t) = s(t) \]
\[ p(t + \Delta t) \neq s(t + \Delta t) \]

Mismatch

With Delay Compensation: FLE

\[ p(t) = s(t) \]
\[ p(t + \Delta t) \equiv s(t + \Delta t) \]

Match
Research Questions

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

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.

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).

Dynamic Synapses

(Markram et al. 1998)
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)

Alternative Role of Dynamic Synapses

- Previous: temporal information processing (Fuhrmann et al. 2002; Markram et al. 1998; Fortune and Rose 2001).
- Proposed: extrapolation (facilitating synapses).

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.

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

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

- Synaptic efficacy $U$ (Markram et al. 1998; Fuhrmann et al. 2002):
  \[
  \frac{dU}{dt} = -\frac{U}{\tau_f} + C(1 - U)\delta(t - t_s),
  \]
  (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:
  \[
  C = \left( \frac{I(n - 1) - I(n)}{|I(n - 1) - I(n)|} \right) \left( \frac{I(n - 1)}{I(n)} \right) r,
  \]
  (2)
  where $I(n)$ is the inter-spike interval.

Model: Membrane Potential

- Postsynaptic current $P(t)$:
  \[
  P(t) = E e^{-\frac{t}{\tau_p}},
  \]
  (3)
  \[
  E = AU,
  \]
  (4)

- Membrane potential $V_m(t)$:
  \[
  V_m(t) = V_m(t - 1)e^{-\frac{t}{\tau_m}} + P(t)(1 - e^{-\frac{t}{\tau_m}}).
  \]
  (5)
  - Once $V_m$ exceeds the spike threshold $\theta$, a spike is generated, followed by an absolute refractory period of $\tau_{\text{refrac}}$.

Results

- 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

Luminance FLE: Summary
**Target Experiment: Orientation FLE**

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

**Model: A Ring of Orientation Cells**

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

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**Model: STDP and Facil. Synapses**

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

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**Results: Learned Weights**

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

- Peak firing neuron shifts in the direction of rotation.

Orientation FLE: Summary

For cross-neuronal facilitation, both

- STDP
- Facilitating synapses

are needed.

Results: STDP or Facil. Synapse Alone

- STDP or facilitating synapses alone was insufficient.

Application: Pole Balancing
Modified Pole-Balancing Problem

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

Neuroevolution of Recurrent Neural Network Controller

- Fully recurrent neural network controller.

ESP Activation

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

\[ X_i(t) = g(\sum_{j \in N_i} w_{ij} X_j(t)), \]

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 \( i \).

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): \( A(t) = A(t-1)r + X(t)(1-r). \)
**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.

**Experiment**

Compare task performance under three types of dynamics:
- Control: Basic ESP implementation.
- FAN: Facilitatory Activation Network.
- DAN: Decaying Activation Network.

**Results: Activation Pattern**

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

**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.
Results: Success Rate

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

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).

Results: Effect of Increased Delay

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

Blank-Out as External Delay

- 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.
Analysis: Evolution of \( r \)

<table>
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<tr>
<th>Diagram</th>
<th>Description</th>
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<tr>
<td>(a) DAN: Initial state</td>
<td>(b) DAN: Final state</td>
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<tr>
<td>(c) FAN: Initial state</td>
<td>(d) FAN: Final state</td>
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- DAN: Initial state
- DAN: Final state
- FAN: Initial state
- FAN: Final state

- **FAN:** best neurons had high \( r \)
- **DAN:** best neurons had low \( r \)

Summary: Pole Balancing

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

Discussion

- Can predictive traces be found in cortical/cerebellar dynamics? (cf. Harter; Kozma and Freeman; Principe; Werner; Voicu)
- Role of prediction in decision making? (cf. Levine; Wunsch)
- Nonlinear control with delay? (cf. Lewis)
- Facilitating (afferent) and nonfacilitating (associative) synapses in the olfactory system (cf. Gutierrez-Osuna)
- Predicted future state (and goal) as a moving target to be optimized against? (cf. Werbos)
- Use of delay in simulated agents to facilitate the evolution of predictive capabilities (cf. Miikkulainen)
- Differential role of prediction in differentiation-oriented vs. synthesis-oriented cultures (Perelovsky).

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 have outgrown built-in delay compensation mechanisms.
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!
- Such mechanisms may have evolved into predictive mechanisms providing access to estimated future states.

References


