10. Executive Function
Higher Level Cognition: What’s Missing

• Planning, problem solving, reasoning, complex decision-making
• What do all of these have in common?
• Top-down control of behavior: Instead of reacting in a bottom-up fashion to stimuli, behavior is driven (controlled) by an actively maintained representation of what we are supposed to be doing
• Allows us to behave in contextually appropriate fashion instead of just giving the strongest, most dominant response
• Also gives us the ability to link events across time points, and to carry out behaviors that are extended across time
Definition of Executive Function

• A process used to effortfully guide behavior towards a goal, especially in non-routine situations

• Multi-faceted, may include:
  — Inhibiting familiar/stereotyped behavior
  — Maintain an idea of which information is relevant right now
  — Resist distracting information
  — Switch between goals

• Definition from Banich (2009)
Very Relevant Example

• How do I get into grad school?
  — Figuring out what I am interested in
  — Working in a lab to learn about research
  — Contacting professors to get recommendations
  — Looking at schools
  — Sending applications & taking tests on time
  — Going to interviews (social skills, learning skills)
  — Making a decision about where to go
    ➢ Listing pros and cons
Why Do We Care?

- Clinical disorders involve impairments in executive function
- Depression:
  - Enhanced focus on negative stimuli
- Addiction
  - Enhanced focus on & behavior to seek out addictive substance
  - Poor top-down control/inhibition of drug-seeking response
- OCD
  - Habit pathway – prepotent responses to distressing stimuli must be overcome with cognitive control
- Put your favorite disorder here – chances are it involves EF deficits (see Snyder, 2016)
Phineas Gage (d. 1860)
Examples of Different EF Tasks

**Updating: Letter Memory Task** (Always Remember the Last 3 Letters)

- M
- K
- P
- T
- C
- R
- “M”
- “M, K”
- “M, K, P”
- “K, P, T”
- “P, T, C”
- “T, C, R”

**Shifting: Color-Shape Task** (Classify Each Target by Color [C] or by Shape [S])

- C
- C
- S
- S
- C
- S
- Red Circle
- Green Triangle
- Red Triangle
- Green Circle
- Repeat
- Switch
- Repeat
- Switch
- Switch

**Inhibition: Antisaccade Task** (Report the Arrow Direction Presented on the Nonflashed Side)

- +
- +
- +
- +
- Fixate the Cross
- Brief Flash (150 ms)
- Look for the Arrow on the Opposite Side (175 ms)
- Arrow Replaced by a Mask
- Arrow Replacement
Different Parts of EF

Friedman & Miyake (2012)
Prefrontal Cortex Across Species
Prefrontal Cortex Across Life

Does this development of prefrontal cortex link to impairments in decision making you may see with adolescents?
Who is in Charge of Your Brain?

Prefrontal Cortex?
Integrates:
• Cognitive Control
• Planning
• Motivation
• Reward processing
• Decision making
Baddeley/Hitch Model

- Influential account of working memory
- Phonological loop: hold information for a few seconds, maintain through rehearsal
- Central executive: switch & focus attention
- Visuospatial sketchpad: ongoing manipulation of visual/spatial items
Key Idea: Top-Down Biasing

PFC active maintenance provides top-down biasing of posterior-cortical processing
The Homunculus Problem
A. Biology of PFC/BG and Robust Active Maintenance

Mechanisms of “Working Memory”
It Takes a Network

Sensory Input

Motor Output

Posterior Cortex: I/O Mapping

PVLV: DA (Critic)

PFC: Context, Goals, etc

BG: Gating (Actor)

(modulation)

(gating)
What is the PFC maintaining?

- Miller (2000) — Monkey does several different tasks
- During the delay period, you see differences in activity depending on the task, meaning that the PFC encodes “task” rules
PFC Does Active Maintenance

D  Movement Neuron

B  Neuron with delay signal

C  Visual Neurons

E  Visuomovement Neuron

4/9/19

COSC 421/521

(slide < Mollick & O’Reilly)
Active maintenance can do it all

- Cognitive Control
  - Maintained activity drives top-down biasing
- Planning
  - Think about things that are not there (future)
- Motivation
  - Maintain goals
- Reward processing
  - Maintain possible outcomes
- Decision making
  - Maintain alternatives
The Need for Robust Maintenance

• “Every sound has to be an earthquake or tidal wave that topples governments and changes national boundaries and mutates whole species so they suddenly drift off the planet, across galaxies, only to return, years later, when nobody wants to know them cause their credit rating’s bad or because they can’t do the Mashed Potatoes.” — MFU by HC, 1998

• Subjective experience of PFC lesion: dreaming!
  — PFC is deactivated during sleep
Mechanisms of Sustained Active Firing

- Recurrent excitatory connectivity
  - corticocortical loop
  - corticothalamocortical loop
- Intrinsic excitatory maintenance currents
  - NMDA and metabotropic glutamate (mGluR) receptors
  - once opened by high frequency activity, provide longer window of increased excitability
Functional Specialization of PFC Areas

- **Lateral:** “cold” cognitive processing (sensory & motor areas)
  - Dorsal lateral PFC (DLPFC): executive control over motor planning & control
  - Ventral lateral PFC (VLPFC): control over temporal lobe pathways that identify entities and form semantic associations

- **Medial:** “hot” emotional & motivational processing (subcortical areas)
  - Dorsal medial PFC (DMPFC): encodes affective aspects of motor control variables
  - Ventral medial PFC (VMPFC) including orbital frontal cortex (OFC): encodes affective value of sensory stimuli
Medial Frontal Map of Values

This is your emotional life
Orbital Frontal Cortex (OFC)

- OFC abstracts the mores of one’s culture
  - abstracts “rules” (regularities) of social interaction
  - prior to moral reasoning (reflection comes later)
  - similar to brain’s abstraction of language regularities
    - both are regularities in our social interactions
- OFC guides behavior in accord with cultural mores
  - following mores activates endogenous reward system (and vice versa)
  - emotional judgements of morality
  - OFC and related limbic areas are especially active in moral personal dilemmas
Patient “Eliot”

- Patient of Antonio Damasio (*Descartes’ Error*)
- Damage to both PFC (cf. Phineas Gage)
  - they both became obsessive collectors
- Eliot lost *feelings* (capacity to experience emotions)
  - remembered them & understood them intellectually
  - could not make rational decisions
  - could do the analysis
  - could not weigh options and make a choice
- Emotions are an essential foundation for rational behavior
Substructure of PFC Areas

- PFC organized into stripes (= macrocolumns, hypercolumns)
- Stripes are organized into clusters of about 10
- Four clusters in monkey PFC
- ~20 000 stripes in human FC
PFC Stripe Cluster

- **Microcolumn:**
  - ≈50 pyramidal cells
  - ≈50 microns across
  - correspond to rate-coded model neurons

- **Stripe:**
  - ≈100 microcolumns
  - 5 × 20 microcolumns
  - 0.25 × 1 mm²

- Hypothesis: individual stripes updated by loops through BG

- Lower figure (B) shows two stripe clusters
BG Model Extension to Working Memory and Attention

• In the motor domain, the BG selectively facilitates one command while suppressing others (Mink, 1996)

• In parallel circuits, the BG may reinforce the updating of PFC working memory representations (Alexander et al, 1986; Frank, Loughry & O’Reilly, 2001)

• Dopamine (DA) in PFC supports robust maintenance over time (Lewis & O’Donnell, 2000; Durstewitz & Seemans, 2002)

• Phasic DA bursts thought to occur for task-relevant (“positive”) information, reinforcing BG updating signals (O’Reilly & Frank, 2006; Frank & O’Reilly, 2006)

• Time course of DA activity: maintenance in PFC, updating thru BG
(A) Default state, no BG activity or NoGo firing: PFC continues to maintain information in active state. SNr or GPi exhibits tonic activity, inhibits neurons in thalamus, shutting down thalamocortical loop.

(B) Go firing triggers updating of PFC stripe to encode new information by inhibiting SNr/GPi neurons, opening up thalamocortical loop, resulting in activity in PFC that drives updating to new pattern of firing, including intrinsic maintenance currents to sustain new pattern.
Phasic DA & Temporal Credit Assignment

• How does PFC active maintenance system learn what to maintain?
• Initially dopamine (DA) neurons respond to primary rewards
• Later respond to conditioned stimulus (CS) to predict rewards
• Maintenance of useful information in PFC acts as CS, predicting reward
• Phasic DA signal at CS onset drives learning of BG Go neurons that update new information into PFC active maintenance
B. The PBWM Computational Model

Prefrontal Cortex Basal Ganglia Working Memory
Motor Gating ⇒ Cognitive Gating

Motor

Cortex
- SMA

Striatum
- Putamen

Thalamus
- VL

Oculomotor

Cortex
- FEF

Striatum
- Caudate

Thalamus
- VA/MD

Prefrontal

Cortex
- DLPFC, PPC

Striatum
- Caudate

Thalamus
- VA/MD

Orbitofrontal

Cortex
- OFC

Striatum
- Caudate

Thalamus
- VA/MD

Cingulate

Cortex
- ACC

Striatum
- V. Striat.

Thalamus
- MD

Note: Partial diagram of cerebral cortex and possible responses.
Chain of Command

![Diagram showing the chain of command with nodes labeled Cortex, Striatum, Thalamus, SMA, ACC, DLPFC, OFC, DS, MVS, DMS, VS, VL, MD, VA/MD, and arrows connecting them to represent the flow of actions, utilities, plans, and goals.](slide < Mollick & O’Reilly)
PBWM Model

Sensory Input

Motor Output

Posterior Cortex: I/O Mapping

PVLV: DA (Critic)

PFC_{mnt}

PFC_{out} (gating)

BG_{mnt}

BG_{out} (modulation)
BG Gates Flow: Superficial → Deep PFC

- Maintenance via thalamocortical loops, BG disinhibits
- Superficial reflects inputs and maintenance
- Separate Maintenance vs. Output PFC / BG stripes
Details: Maintenance vs. Output

A - Maintenance, pre-Output

B - Output gating

SNr/GPi  Action outputs  SNr/GPi  Action outputs
Trace-based Learning

- System uses trial and error exploration of different gating strategies in the BG
  - DA reinforces strategies associated with positive reward
  - DA punishes those that are not
- Synaptic-tag-based trace mechanism
  - reinforces/punishes all prior gating actions leading to DA outcome
- When a matrix unit in BG fires for a gated action
  - synapses with active input establish a synaptic tag
  - which persists until subsequent phasic DA outcome signal
- Synaptic tags based on actin fiber networks in the synapse
  - can persist for up to 90 minutes
  - when subsequent strong learning event occurs, tagged synapses are also strongly potentiated
Parallel Stripes for Selective Gating

- PFC/BG loops form independent stripes = selective gating
- Different gating strategies to be explored in parallel
- Multiple stripes are critical when more than one piece of information has to be maintained and updated
Multiple Stripes: Competition

Competition in striatum/GP between Maint vs. Output and different stripes
C. Top-down Control
Stroop Task: Top Down Biasing

RED
Stroop Task: Top Down Biasing

GREEN
Stroop Task: Top Down Biasing

RED
Stroop Task: Top Down Biasing

GREEN
Conditions

- **Control**: no color unit active
- **Conflict**: color of word inconsistent with meaning
- **Congruent**: color of word consistent with meaning
Asymmetric Conflict

Stroop Data (Dunbar & MacLeod, 84)

Reaction Time (msec)

Control  Conflict  Congruent

Condition

4/9/19

COSC 421/521

(From slide < Mollick & O’Reilly)
Possible explanation: **differential pathway strength**:

- Two pathways: word reading and color naming
- These **compete** to generate response
- Word reading pathway is much stronger than color naming
- When word identity information doesn’t match color, it **interferes strongly** with color naming
- Because color pathway is relatively weak, incongruent color information does not interfere with word reading
Stroop Effect: GREEN

- **Puzzle**: If the color naming pathway is weaker than word reading, how do we manage to name color of the word “green” above?

- **Solution**: Prefrontal cortex actively maintains a representation of the task that you are supposed to be doing (color naming or word reading)

- This actively maintained task representation biases processing in posterior cortex by activating units in the appropriate pathway

- e.g., color naming task representation in PFC sends activation to the units in color naming pathway
Model of the Stroop Task

FIG. 2. Architecture of the present model.
Stroop emergent Model
Effects of Frontal Damage

- Assess importance of prefrontal (PFC) task units in the model
- Weakened connection strength $\Rightarrow$ much slower in conflict color naming condition
- Same pattern of data observed in frontal and schizophrenic patient populations
- PFC task units are important for controlled-processing necessary to overcome prepotent word reading response
- However, other manipulations could cause this same pattern of behavior without specifically affecting PFC
SOA Timing Data

- SOA = stimulus onset asynchrony
  - in word reading: time by which color precedes (–) or follows (+) word
  - in color naming: time by which word precedes (–) or follow (+) color

- Word reading is relatively impervious to color conditions

- Elimination of interference effect of words on color naming when color precedes word by long time

- Model duplicates these effects except:
  - processing is slowed across all conditions as the two inputs get closer to being presented simultaneously
  - increasingly large interference effect for earlier word SOA's on color naming in the model, but not in people
Simulated SOA Timing Data

Stroop SOA (Glaser & Glaser, 82)
emergent Demonstration: stroop
Development of PFC Active Memory Strength

• Piaget’s A-not-B task:
  — toy hidden several time in location A
  — toy hidden in different location B
  — child looks for toy in location A

• Captured by “A Not B” model
  — development modeled by increasing strength of reverberant excitatory connections among PFC neurons
  — improves active maintenance, so “older” networks can hold onto information for longer period of time
“A Not B” Model

• Inputs:
  • Location: 3 possible
  • Cover: 2 cover types
  • Toy: 2 toy types
  • Hidden: represents PFC

• Outputs:
  • Gaze: updated continuously
  • Reach: has to wait
Trials

1. **start**: covers sit in place on apparatus, before experimenter draws infant’s attention to particular location
   — weak equal activation on locations and cover inputs

2. **toy presentation** (toy-pres): experimenter draws infant’s attention to and places it into one location
   — one location more strongly active, and toy T1 active

3. **lid presentation** (lid-pres): experimenter further draws infant’s attention to the location while placing lid over the toy location
   — toy fading out in activation while cover is more active, and location less active

4. **delay**: the apparatus sits with all covers in place
   — equal weak location and toy activation

5. **choice**: experimenter makes apparatus accessible (with covers in place) for infant’s response (reaching is possible/permitted only during this segment)
   — inputs more active than delay but same pattern; reach layer is disinhibited
emergent Demonstration: A Not B
Dynamic Updating of PFC Active Memory: The SIR Model

• SIR (Store, Ignore, Recall) task. Example sequence:
  — S - A — this means that the network should store the A stimulus for later recall — network responds A
  — I - C — ignore the C stimulus, but you still have to respond to it — network responds C
  — I - B — ignore the B stimulus — network responds B
  — R — recall the most recently stored stimulus — network responds A
• BG has to learn:
  — to fire Go to drive updating of PFC on store trials
  — to fire NoGo to ignore stimuli, so don’t overwrite previously information
  — on recall trials, output BG gating mechanism should drive output of stored information
• Network starts out knowing nothing about semantics of various inputs
SIR Model
emergent Demonstration: SIR
D. Hierarchical Control

Subtasks, Goals, Cognitive Sequencing
Hierarchical Control Over Action

- Consider situations:
  - where there are multiple potential rule sets signifying which actions to select in particular sensory states, and
  - where appropriate rule set might depend on a higher level context (a “task set”)

- Hierarchical PFC-BG networks can simultaneously:
  - learn to create these PFC task-sets
  - learn which actions to select in each task-set

- Learned PFC representations are abstract and independent of contexts that cue them, facilitating transfer
Hierarchical Action Selection Across Multiple Prefrontal Basal Ganglia Loops

- At most anterior level, PFC represents contextual information gated by corresponding BG loop based on probability that maintaining this context is predictive of reward.
- Middle loop involves input and output gating:
  - Input gating allows stimulus representations S to update PFC_maint layer.
  - Output gating gates out subset of maintained information conditional on context in anterior PFC.
- Left-most motor loop learns to gate simple motor responses based on reward probabilities conditional on the stimulus; here relevant stimulus features are selected by more anterior loops.
Summary of Hierarchical Control

• Higher (more anterior) levels of PFC
  — encode context/goals/plans to organize a sequence of cognitive actions
    ➢ driven by more lower, more posterior PFC areas
  — do not specify rigid sequences of actions, but rather encode desired outcome states of a sequence of actions
  — provide context so appropriate lower-level steps will be selected

• Each step in a sequence of actions involves a consideration of the reward outcomes and effort costs of the action relative to other possible options
Affective Influences over Executive Function

- PFC and executive function (EF) integrate:
  - emotional and motivational influences
  - high-level cognitive control and planning

- Medial and ventral regions of PFC are particularly important for processing emotional and motivational factors
  - ventral medial areas including OFC: important for encoding the affective value of stimuli,
  - dorsal medial areas (esp. anterior cingulate cortex (ACC)): important for encoding affective value of motor actions and plans
Summary of Key Points

• PFC encodes information in active state through sustained firing (more flexible and rapidly updatable than synaptic changes)

• BG drives updating (dynamic gating) of PFC active memory states, enhancing flexibility

• Phasic DA signals from midbrain nuclei can train BG gating, by transferring reward associations earlier in time to onset of stimuli that predict subsequent rewards

• The PFC influences cognitive processing elsewhere via top-down excitatory biasing (e.g., Stroop model)

• Developmental changes in active memory can be explained in terms of stronger PFC active maintenance abilities (e.g., A-not-B model)

• BG dynamic gating can support flexible cognitive function by dynamically encoding some information while ignoring other irrelevant information, and updating the contents of active memory (e.g., SIR and n-back models)

• Medial and ventral areas of PFC (OFC and ACC) convey affective information about stimuli and actions, respectively, and are important for properly evaluating potential actions to be taken (decision making, problem solving, etc.)
Other Executive Functions

• Highly structured cognitive activities, often involving formal symbol systems
  — mental activities like learning and/or using mathematics, formal logic, computer programming, creative and/or non-fiction writing, and structured, rational decision-making
  — require temporally-extended maintenance of task-relevant information, especially of highly abstract, symbolic nature.
  — important role of language in these and many other executive functions

• Control over encoding and retrieval of episodic information in HC
  — HC and PFC/BG systems interact significantly in many forms of EF
  — rapid learning abilities of the hippocampus complement transient, flexible active maintenance properties of PFC
Symbolic AI

- “Good Old Fashioned AI” (GOFAI) tried to start with executive function, working from top down, like a computer program
- Unfortunately, the symbolic foundation is weak and brittle
  — few factors involved
- Subsymbolic neural representation and processing provides a more robust and flexible foundation on which to build higher cognitive processes
Higher Level Cognition: What’s Missing

- Planning
- Reasoning
- Decision-making
- Emotion
- Consciousness, sense of self
- Free will
- Social interaction
Supplementary:
Dynamic Field Theory Approach to EF

Dimensional Change Card Sort (DCCS) Task
Architecture of DCCS Model & Mapping to Brain

To make a decision in the context of the DCCS, then, the model must bind the features presented on the test cards to a left or right location in the task space. In this case, EF processes involve the application of rules under conditions in which bottom-up information is insufficient. That is, a given test card could be sorted to different locations depending on whether it is being sorted by shape or color. This requires some form of top-down biasing that can be recruited from trial to trial. This presents a real challenge to any theory of EF: How are rules represented, and how can top-down goals resolve competition among different representations of rules?

To simulate performance in the DCCS task, we use autonomous resting level modulation of neural populations tuned to shape or color information to get "rule-like" decisions from the model. Autonomous resting level modulation is grounded in a dimensional attention system composed of a set of nodes that encode either a shape or color dimension (see bottom left of Figure 13.3). These nodes are self-excitatory and bistable with mutual inhibition (see arrows in Figure 13.3). As with the dynamics operating within fields, self-excitation allows the nodes to achieve stabilized suprathreshold activation. Mutual inhibition, on the other hand, creates suppression of one node when the other is activated, creating a winner-take-all type of interaction. This allows for the selective activation of a single dimensional representation. Finally, each node has learned reciprocal connections with the shape and color WM fields which serves as the basis for resting level modulation. Conceptually, these connections are established through associating labels for "shape" and "color" with neural populations tuned to the metric properties of those dimensions. Thus, these nodes receive input when activation accumulates near threshold in the shape or color WM field. When a dimensional node gains suprathreshold activation, it projects global activation, that is, a boost in the resting-level to the shape or color WM fields based on the strength of the connection weight between the dimensional node and the feature WM fields. By selectively activating a dimensional node, then, the processing of information within the associated dimension becomes enhanced, serving as a form of dimensional attention.

A final component of the model is a memory trace mechanism (see Chapter 2). As the model builds peaks in the WM fields, memory traces are laid down that boost the level of activation corresponding to where features were sorted. Further, as the model activates the shape or color nodes and attends to these dimensions, the baseline level of activation of these nodes becomes boosted, which can lead to perseverative errors in certain circumstances. As will be illustrated in the examples presented here, the influence of these memory traces depends on the developmental state of the model and the relationship between the memory traces and the target inputs during the post-switch phase.
“Old” and “Young” DCCS Models

FIGURE 13.4: “Old” and “young” DCCS models during the pre- and post-switch phases. In this example, color is the pre-switch dimension and shape is the post-switch dimension. The top panel shows the activation of the shape and color nodes over the course of six pre- and six post-switch trials. The bottom panel shows the activation of the shape and color nodes over the course of these trials for the old model. Note the larger activation of the relevant node and stronger suppression of the irrelevant node. The middle panel shows a series of “snapshots” of the object WM model at key points during the simulation. Panel (a) shows the object WM model before the first pre-switch trial. At this point the model has a pattern of subthreshold inputs corresponding to the target cards and trays. Panel (b) shows the fields just after a red circle test card is presented. In panel (c) the model has bound the features to the rightward sorting location, making a decision to sort the red circle to the right. Panel (d) shows the model during the intertrial interval with the memory traces acquired from the first trial. The black ovals highlight the locations of the target card inputs and the white circles highlight the locations of the memory traces. The target input and memory traces for the circle feature conflict with one another, while these sources of activation overlap and cooperate for the red feature. Panel (e) shows the presentation of a blue-star test card on the third pre-switch trial. Panel (f) shows the binding of features and decision to sort the test card to the left. Panel (g) shows the model just before the start of the post-switch phase. Now there is conflict for both features in the post-switch shape field and cooperation for both features in the color field. Panel (h) shows the presentation of a red-circle test card on the first post-switch trial. Panel (i) shows the fields corresponding to the young model. Here the model perseverates and sorts the test card by color even though it was instructed to sort by shape. Panel (j) shows the fields corresponding to the old model during the critical post-switch trial. Now it correctly sorts the red circle by shape due to the stronger influence from dimensional attention system.
Simulation and Behavioral Data Across Variations of DCCS Task

There are various manipulations to the DCCS task that have been conducted with 3- and 5-year-olds that have revealed a complex pattern of results. Can the same model with the same parameters generalize to capture these results as well? Previous research has isolated the influences of memory traces across different feature fields and has shown that 3-year-olds still perseverate even when only one influence (cooperation with the pre-switch field or competition within the post-switch field) is present. For example, in a Negative-Priming (NP) version, the features that were relevant for the pre-switch phase are changed for the post-switch phase (see Figure 13.7b). For example, if children sorted red and blue stars and circles by color during the pre-switch phase, then they would be told to sort green and yellow stars and circles by shape during the post-switch phase. In this situation, 3-year-olds still perseverate (Müller, Dick, Gela, Overton, & Zelazo, 2006; Zelazo et al., 2003). This is particularly interesting because children are not told anything about green or yellow cards, yet they spontaneously sort by those features. Conversely, in the Partial Change version, the features for the dimension that is to be relevant for the post-switch phase are changed before the rule switch (see Figure 13.7c). For example, if children sorted red and blue stars and circles by color...