Mechanisms of executive control in the mind and brain

Todd Braver

Cognitive Control and Psychopathology Lab,

Washington University

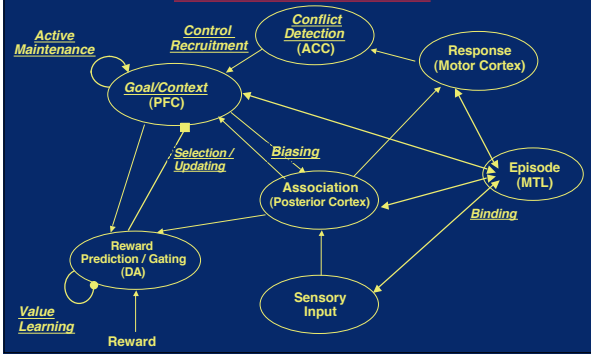
The Problem with Executive Control

- On the one hand….
  - Clearly central to understanding human cognitive sophistication and flexibility
    - What we mean when we talk about intelligent, goal-driven behavior
  - Obviously important for understanding cognitive deficits in schizophrenia
    - And many other neuropsychiatric disorders as well (interesting side issue is how to distinguish these)
- On the other hand….
  - Huge challenge for scientific understanding: the insidious "homunculus" problem
    - Our intuitions get in the way of developing coherent theories
  - Even terminology (" central executive") suggests a monolithic function or process
    - But, the best chance for progress is to "deconstruct" the homunculus
  - Also, executive control processes involved in most tasks
    - But, sits outside of task processing (domain-general vs. task-embedded)

Specifying Executive Functions & Mechanisms

- One influential taxonomy (Jonides & Smith, Science 1999):
  - Attention & Inhibition
  - Task-Management
  - Planning
  - Monitoring
  - Temporal Coding
- This is a good starting list
  - Potentially distinct functions that need to be accomplished by executive control system
- But…
  - It is not a list of mechanisms
- A mechanism:
  - specifies the computation or transformation that enables accomplishment of a function or process
  - may not map in a one-to-one way to function
  - for cognitive neuroscientists, will be more closely linked to neurobiology & neurophysiology
- What would a brain-based specification of mechanisms look like?

One view of executive mechanisms



Talk Approach

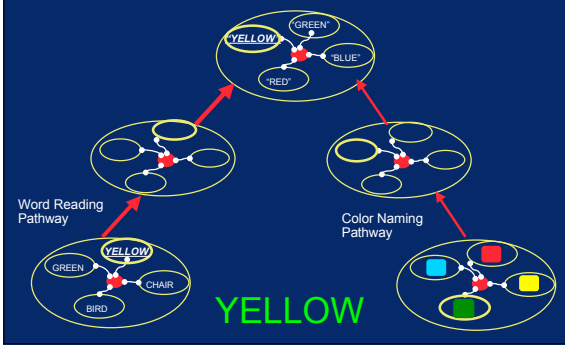
- **Start with well-known neuropsychological tasks for examining executive functions**
  - **Stroop:** Attention & Inhibition
  - **Wisconsin Card Sort (WCST):** Task-Management (Switching)
  - **Tower of London:** Planning
- **Apply cognitive neuroscience approach**
  - Process analysis / Task deconstruction
  - Formulation of potential mechanisms and neural substrates

The Stroop Task

YELLOW

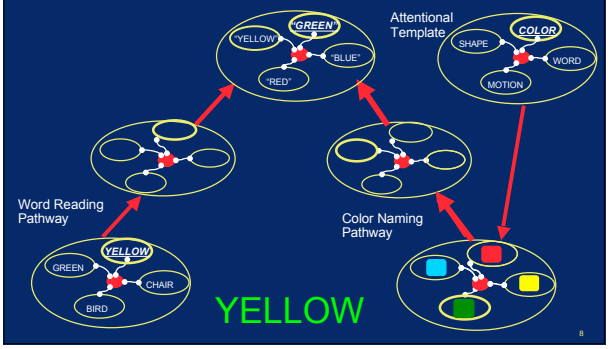
- **Task requires both selective attention & inhibition**
  - High Stroop interference taken as an index of inhibitory impairment
  - But does the task actually demand a specialized executive mechanism of inhibition?
- **A cognitive neuroscience framework**
  - Biased competition (Desimone & Duncan, Ann Rev Neuro, 1995)

Biased Competition: No selective attention



YELLOW

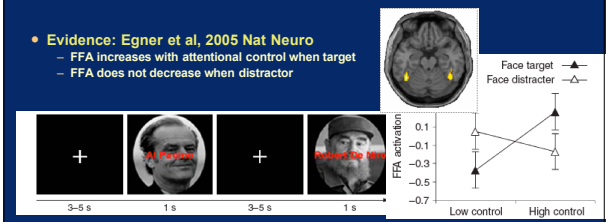
Biased Competition: With selective attention



YELLOW

Biased Competition: Attention vs. Inhibition

- **Biased competition framework**
  - Inhibitory mechanism might be a local and ubiquitous component of cortical processing
  - Top-down selective attentional biases alters outcome of local competitive interactions
    - Can produce indirect inhibitory effects even though mechanism is excitatory
  - Interference control can occur without dedicated executive inhibitory mechanism
- **Evidence: Egner et al, 2005 Nat Neuro**
  - FFA increases with attentional control when target
  - FFA does not decrease when distractor



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But what about inhibition?

- **Seems like a prototypical executive control mechanism**
  - Invoked for many tasks: Stroop, Eriksen flanker, Simon, go-nogo, stop-signal, anti-saccade, etc.
  - Impairments generally observed in schizophrenia
- **Not great evidence for unitary construct**
  - Behavioral correlation data (Kramer et al., 1994; Keys et al., 2006, others)
  - Imaging data: Wide variety of PFC regions engaged (e.g,. ventral/orbital, dorsal, superior)
- **But yet…**
  - Some suggestion that the right ventrolateral PFC might be preferentially involved in inhibition (e.g., Aron et al., 2004 TICS)
  - At least for motor inhibition tasks: go-nogo, stop-signal

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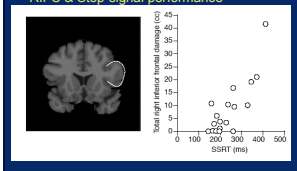
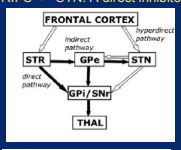
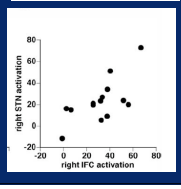
Right ventrolateral PFC (RIFC)

RIFC & Stop-signal performance



RIFC -> STN: A direct inhibitory route?





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- **Of course…**
  - Motor inhibition deficits are not that prominent in schizophrenia (Chambers et al., 2006; Badcock et al., 2002)

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Back to the Stroop

Interference (inhibitory) control is needed here

YELLOW

GREEN

But it is not needed here

In fact, it is maladaptive to filter out word information if all (most) trials are congruent

A mechanism seems required:
- detect and adapt to the presence/absence of interference

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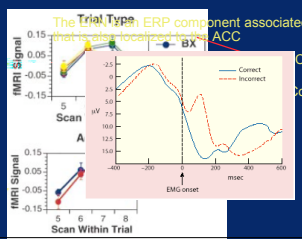
⇤Conflict (interference) detection and the Anterior Cingulate Cortex (ACC)

- **Conflict monitoring theory** (Carter et al., Science 1998)
  - The ACC detects the presence of decision-level conflict or interference
  - The ACC also responds to presence of errors (ERN literature)
  - Errors are just a special case of high conflict



The [illegible] ERP component associated with errors that [illegible] localizes to the ACC

Conflict

Conflict

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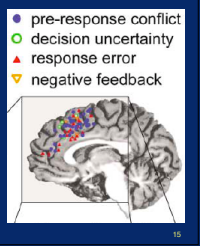
⇤Performance monitoring and the Anterior Cingulate Cortex (ACC)

- **Basic findings have been replicated many times**
  - Dorsal ACC is reliably engaged when errors are committed
    - Additional effects may be related to error awareness (e.g., Pe component)
  - Dorsal ACC is reliably engaged across a range of conflict tasks (Stroop, Eriksen, Simon, go-nogo, etc)
- **Functions may be a bit more broadly described**
  - Decision-level uncertainty (Barch et al., 2000)
  - Negative feedback (Holroyd et al., 2004)
  - Error expectation (Brown & Braver, 2005)

Dorsal ACC may be generically involved in monitoring on-going performance to detect when poorer than desired



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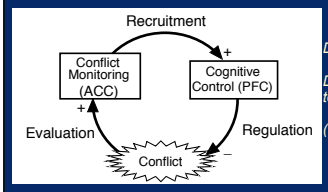
⇤Performance monitoring and the Feedback Control Loop

- **What is the point of performance monitoring in the ACC?**
  - To provide signals that indicate when control processes need to be adjusted
  - Control state needs to adapt to environmental demands & contingencies
    - Low interference = low control (unbiased attention)
    - High interference = high control (focused attention)



Dorsal ACC & PFC form a feedback loop

Dynamically adjusts control in response to experienced conflict

(Botvinick et al., 2001 Psych Review)

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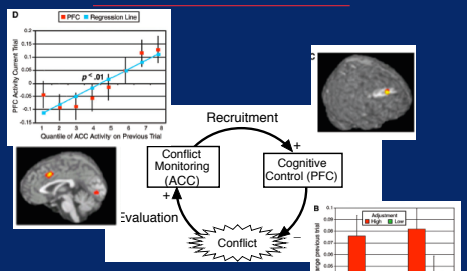
ACC-PFC feedback loop (Kerns et al., 2003)



Recruitment

Conflict Monitoring (ACC)

+

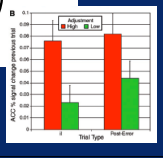
Cognitive Control (PFC)

+

Evaluation

Conflict

−



ACC activity increases following conflict (incongruent) or error trials

Increased PFC activity and decreased interference on subsequent trial

Summary: Attention & Inhibition

- **Primary mechanisms in interference tasks such as Stroop**
  - Biased competition: Top-down focus + local inhibition
    - Focus may come from lateral PFC
    - Don't need top-down inhibition: but maybe from RIFC in some domains
  - Performance Monitoring: ACC
  - Dynamic Control Adjustment: ACC-PFC Feedback Loop
- **Also, should mention**
  - These systems are richly innervated by DA
  - Also, may be important NE component
    - ACC-LC connections

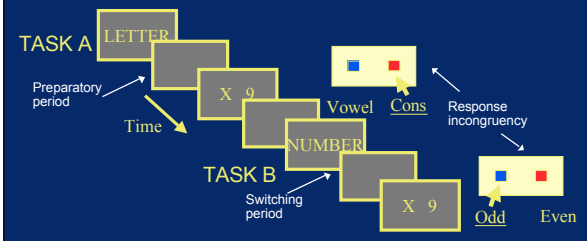
The Wisconsin Card Sort Test (WCST)

- **Task requires formation, maintenance, and shifting of "task-set"**
- **Task deconstruction: Similar to Stroop**
  - Performance monitoring: Detection of negative feedback
  - Attentional biasing: Focus on task-relevant dimension
  - Feedback loop: Performance monitoring leads to attentional adjustments
- **The critical difference**
  - Attention shifting (updating) to new dimension
    - In Stroop same dimension always relevant
  - Forming new set based on search + positive feedback
    - A hard problem -- won't discuss further

Set-Shifting

- **Are there important distinctions between shifting attention to:**
  - different features within a dimension
  - different dimensions
  - different tasks
- **Some positive evidence: ID/ED task (Owen et al,1991; Dias et al., 1997)**
  - Neurochemical dissociations: ED - Norepinephrine, ID - Dopamine
  - Cortical vs. subcortical dissociations: ED - lateral PFC; ID - ? (basal ganglia)
  - Intra-dimensional shifting engages parietal cortex; extradimensional shifting engages ventral PFC (Hampshire & Owen, 2006)
- **Some negative evidence: Meta-analysis of shifting tasks (Wager et al., 2004)**
  - Overlapping brain areas engaged by different types of shifting
  - Superior parietal cortex is reliably engaged
- **Switching studies in cognitive psychology & cognitive neuroscience**
  - Typically focused on switching between tasks

Standard Experimental Paradigm: Cued Task-Switching

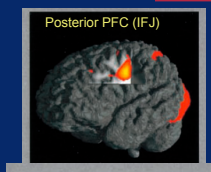


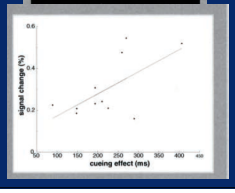
- **This paradigm enables examination of:**
  - Task switching effects (task switch vs. task repeat trials or single task trials)
  - Preparatory effects on task-switching (manipulation of preparatory period)
  - Other subtle effects (response congruency, cue vs. target repetition priming

Unresolved issues in task-switching

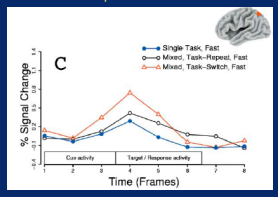
- **Some surprising findings: Behavioral**
  - Task-set updating may not be occurring in a preparatory fashion (Allport et al., 1994; Schneider & Logan, 2005)
  - Task-set preparation may be probabilistic and intermittent (De Jong et al., 1999; Reynolds et al., 2006)
- **Some surprising findings: Imaging**
  - May not be any switch-specific effects in preparatory brain activity (Brass et al., 2002; Ruge et al., 2005)
  - Task-cueing may involve preparation of S-R mappings rather than preparation of attention (Brass et al., 2003; Ruge & Braver, in press)
- **What does seem reliable:**
  - Parietal cortex is selectively engaged on task-switch trials, but maybe not in a preparatory fashion
  - Posterior PFC (inferior frontal junction) is reliably engaged by preparatory task-cues, but maybe not switch specific

Task-switching findings





Superior Parietal Cortex

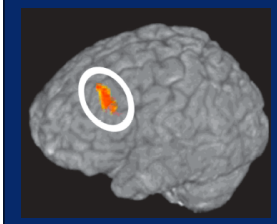


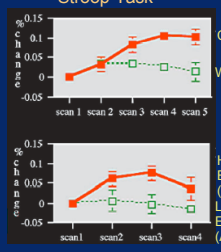
Task representations: The role of lateral PFC

- **Lateral PFC regions (dorsolateral, ventrolateral, anterior)**
  - Typically engaged in WM tasks
  - Typically engaged in attentional tasks
  - Typically engaged in task-cuing situations
- **But…**
  - Most often modality-specific (c.f. Ed Smith talk)
  - Sometimes transient rather than sustained activity in WM and preparatory situations (e.g., Rowe & Passingham)
  - Primarily engaged by difficult WM / attentional tasks
    - Interference, Manipulation, Distraction (e.g., Rowe & Passingham)
- **An account: Goal maintenance** (Miller & Cohen, 2001; Engle - many papers)
  - Lateral PFC representations encode task goals / rules, intended outcomes
  - May be primarily engaged when interference expectancy is high
  - Can be flexibly utilized in transient vs. sustained manner
    - Proactive vs. Reactive control (DMC model; Braver et al., 2007)

DLPFC Activity

Stroop Task





Color Naming

Word Reading

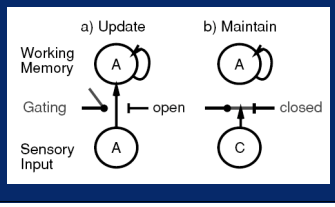
High Conflict Expectancy (B-Cues)

Low Conflict Expectancy (A-Cues)

AX-CPT

Updating: Computational Mechanisms

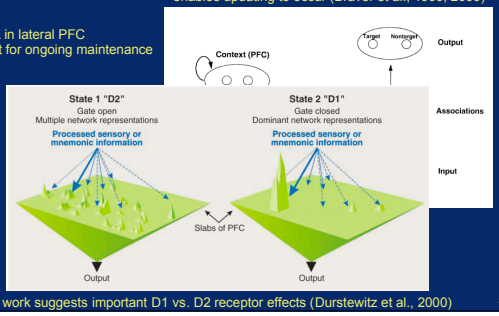
- **Task-set (Goal / WM) maintenance may involve gating mechanism**
  - **Protects maintained information from afferent input**
  - **Enables robust maintenance in the face of distraction**
- **Updating (of task-set / goals / WM) may require "opening the gate"**
  - **What serves as the gating mechanism?**
  - **Two different accounts have been proposed…**



DA-PFC Gating

Phasic dopamine (DA) activity in lateral PFC serves as gating signal
- enables updating to occur (Braver et al., 1999, 2000)

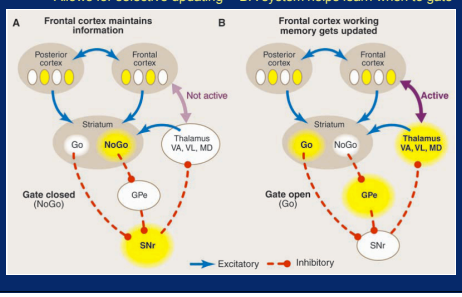
Tonic DA in lateral PFC
Important for ongoing maintenance



More recent work suggests important D1 vs. D2 receptor effects (Durstewitz et al., 2000)

BG-PFC Gating

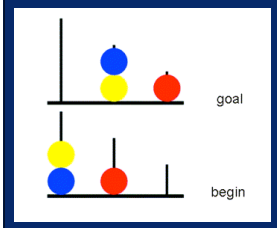
Basal ganglia (BG) disinhibition of thalamus can also serve as gating signal
Allows for selective updating -- DA system helps learn when to gate



Summary: Task Management

- Basic mechanisms in set-shifting tasks such as WCST
  - May be similar to interference tasks such as Stroop:
    - Performance monitoring, biased competition, dynamic control adjustment
- Specialized mechanisms for task-set updating
  - Parietal cortex may be important: Still not good accounts of mechanism
    - Re-mapping of S-R associations?
  - Gating mechanisms: Maintenance vs. Updating
    - Tonic vs. Phasic DA
    - BG - PFC: Selective updating (learning through DA)
- Task-set / Goal representations
  - Lateral PFC representations related to storage of task goals
  - KEY POINT: These representations are probably not simple WM buffers! (cf. Ed Smith)
  - May be dynamically flexible: sustained vs. transient
  - Potential dissociations:
    - Posterior PFC: Preparation of S-R associations
    - DLPFC: Preparation for interference

The Tower of London Task



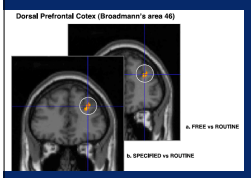
- Task requires planning & problem-solving
- Task deconstruction
  - Generate possible actions
  - Generate subgoals
  - Select action which best matches subgoal
  - Integrate (chain) subgoals together
- Similar to other task situations
  - Free selection tasks: Generate actions + select
  - Verbal fluency tasks: Select action which best matches goal (or subgoal)

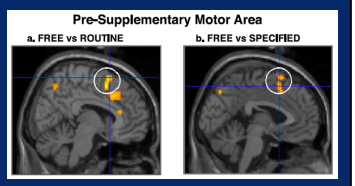
Free Selection Tasks

- Very reliably engage both DLPFC and MFC (ACC / pre-SMA)
  - Random number generation
  - Motor selection
  - Verbal fluency
- May be one of the core deficits in schizophrenia
  - "Willed action" (Frith)
  - Volition, Goal-driven initation of actions
- But is this a single process?
  - Generation of potential actions
  - Selection according to goal-based (attentional) criteria
- Evidence for a double dissociation….

Free Selection Tasks

- Potential dissociation (Lau et al., 2004)
  - MFC: Involved with response generation component (when response is FREE)
  - DLPFC: Involved with goal-based response selection component (when response is SPECIFIED)

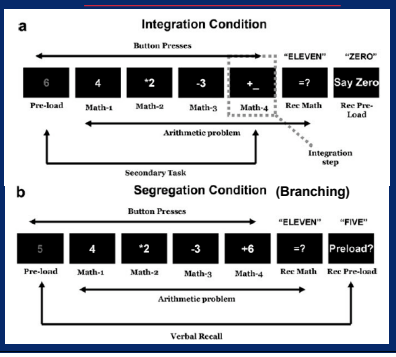




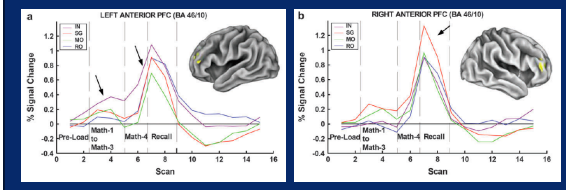
Goal-Subgoal Coordination

- **Prominent in many high-level cognitive tasks**
  - Problem-solving (e.g., Ravens task: Intelligence test)
  - Reasoning (e.g., analogies, logic)
  - Planning
- **Neuroimaging studies in these domains reliably engage anterior PFC (aPFC) regions** (Christoff & Gabrieli, 2000; Ramnani & Owen, 2004)
- **Is there a core process that engages aPFC?**
- **Possibilities from cognitive neuroscience**
  - Cognitive branching, Integration, Coordination
  - Main idea: Maintenance of primary task goal information (outer loop) while carrying out subgoal processes (inner loop)
  - Can these ideas be distinguished?

Integration vs. Branching (De Pisapia et al, 2006)



APFC Activity



Left aPFC selectively engaged by integration

Preparation for integration, rather than integration computation per se

Right aPFC selectively engaged in branching condition

Resumption of primary task after subgoal is completed

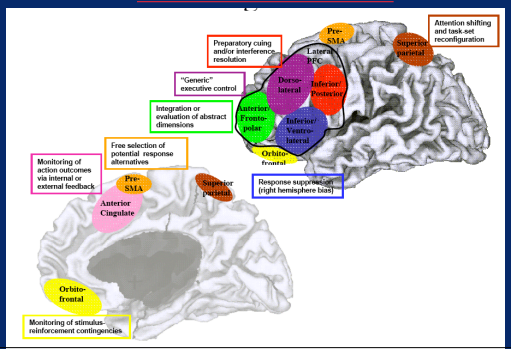
(But, this pattern has not replicated in a follow-up study)

Summary: Planning

- **Planning might be composed of separable subprocesses**
  - Response generation: Volitional component
  - Goal-based response selection
  - Goal-subgoal integration and coordination
- **Generation vs. Selection**
  - MFC might be the generation component: Volitional
  - DLPFC might be more involved with selection
    - Shifts emphasis away from DLPFC in volition
- **Anterior PFC**
  - Could be critical for goal-subgoal integration: A core component of many higher cognitive tasks
  - Potential candidate mechanisms: Branching, Preparation for integration

Neuroimaging of executive functions: A summary

(Braver & Ruge, 2006)



Conclusion: Evaluating constructs

- These mechanisms are most likely impaired in schizophrenia (IMHO!)
  - Biased competition effects
  - Conflict-control feedback loop
  - Goal maintenance
- But the story is complex…
  - Biased competition: Top-down attention vs. local competition (or both)
  - Conflict-control loop: Deficit in ACC vs. PFC component?
  - Goal maintenance: Is it really a maintenance or updating problem?
    - Sustained vs. transient activation dynamics
- Other interesting candidates that should get more study
  - Volitional response generation (MFC)
  - Interference expectancy (DLPFC)
  - Integration demands (aPFC)
  - Maybe: motor inhibition (RIFC - STN circuit)