Lecture 28. Vocal Learning in Songbirds

Dr. Jesse Goldberg

Pre lecture materials (you will be tested on this content)

None.

Supplemental Reading:

Gadagkar, V, Puzery, PA, Chen, R, Baird-Daniel, E, Farhang, AR, Goldberg, JH. 2016. Dopamine neurons encode performance error in singing birds. Science 354(6317):1278-1282.

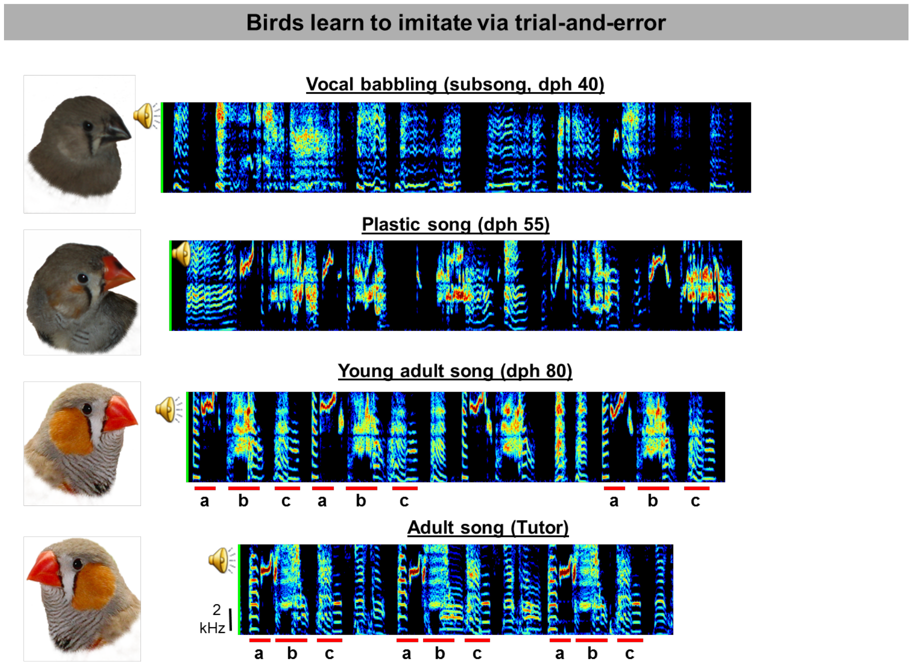
Learning Objectives

1. Explain how vocal learning can by implemented using similar neural mechanisms as reinforcement learning.
2. Explain why motor exploration (the 'trial' part of trial and error learning) might be actively driven by specific parts of cortex.
3. Explain what a 'synfire chain' is, and how it might drive stereotyped motor sequences such as speech or birdsong.
4. Provide evidence that dopamine can evaluate the quality of vocal performance (the 'error' part of learning).
5. Understand how *dopamine-modulated corticostriatal plasticity* can contribute to vocal learning, i.e. by linking context (time-step in the song sequence) to the right vocalization.

Lecture Outline

I. Birds learn to imitate a tutor song through a gradual process of trial and error

Baby birds babble as they gradually learn to imitate a tutor song
Birds deprived of auditory feedback (e.g. by deafening) cannot learn to sing
Adult song is a highly stereotyped vocal sequence



II. The song system is a basal ganglia thalamocortical loop

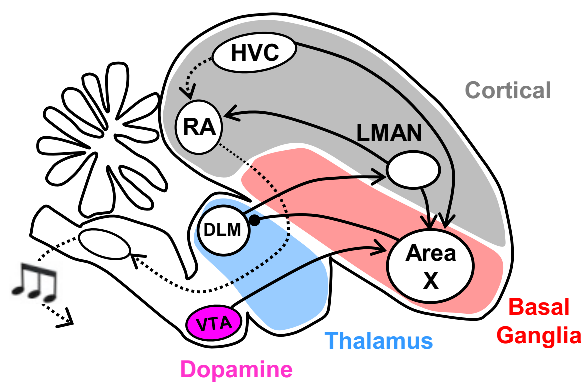
Specific motor cortical areas in songbirds have different functions

Variable firing in LMAN drives vocal variability and babbling

Synfire chains in HVC drive stereotyped / skilled vocal output in adults

HVC and LMAN converge on RA – which is like primary motor cortex.

The basal ganglia is required for vocal learning but not vocal production



III. Just as basal ganglia *link context to action* to implement reinforcement learning, the basal ganglia link time-step to vocalization to implement birdsong learning

Learning boils down to knowing *what* to do (the action) and *when* to do it (the situation or context). The striatum implements this learning by integrating three key signals: (1) Context, (2) Action and (3) Outcome.

(1) Context: Comes from corticostriatal inputs from HVC
The HVC synfire chain encodes what time-step it is in the song

(2) Action: Comes from corticostriatal inputs from LMAN

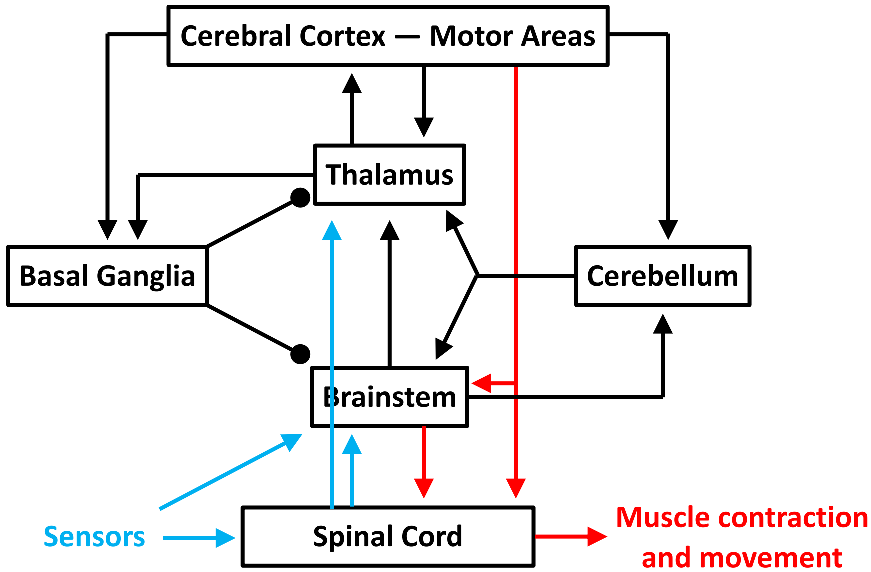
(3) Outcome: Dopamine evaluates performance quality (e.g. good or bad)

By integrating these three inputs, the medium spiny neurons in the striatum can implement the three-factor learning rule you learned about in Lecture 19 (DA-modulated corticostriatal plasticity) to learn what action to take at each time-step.

Study Questions

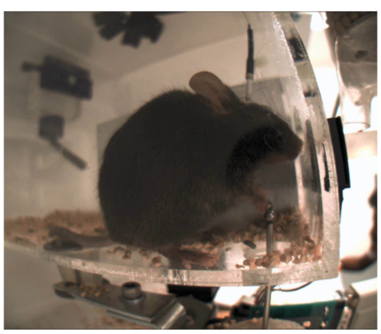
1. Design two experiments to test if reinforcement learning mechanisms can apply to a behavior like birdsong – one using neural recording and one using neural stimulation.
2. Design an experiment using optogenetic silencing to test if mammals have a part of their brain that actively drives trial-to-trial variability.

Your motor system is hierarchically organized



'Systems' neuroscience, a microcircuit-level understanding, and disease pathogenesis

Neural circuits for trial and error learning



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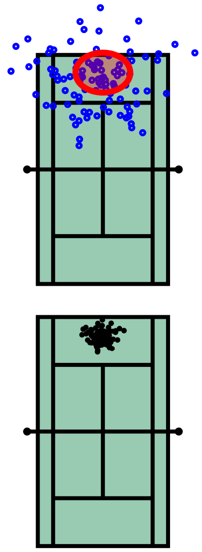
Neural circuits for trial and error learning



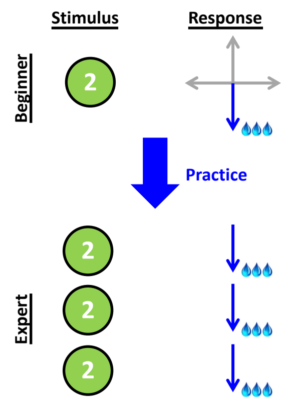
1. Generate variability
   (Trial)

2. Evaluate performance
   (Error)

Learned sequence

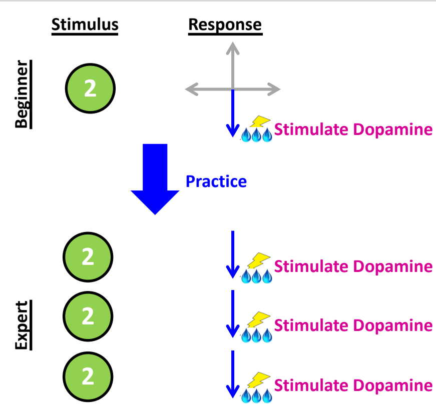
Animals learn things for primary rewards

Reinforcement learning: Link 'stimulus' to 'response' to maximize 'reward'



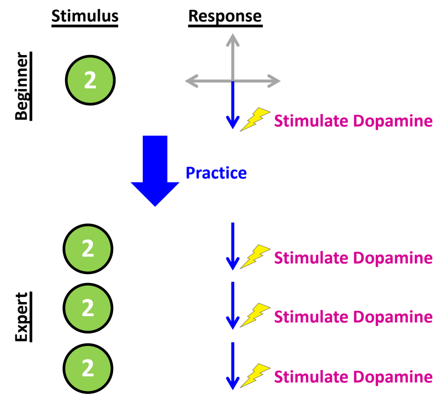
stimulus – response – reward

Reinforcement learning: Link 'stimulus' to 'response' to maximize 'reward'



stimulus – response – reward

Reinforcement learning: Link 'stimulus' to 'response' to maximize 'reward'



dopamine
stimulus – response – reward

(Olds and Millner, 1954; Redgrave, 1978; Reynolds et al, 2001; Tsai et al, 2009)

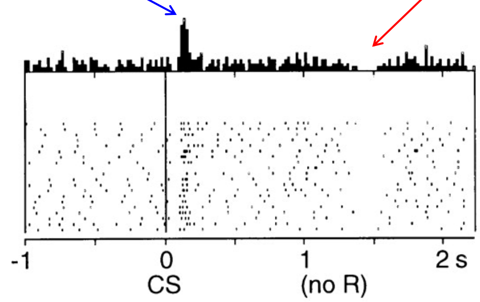
Dopamine stimulation can stand-in for reward as a reinforcer

Dopamine reinforces S-R associations by encoding 'reward prediction error'

REWARD PREDICTION ERROR = Actual reward – Predicted reward

Positive prediction error
(Surprisingly good)

Negative prediction error
(disappointingly bad)



Schultz et al, 1997

RPE signals are ideal for linking a stimulus to a rewarding action

Graybiel et al, 1994; Suri and Schultz, 2001;Daw et al, 2011; Doya, 1999; Glimcher, 2011;

Many natural behaviors lack primary rewards and external cues.

Desired (auditory) A really fast car

f ≠ c

- ERROR!

Inverse model

+ ERROR

Produced (motor) A really fast far

Dopamine signal

Recent history A reawy fast car

Do DA error signals and associated reinforcement learning principles apply?

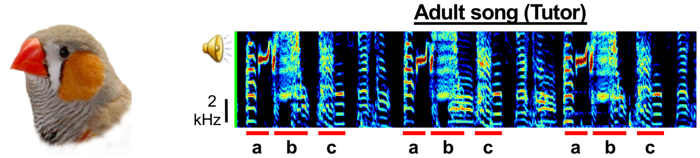
Outline

1. An introduction to the songbird as a model system for BG-dependent learning

2. Experimental methods and design: How to study brain function

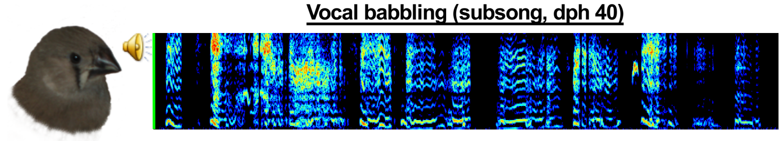
Birds learn to imitate their tutor through a gradual process of trial-and-error

Adult song (Tutor)

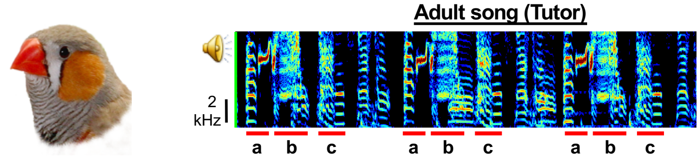


Birds learn to imitate their tutor through a gradual process of trial-and-error

Vocal babbling (subsong, dph 40)



Adult song (Tutor)



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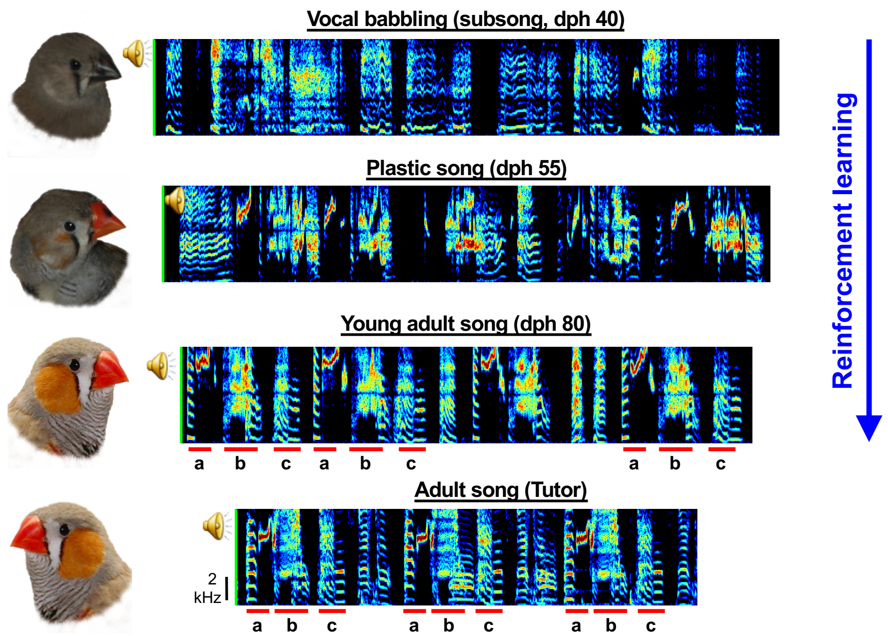

Dopamine reinforces behaviors by encoding 'reward prediction error'

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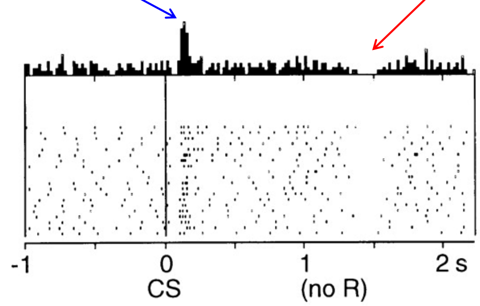
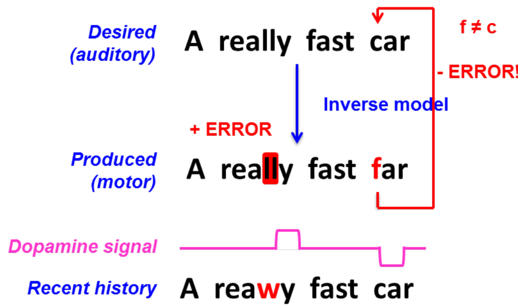
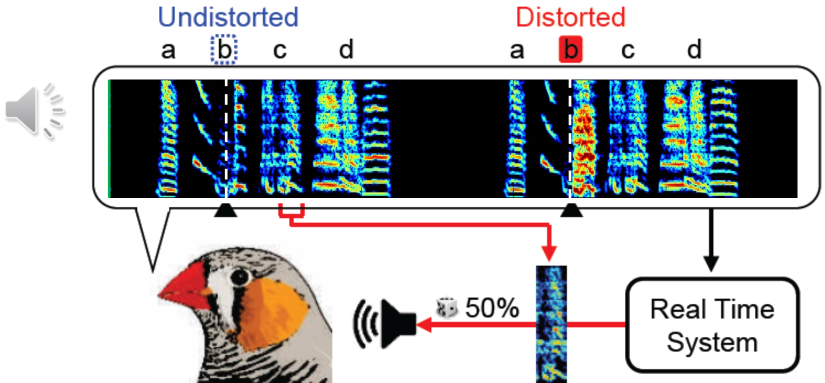


Schultz et al, 1997

Discussion: Design an experiment to test if dopaminergic error signals apply to internally evaluated behaviors like birdsong



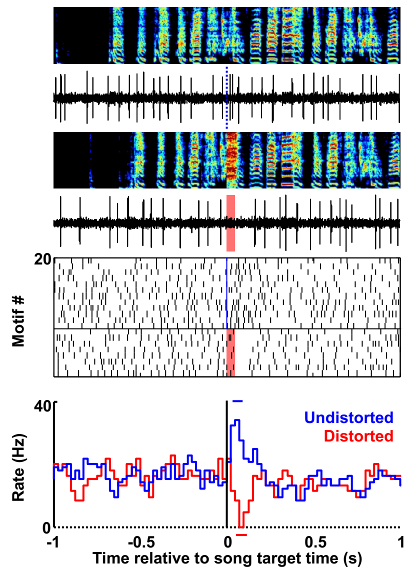
A method for controlling perceived song quality



Displaced syllable
distorted auditory feedback (DAF)

(Tumer and Brainard, 2007; Andalman and Fee, 2009; Ali et al, 2013 Canapoli et al, 2014; Hamaguchi et al, 2014)

Shown below is the activity of a dopamine neuron recorded during syllable-targeted distorted auditory feedback



Does this neuron support a role for dopamine error signals in birdsong learning?

(A) No, because it's lack of modulation by error indicates that cannot be evaluating song quality

(B) Yes, because dopamine can both burst (following distortion-errors, and pause following undistorted renditions.)

(C) Yes, dopamine pauses resemble a worse-than-predicted outcome following distortions.

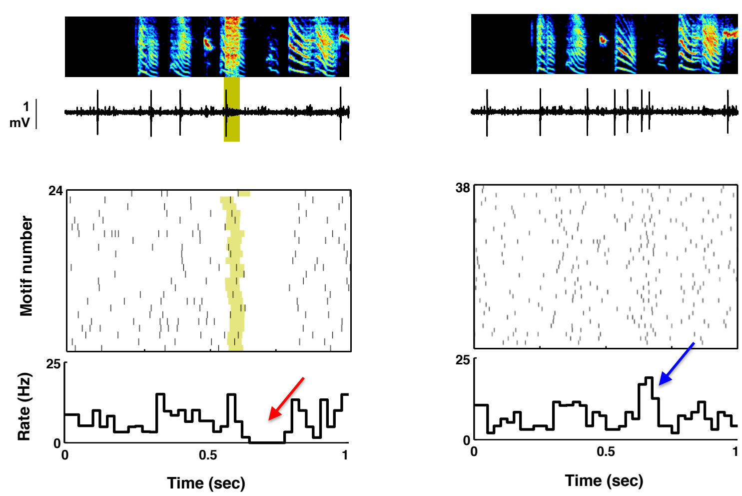
(D) Yes, dopamine bursts following undistorted renditions is consistent with a better than predicted outcome.

(E) C and D

Dopamine neuron recorded during song distortion

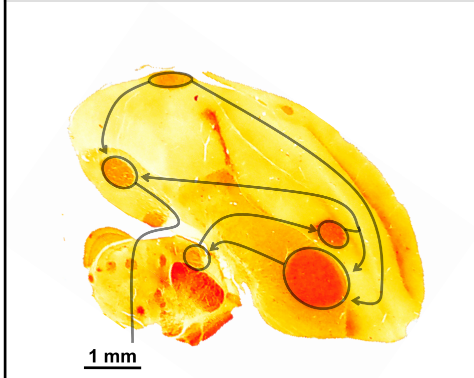
Distorted rendition

Undistorted rendition



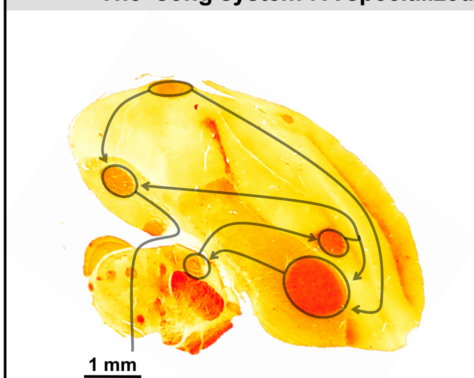
'Worse than expected' 'Better than expected'

The 'song system': A specialized neural circuit for singing behavior

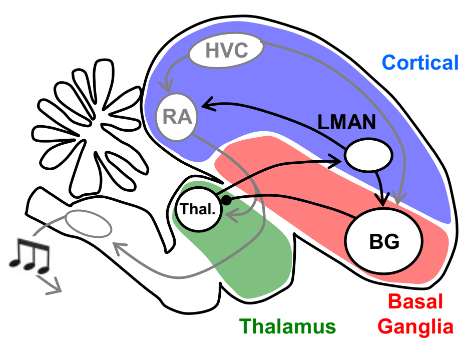


Nottebohm et al, 1976

The 'song system': A specialized neural circuit for singing behavior

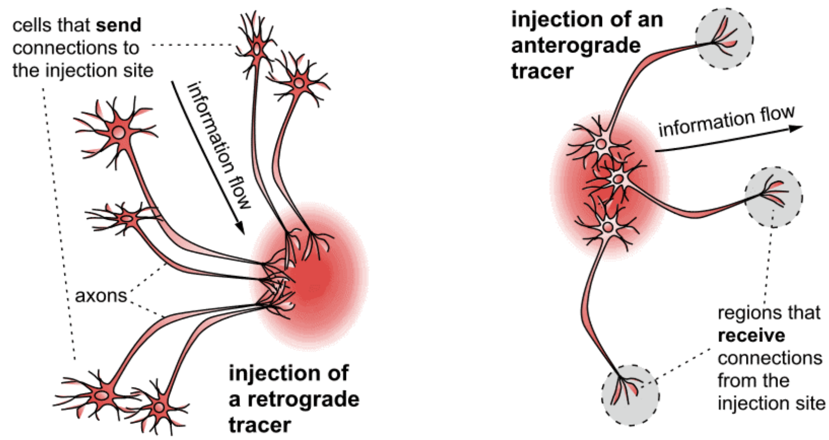


Nottebohm et al, 1976



Avian Brain Nomenclature Consortium, 2004

Neuronal tracers map connections between brain areas



Retrograde tracers label cell bodies in areas that project to site of tracer

Anterograde tracers label axon terminals in areas that receive projections from site of tracer

Graded Clicker question: You inject a fluorescent retrograde tracer in the Gpi. Where will you see labeled cell bodies?

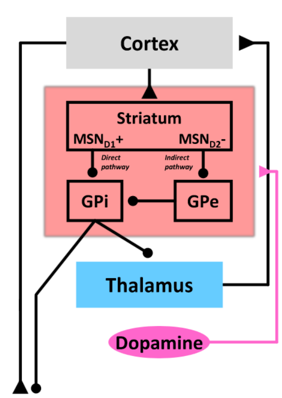
(A) Thalamus and brainstem

(B) Inferior Olive and Pontine nuclei

(C) Cortex and brainstem

(D) Only in the striatum

(E) Striatum and GPe



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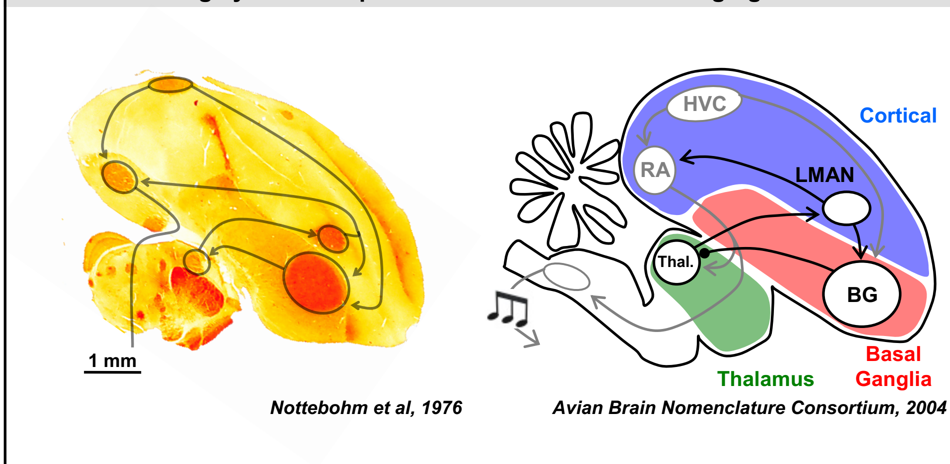
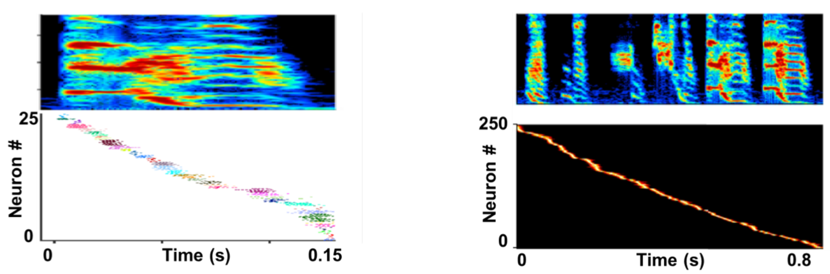


Nottebohm et al, 1976 *Avian Brain Nomenclature Consortium, 2004*

HVC neurons encode a 'synfire chain' that encodes precise song time-step



Hahnloser et al, (2002)
Long and Fee (2010)
Lynch et al,(2016)

A 'synfire chain' is a group of synaptically connected excitatory neurons that form a functional network resembling a chain of dominoes

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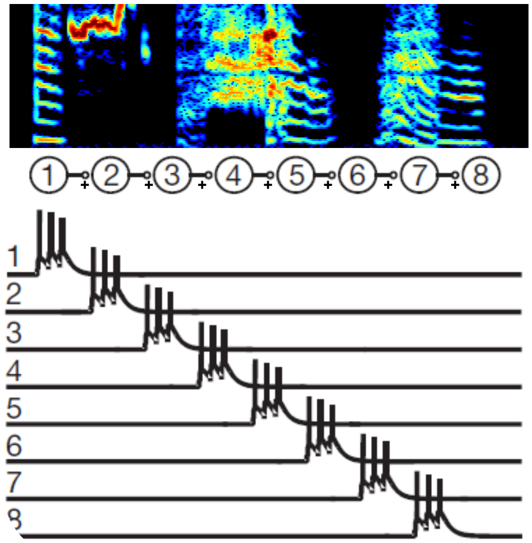


Each timestep of the song is discretely encoded by HVC
Learning the song is learning what action to take at each timestep (context)

Clicker: Which statement about organization of BG microcircuit is FALSE?

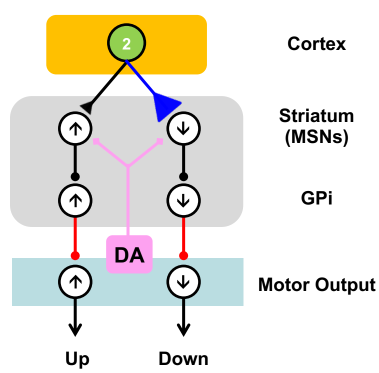
A) **The corticostriatal synaptic weight will make this animal to go down at #2.**

B) **Context inputs are not-topographically organized**

C) **Motor output channels are topographically organized**

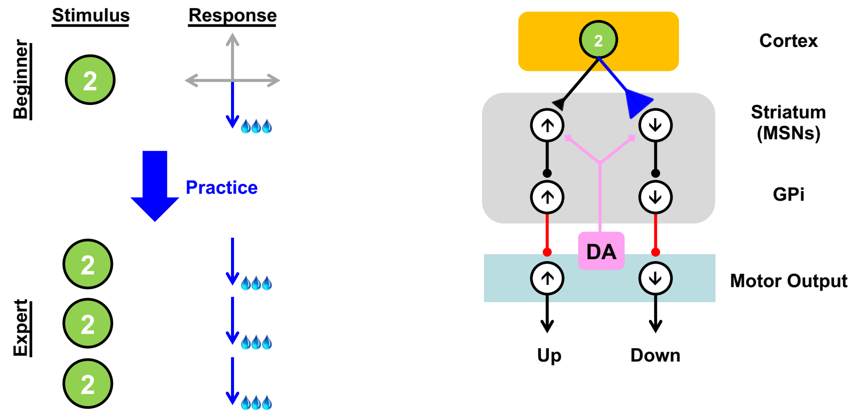
D) **Dopamine inputs are non-topographically organized**

E) **This schematic shows direct and indirect pathways through the BG**



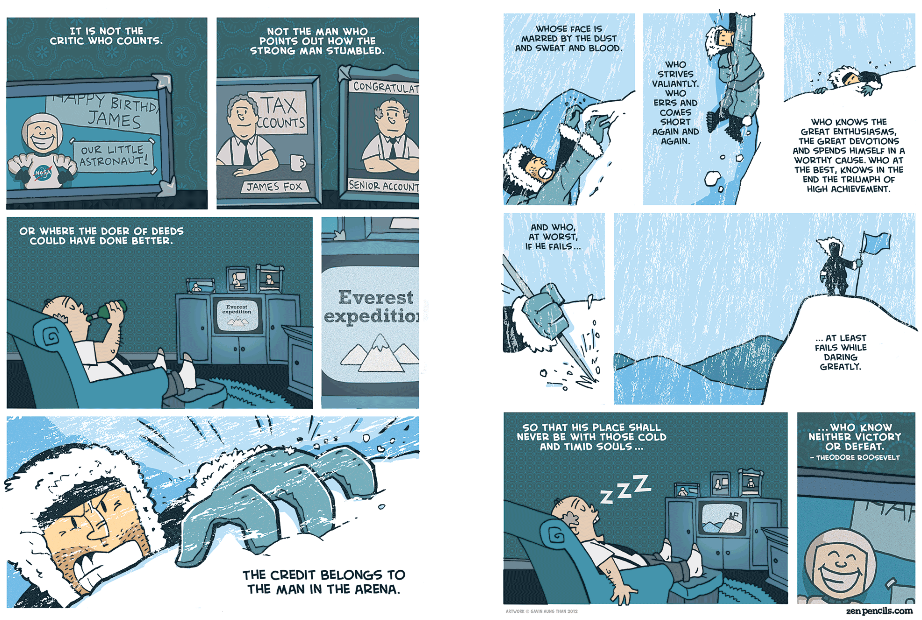
Three-factor learning rule implemented in the BG

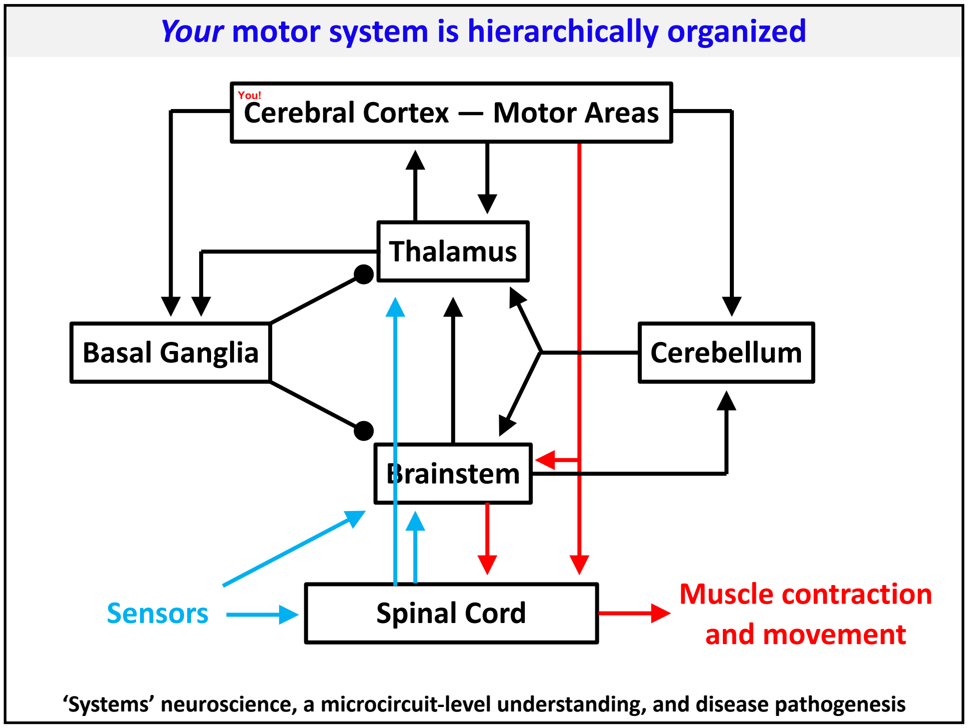
2 → ↓ → +Outcome



Dopamine-modulated corticostriatal plasticity links 'context' to 'action'

April 23, 1910, Theodore Roosevelt, "Citizenship in a Republic" (aka (wo)man in the Arena




Your motor system is hierarchically organized
You!
Cerebral Cortex — Motor Areas
Thalamus
Basal Ganglia
Cerebellum
Brainstem
Sensors
Spinal Cord
Muscle contraction
and movement
'Systems' neuroscience, a microcircuit-level understanding, and disease pathogenesis