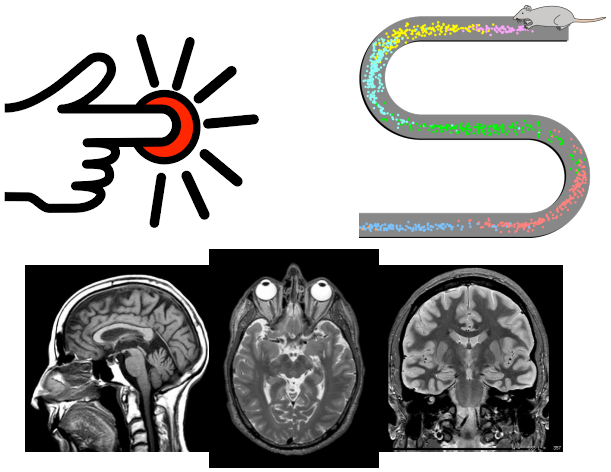
Experimental Methods & Working Memory



Outline

Types of Experimental Evidence

Working memory

Outline

How do we study Learning and Memory?

Historical traditions
- Birth of experimental psychology
- Behaviorism
- Cognitive revolution

Types of experimental evidence
- Behavior
- Neuropsychology
- Neurophysiology

Neuroanatomy primer

Neurophysiology

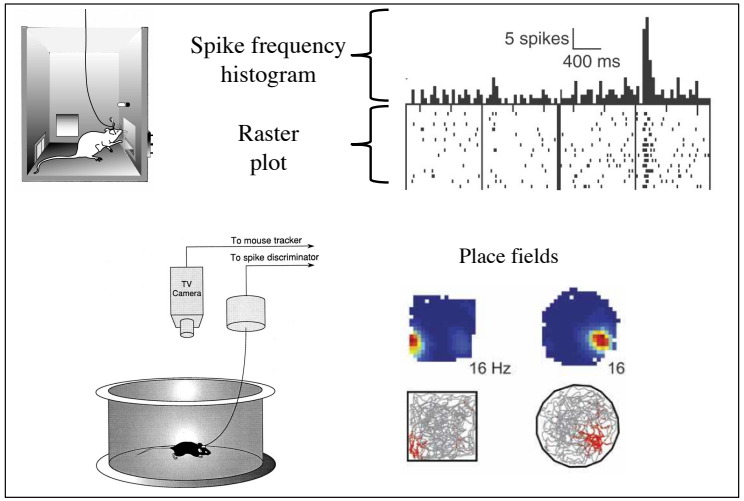
Non-human animal studies
- Direct recordings of neural activity

Human studies
- Neuroimaging
- Direct recordings of neural activity

Direct Recordings using Implanted Electrodes

(Neurophysiological data / Unit recordings)

– "The workhorse of neuroscience"



Direct Recordings using Implanted Electrodes

(Neurophysiological data / Unit recordings)

- Pros

  Direct recordings from neurons allow for excellent spatial and temporal resolution

- Cons

  Can't tell you about causation, only correlation

  Limited coverage of the brain

  Can be difficult to translate animal findings to humans

Neuroimaging in Humans

Two types of brain imaging:

1) Structural imaging
   - Images the structure/composition of tissue
   - e.g., MRI; diffusion tensor imaging (DTI)

2) Functional imaging
   - Images brain function
   - e.g., functional MRI

Functional Neuroimaging

Electrophysiological

- Measure electrical or magnetic signals related to neural activity
  - Electroencephalography (EEG)
  - Magnetoencephalography (MEG)
- Better temporal resolution; worse spatial resolution

Hemodynamic

- Measure changes in blood flow, oxygenation, or metabolism correlated with neural activity
  - Positron emission tomography (PET)
  - fMRI
- Worse temporal resolution; better spatial resolution

Functional Neuroimaging

Both electrophysiological and hemodynamic techniques are *relative*

Brain is always active

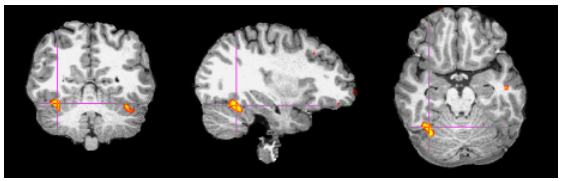
To measure the brain's response to stimuli, need to compare two conditions (subtraction technique)

Condition 2 – Condition 1 = difference image

Neuroimaging "Subtractive" Logic

What regions are used for perceive faces?

Experimental condition Baseline condition

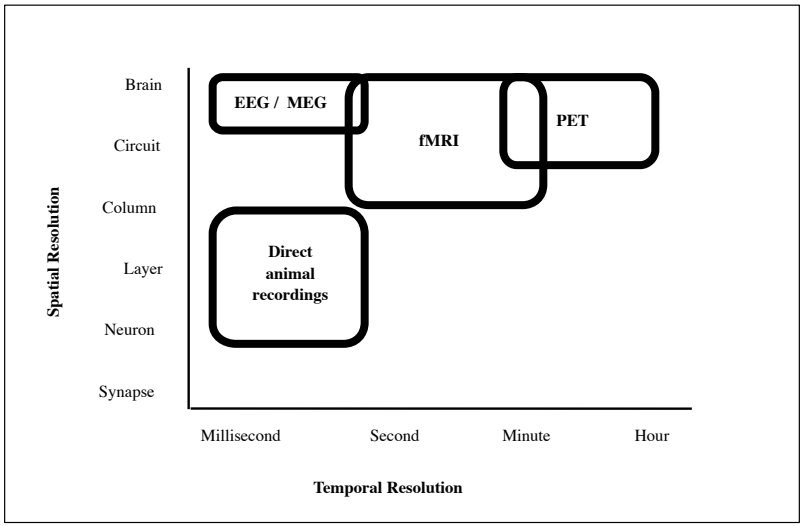


Difference image: experimental condition – baseline condition

Functional Neuroimaging

- Pros
  - Non-invasive technique for measuring brain function in humans
  - Can evaluate function across multiple regions simultaneously
- Cons
  - Can't tell you about causation, only correlation
  - Relative to direct animal recordings, relatively poor spatial resolution

Neurophysiology Summary



Outline

How do we study Learning and Memory?

Historical traditions
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Types of experimental evidence
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- Neuropsychology
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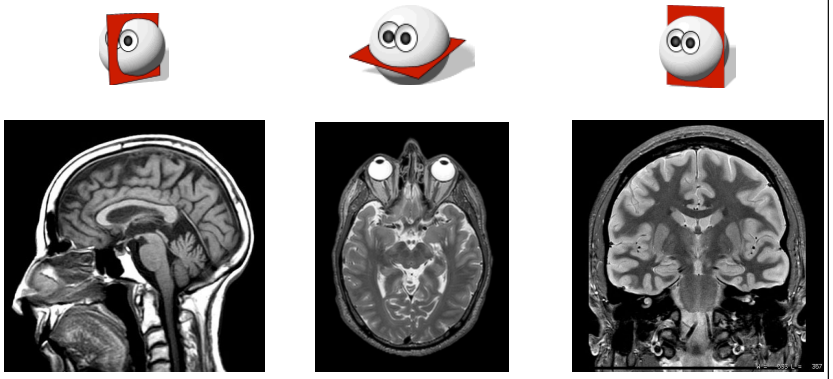
- Neuroanatomy primer

Brain Sections

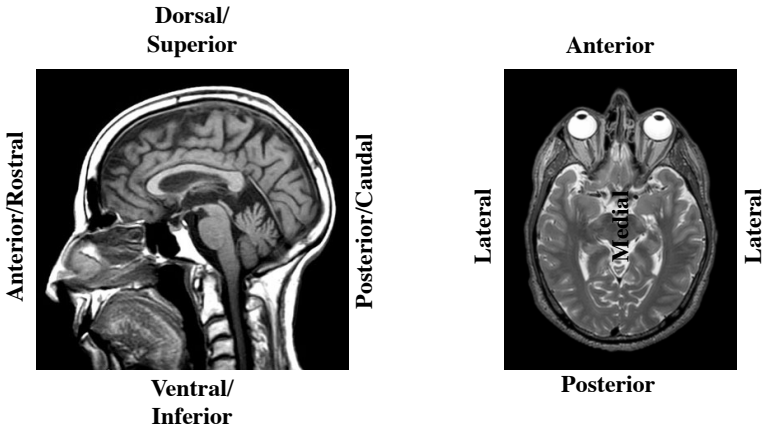


Sagittal
(Brain from the side)

Horizontal / Axial
(Brain from above)

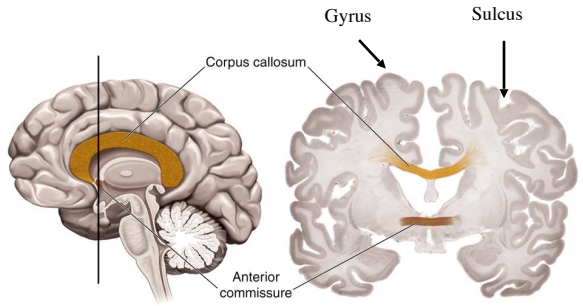
Coronal
(Brain from the front)

Directional Terminology

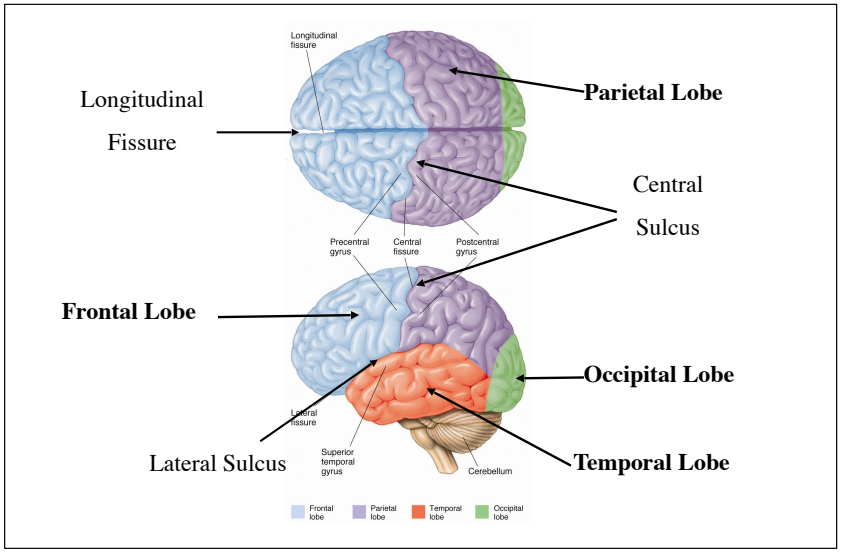


Cerebral Cortex

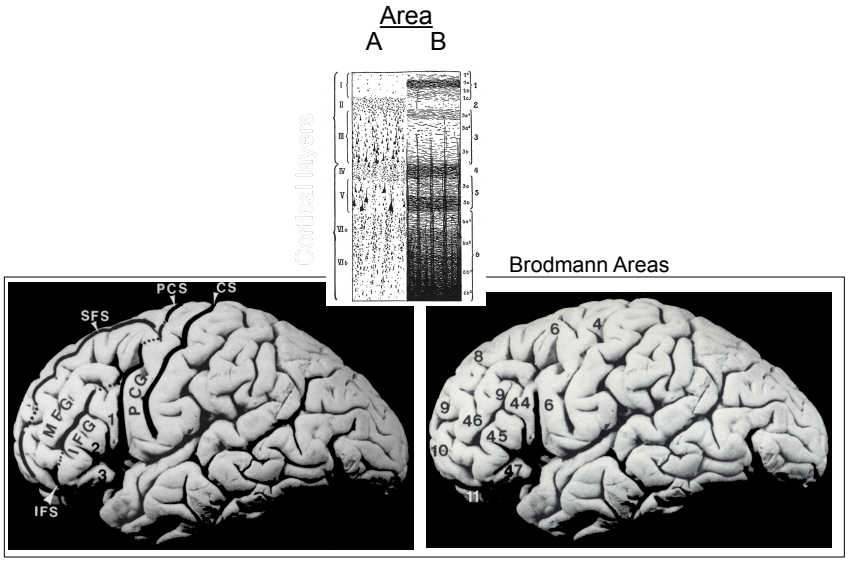
- Cortex ("bark"): outermost layer of the brain
- Deeply folded structure



Cerebral Cortex

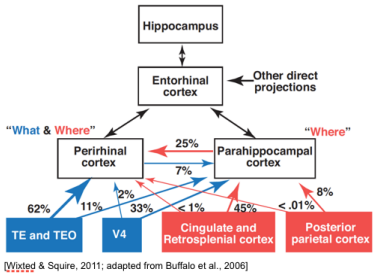


Anatomical Areas and Cytoarchitecture



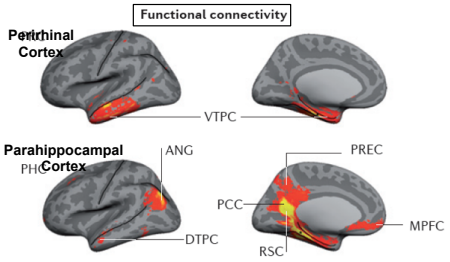
Anatomical Areas and Connectivity

Structural Connectivity



[Wixted & Squire, 2011; adapted from Buffalo et al., 2006]

Functional Connectivity



[Ranganath & Ritchey, 2012]

Outline – Working Memory

What is Working Memory (WM)?

Why is WM important?

Capacity limits of WM

Contrasting WM and LTM

Forms of WM

Neurobiology of WM

Outline – Working Memory

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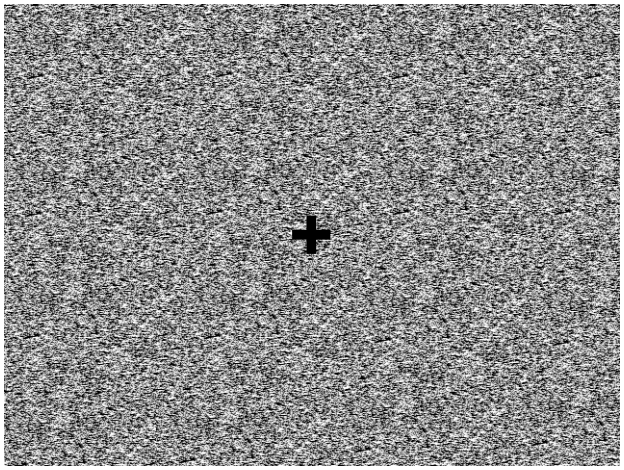
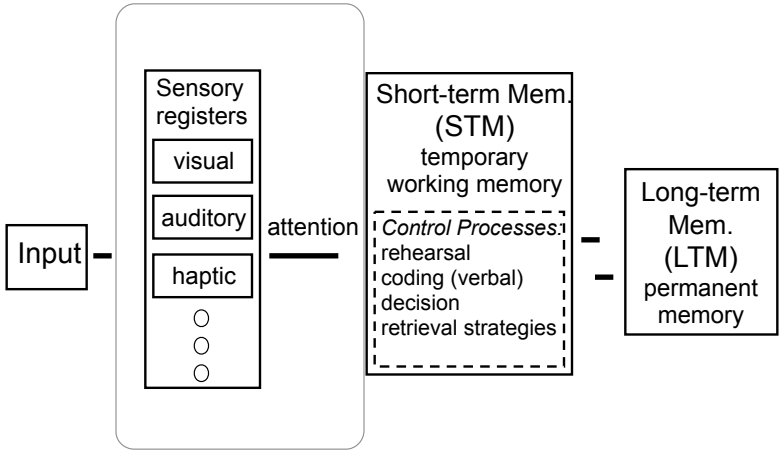
The Beginning of Memories
What is Registered?



"Modal Model" of Memory



Atkinson & Shiffrin (1968)

Sensory Memory

How does information from the outside world get registered in memory?

sensory systems convert sensory energy (photons, sound waves, etc) into neural representations

information must be represented in sensory systems long enough so that we can identify (perceive) what is being sensed and create a more stable internal representation

– sensory systems support brief 'sensory memories'
– fleeting representations of stimuli just experienced

Visual Sensory Memory: 'Iconic Memory'

X	M	R	J
C	N	K	P
V	F	L	B

after brief presentation (e.g., 50 msec), participants immediately report what they saw

typically can report ~4 items

subjective perception of visual after-effect

subjective perception that after-effect fades before it can be reported

capacity does not depend on # of items in display or their spatial arrangement

How Much Information is in Iconic Memory? Sperling's (1960) Partial Report Procedure

X	M	R	J
C	N	K	P
V	F	L	B

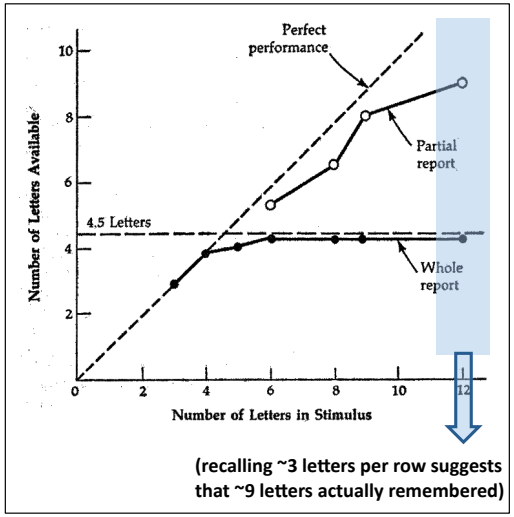
50 msec

e.g. 200 msec delay

tone cues which row to report

allows subject to shift attention to the cued sensory information

How Much Information is in Iconic Memory? Sperling's (1960) Partial Report Procedure



(recalling ~3 letters per row suggests that ~9 letters actually remembered)

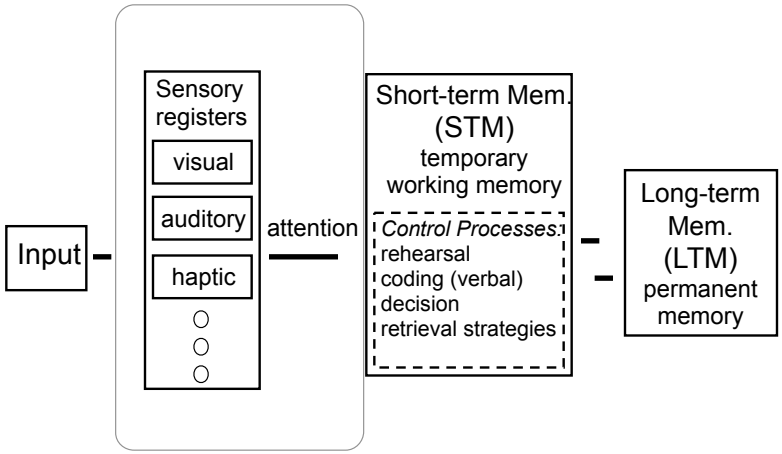
capacity: visual sensory memory seemingly contains all presented visual input

can report attended items that are converted to a more stable internal representation

information-processing / attentional capacity is limited

attentional cue needs to appear within 500-1000 msec to have an effect; sensory memory is fleeting

"Modal Model" of Memory



Atkinson & Shiffrin (1968)

Short-term vs. Long-term Memory

William James
(1890/1905)

- ***primary memory:*** **"the specious present", refers to this moment in time**

  "never lost, its date was never cut off in consciousness from that of the immediately present moment. In fact, it comes to us as belonging to the rearward portion of the present space of time, and not to the genuine past."

- ***secondary memory:*** **"memory proper"; long-term memories**

James and Hebb

James (1890): postulated two forms of memory

- Primary memory
  - The immediate contents of consciousness / information about which you are currently aware
  - Effortlessly available but fleeting
  - Limited capacity
- Secondary memory
  - Memories of the past
  - Permanent but available with effort
  - Unlimited capacity

Hebb (1949): proposed distinction between STM & LTM mechanisms

- STM: relies upon temporary neural activation
- LTM: relies upon structural changes in neurons / connections

Working Memory

Atkinson & Shiffrin (1971)

"…we tend to equate the short-term *store* with 'consciousness,' that is, the thoughts and information of which we are currently aware can be considered part of the contents of the short-term store…Because consciousness is equated with the short-term store and because *control processes* are centered in and act through it, the short-term store is considered a working memory: a system in which decisions are made, problems are solved and information flow is directed."

Working Memory = a system for **maintaining** and **manipulating** active representations

Outline – Working Memory

What is Working Memory (WM)?

Why is WM important?

Capacity limits of WM

Contrasting WM and LTM

Forms of WM

Neurobiology of WM

Importance of WM

Working memory capacity (WMC) is correlated with

- Reading comprehension and numeracy (Daneman & Carpenter, 1980; Cowan & Alloway, 2008)
- Reasoning and problem solving (Kyllonen & Christal, 1990)
  WMC x reasoning ability: r = 0.80-0.90
- General intelligence
  Fluid intelligence (*Gf*) refers to the ability to reason and to solve new problems independently of previously acquired knowledge
  WMC x fluid intelligence: r = 0.59 (Engle et al., 1999)
- Academic success (Alloway & Alloway, 2010)
  WMC at 5 yrs of age is a better predictor of academic success than IQ

Impairments in WM are core to a number of clinical conditions

- Specific language impairment (Baddeley et al., 1998)
- Schizophrenia (Cohen & Servan-Schreiber, 1992)
- Attention-deficit/hyperactivity disorder (ADHD)

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How Do We Measure WM Capacity: Span Tasks

- Forward span (digits, words, symbols)
  - 174
  - 0853
  - 92421
  - 493759
  - 6715247
  - 05369417
  - 265070193
  - 8167049716
  - 04862517290

span = correct 50% of time

"Magic number seven, plus or minus two"
(G. Miller, 1956)

"Magic number seven, plus or minus two"

(G. Miller, 1956)

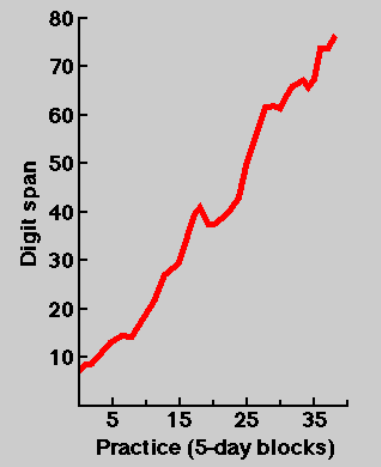
What do Span tests measure?
What is an item?

chunks
  a unit of knowledge that organizes together a few sub-items
  remembering part of the information assists is remembering the rest
  capitalizes on LTM

span increases by increasing the # of items in a chunk
  CA-TFL-YBU-G vs. CAT-FLY-BUG
  interplay between STM and LTM

Effects of Chunking on 'WM' Test Performance

(Ericsson & Chase, 1982)



with practice "WM capacity" improved

achieved by chunking numbers as running times, etc.

Did practice increase WM capacity?

- normal letter span: not a change in WM capacity per se

San Antonio Express-News — This page is recyclable — Monday, February 22, 1999 5A

Two-time memory champion still lives by Post-its

Long on facts, but short on remembering the milk

If we want to know what memory can and cannot do, there may be no better example than Tatiana Cooley, 27, a vivacious working woman in Manhattan and the USA National Memory Championship winner for the last two years in a row.

Cooley won the title by memorizing lengthy passages of poetry and complex series of numbers during a grueling competition. She discovered her ability to remember while in college, when she went into an exam and found she could recall verbatim the notes she had taken in class.

Taliana Cooley with her 1999 memory championship award

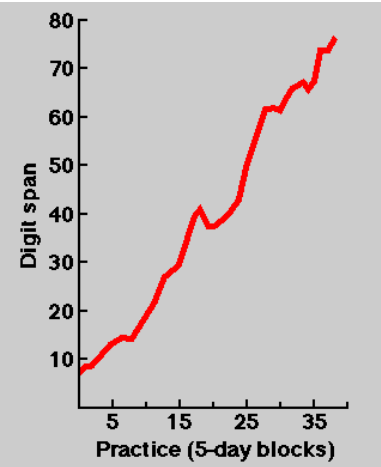
Today, as an executive assistant in a large office, Tatiana does not have to refer to the Rolodex on her desk, as the telephone numbers are all in her head.

Still, she says, there is a big difference between her ability to memorize things and her ability to keep a simple "to do" list in her head.

"They are two different worlds," she insisted. "I'm horribly absent-minded. I live by Post-it Notes."

Effects of Chunking on 'WM' Test Performance

(Ericsson & Chase, 1982)



achieved by chunking numbers as running times, etc.

- normal letter span: not a change in WM capacity

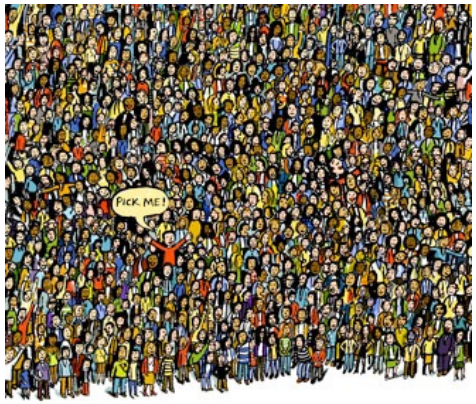
WM is capacity-constrained; performance at short-delays can be supplemented by LTM

performance is often a blend of contributions from multiple types of memory — WM and LTM

What Determines WM Capacity? Filtering Efficiency

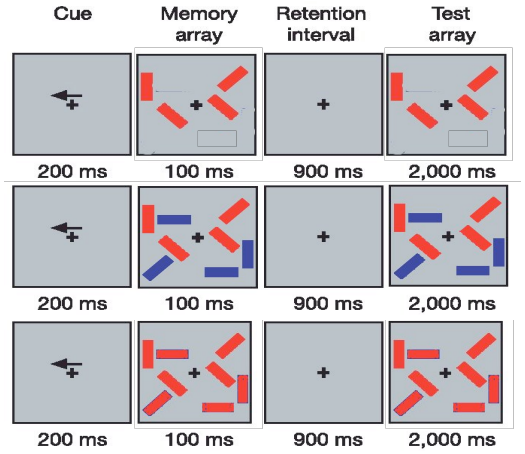
Hypothesis: WM performance rests on the ability to focus attention on relevant information and prevent distraction from irrelevant information

WM capacity is affected by how well a person can filter out distracting information (*Filtering Efficiency*)



Los Angeles Times, 4/4/09

What Determines WM Capacity? Filtering Efficiency



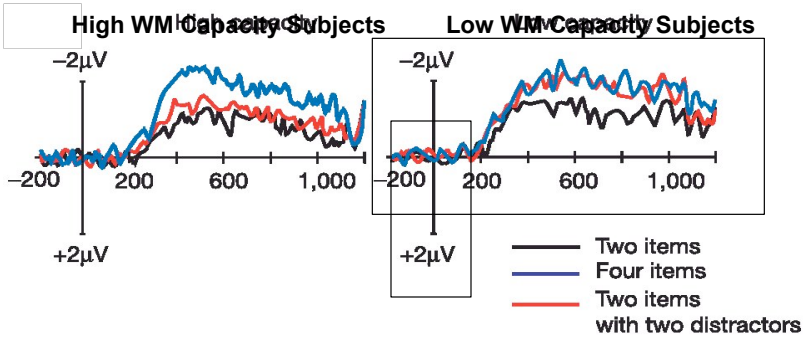
2 Items

2 Items, 2 Distractors

4 Items

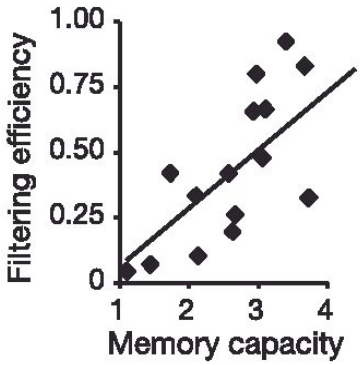
[Vogel et al, (2005) *Nature*]

What Determines WM Capacity? EEG Measure of Filtering Efficiency



[Vogel et al, (2005) *Nature*]

What Determines WM Capacity? Filtering Efficiency



r = .69,
p<.001

WM capacity is partly determined by the ability to filter out irrelevant environmental inputs and thoughts

[Vogel et al, (2005) *Nature*]

Can You Make Yourself Smarter?

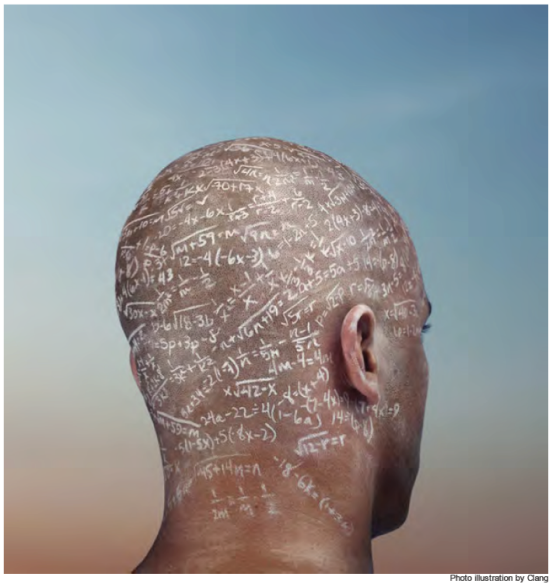


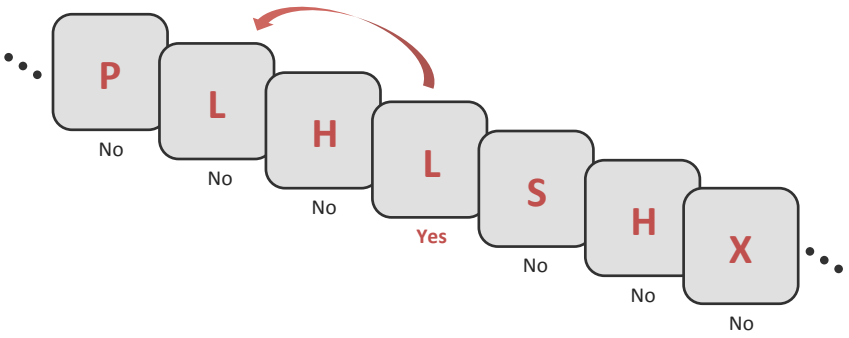
Photo illustration by Clang

New York Times, April 18, 2012

WM Training and Cognition

Does WM training increase *Gf* ? (Jaeggi et al., 2008)

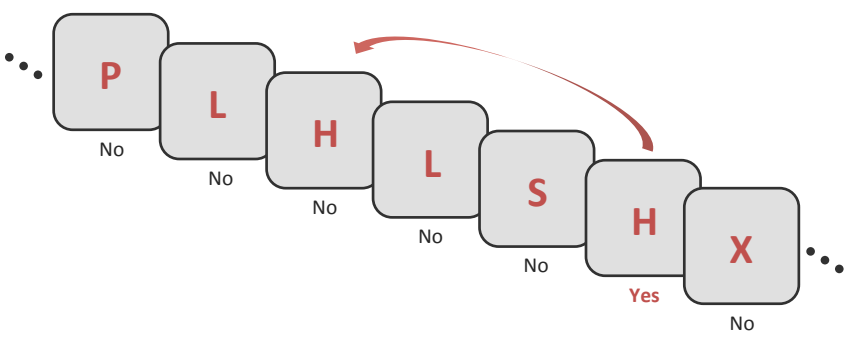
- 2-back



WM Training and Cognition

Does WM training increase *Gf* ? (Jaeggi et al., 2008)

- 3-back



*Training group: Trained on dual 3-back WM task between **Pre-** and **Post-** Gf test sessions (# of training days varied across subjects)*

WM Training and Cognition

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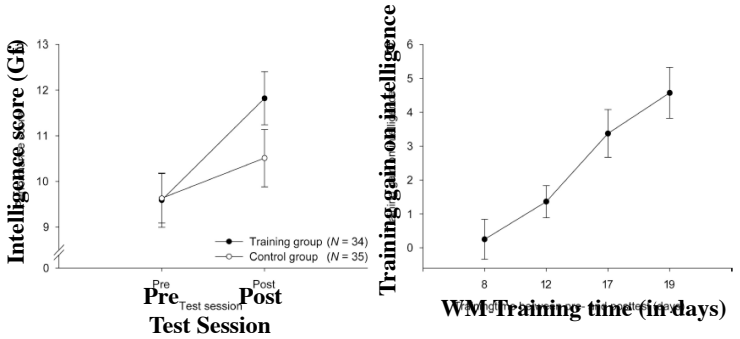
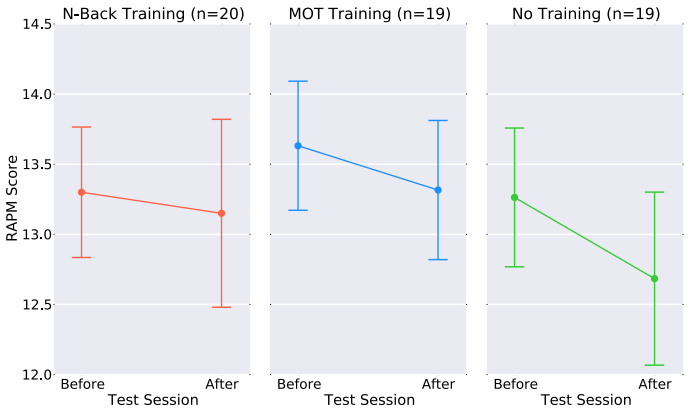


*Training group: Trained on dual 3-back WM task between **Pre-** and **Post-** Gf test sessions (# of training days varied across subjects)*

Challenges to WM Training Effects

WM training and *Gf* (Thompson et al., 2013; see also Redick et al., 2012)



*Training group: Trained on either dual 3-back WM task OR a multi-object tracking (MOT) attention task. **Before-** and **After-** scores on Ravens Progressive Matrices test (Gf) did not increase*

Outline – Working Memory

What is Working Memory (WM)?

– ability to keep active (maintain) and manipulate mental representations

Why is WM important?

– WM capacity correlates with other cognitive abilities

Capacity limits of WM

– WM is capacity limited, but performance at short delays can also be supported by LTM
– attention is required to transform sensory information into WM representations
– WM capacity is correlated with ability to filter out distracting information

Next time…

What is Working Memory (WM)?

Why is WM important?

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Contrasting WM and LTM

Forms of WM

Neurobiology of WM

Outline

What is Working Memory (WM)?

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Neurobiology of WM

Outline

What is Working Memory (WM)?

Why is WM important?

Capacity limits of WM

Contrasting WM and LTM

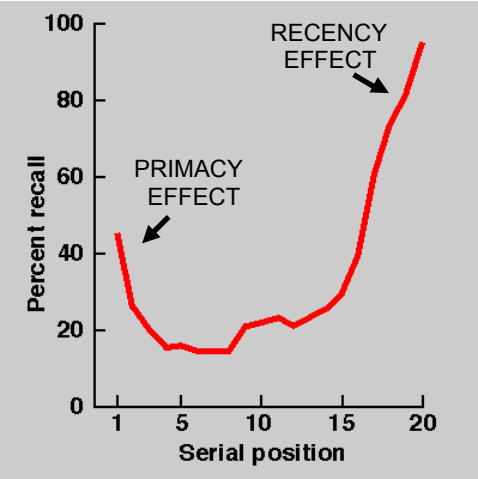
– Evidence for separate WM & LTM systems?

Forms of WM

Neurobiology of WM

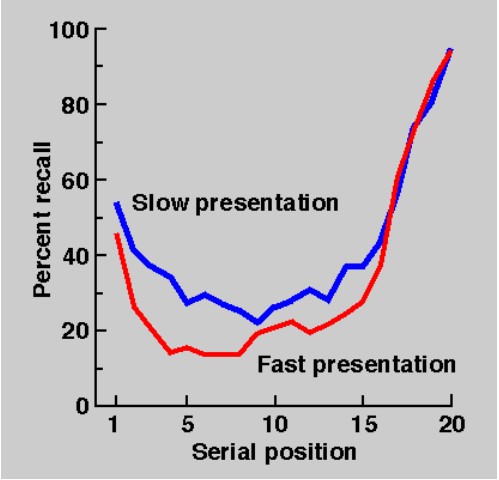
Serial Position Function in Free Recall

Serial Position Function in Free Recall



Primacy Component – LTM

Dissociable effects of rate of presentation

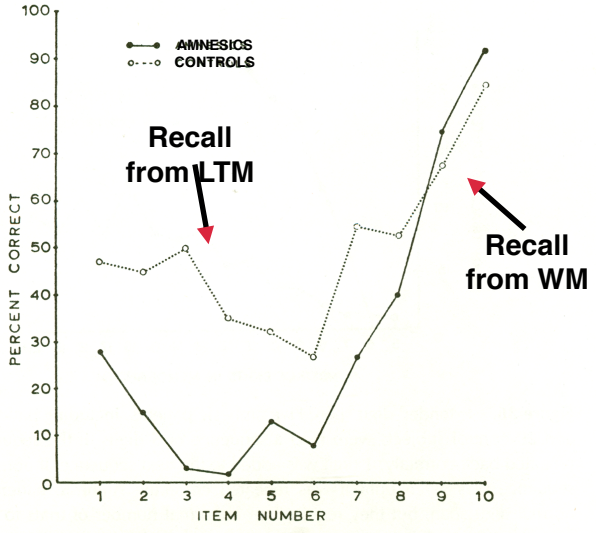


Why?

two-store model's account: longer rehearsal time in WM = greater transfer to LTM

alternatively: elaboration; encode inter-item associations

Impaired Primacy in Amnesia



Baddeley & Warrington (1970)

Factors Affecting the Primacy Effect

- Rate of presentation
  - rehearsal time; encode inter-item associations
- List length
  - less between-item interference (forgetting)
- Familiarity of materials
  - elaborative / depth of encoding
- Aging
- Medial temporal lobe lesions (amnesia)

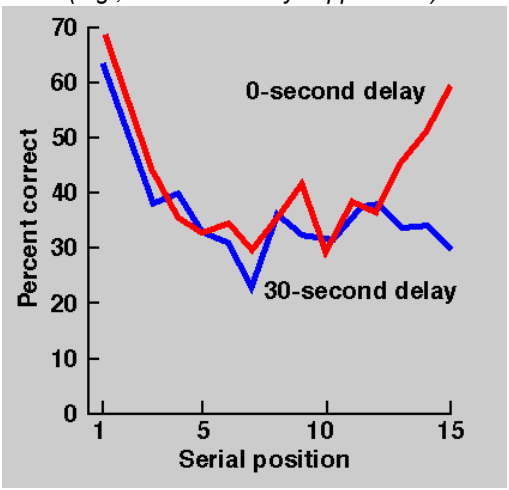
All of these affect LTM encoding/storage

Articulatory Suppression & WM

Recency Component – WM

Dissociable effects of filled delay

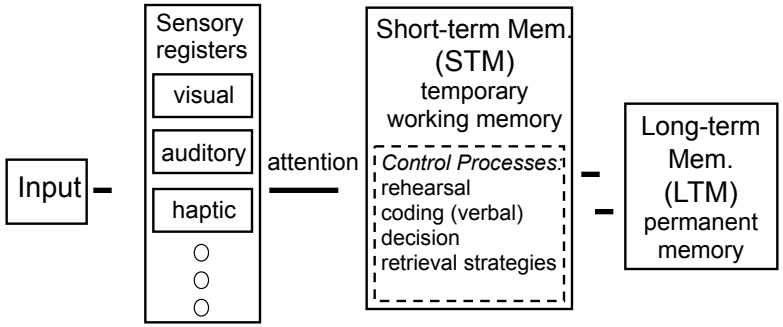
(e.g., with articulatory suppression)



Double Dissociation:

WM and LTM depend on different systems or processes

Two-Store "Modal Model" of Memory

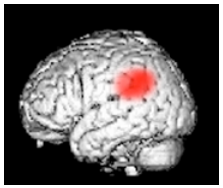


Atkinson & Shiffrin (1968)

Evidence for Separate WM / LTM Stores

H.M. & AMNs → intact WM, but impaired LTM

K.F. → impaired WM, but relatively intact LTM



left temporal/parietal lesion

limited span for auditory material (letters)
- span 1: 19/20 trials correct
- span 2: 7/20 trials correct
- span 3: 2/20 trials correct

Evidence for Separate WM / LTM Stores

K.F.'s intact LTM despite impaired WM

Table 3.3. *Performance of STM patients on tests of LTM*

	KF[a]	JB[b]	WH[b]	PV[c]	Control
Wechsler paired-associate learning (success score)	14	18	11	19	14.8
Ten-word learning (no. trials)	7	10	9	4	9
Warrington recognition memory (words correct)	—	45	—	—	45

[a] Warrington and Shallice (1969)
[b] Warrington, Logue, and Pratt (1971)
[c] Basso, Spinnler, Vallar, and Zanobia (1982)

From Shallice, 1988

Double Dissociation:
WM and LTM depend on different systems or processes

Implications for the Modal Model?

Distinctions between STM and LTM

STM	*LTM*
Active contents of consciousness	Not currently in consciousness
Active nodes in LTM	Inactive until cued
Fast access to contents	Slower access
Limited capacity	Unlimited capacity
Fast forgetting	Slower forgetting
Increased neural firing relative to baseline	Unit-to-unit changes in synaptic/connection strength

Outline

What is Working Memory (WM)?

Why is WM important?

Capacity limits of WM

Contrasting WM and LTM

Forms of WM

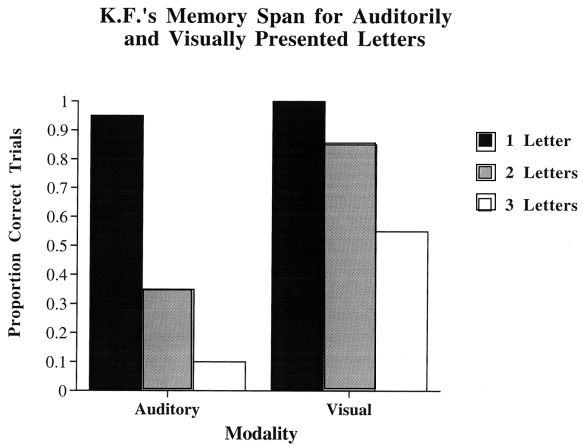
Neurobiology of WM

Is WM Unitary?

- In the modal model, all sensory modalities and types of information pass through a common STM buffer
- Neuropsychological and behavioral studies suggest WM can be fractionated

Auditory vs. Visual Letter Span: Patient KF

Patient K.F.



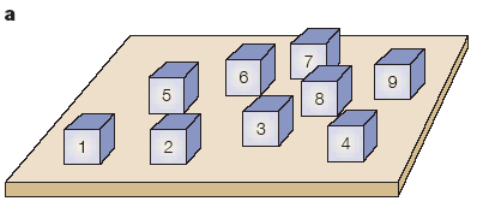
Patient E.L.D.

Suffered stroke to right fronto-temporal region

- Reported difficulties in finding her way home, and memory problems for unfamiliar material

Severe deficit in visuospatial memory

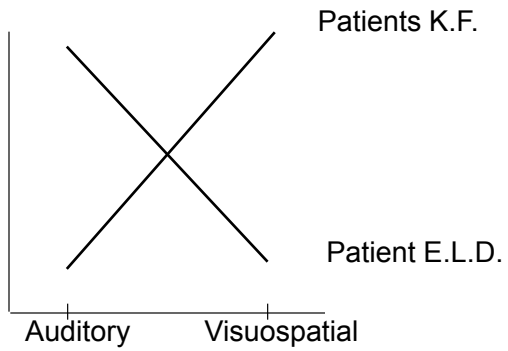
- Corsi blocks



Normal auditory short-term memory

(Hanley et al., 1991)

Double Dissociation within WM



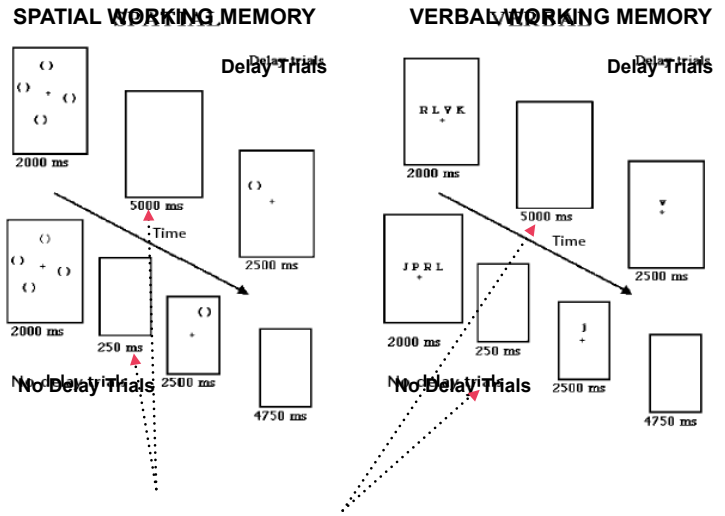
suggests that WM is not a unitary function
similar double dissociations seen in healthy Ss using dual-task distraction paradigms

Brain Imaging Evidence on WM: Reminder about Neuroimaging "Subtractive" Logic

Brain is always "active"
- "baseline" firing rates
- "baseline" blood flow/blood oxygenation levels

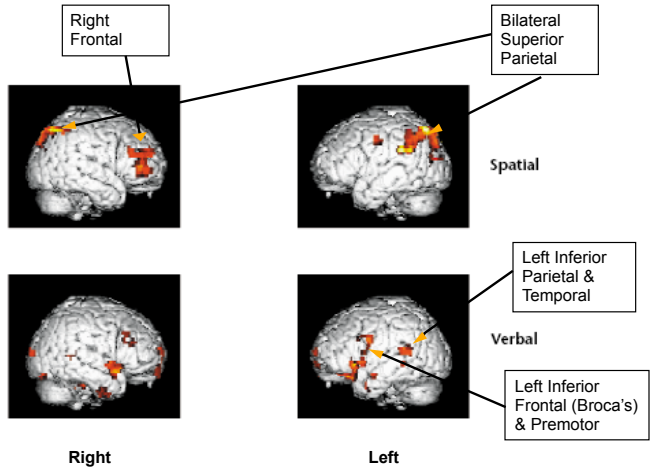
To measure a response, need to **COMPARE** at least two conditions
Condition 2 – Condition 1 ("difference image")

(Prabhakaran et al., 2000)



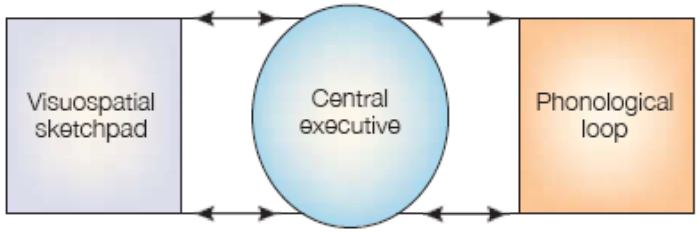
Assumption: differences in brain response are only due to different cognitive demands of having to maintain information across a 5000 vs 250 ms delay

Spatial and Verbal WM Maintenance



Tripartite Model of WM

(Baddeley & Hitch, 1974)



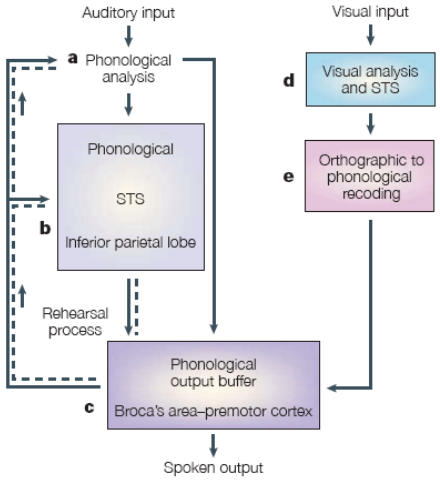
Multi-component model

Combined processing & storage model

The Phonological Loop

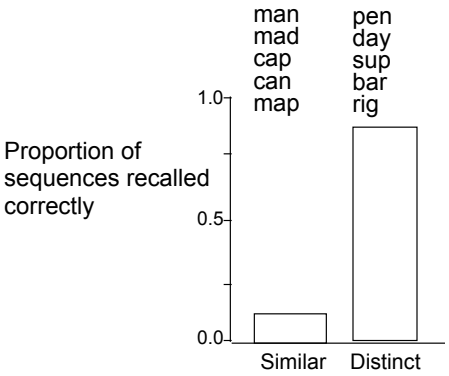
Phonological store
stores active phonological representations

Phonological rehearsal/ control
subvocal rehearsal accesses and maintains representations



What is the Nature of the PL?

Phonological similarity effect:



inference: maintained representations are in a phonological code

What is the Nature of the PL?

Articulatory suppression:

PL disrupted by overt or covert articulation of irrelevant phonological codes

e.g., "bla, bla, bla" hinders digit span

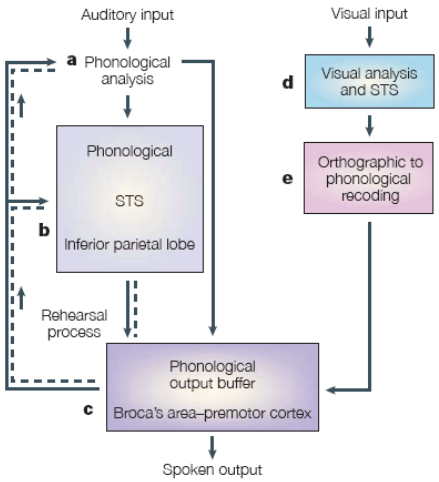
PL not disrupted by rhythmic finger tapping

inference: articulatory rehearsal mechanism is required to maintain phonological codes

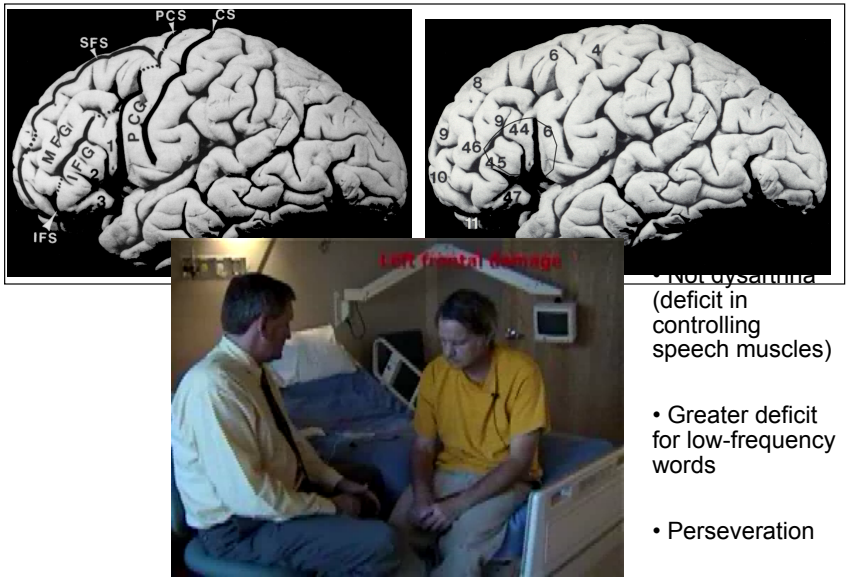
The Phonological Loop

Phonological store
- stores active phonological representations

Phonological rehearsal/ control
- subvocal rehearsal accesses and maintains representations

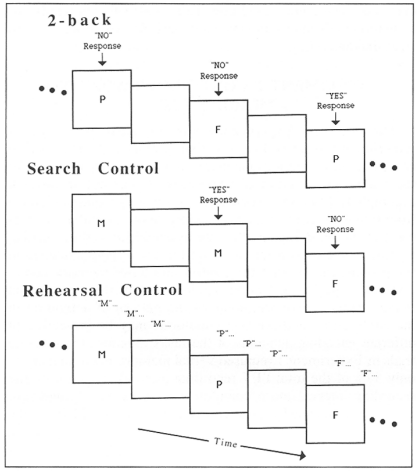


Broca's Aphasia



- (deficit in controlling speech muscles)
- Greater deficit for low-frequency words
- Perseveration

PET: Separating Rehearsal from Storage



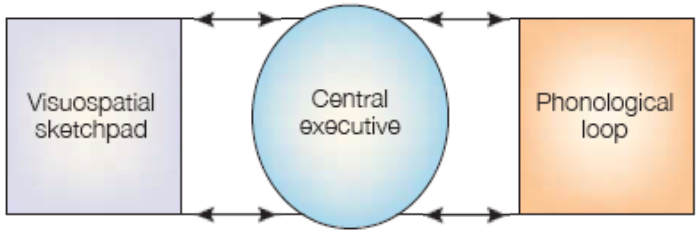
2-Back > Search Control
left frontal (Broca's area)
left inferior parietal lobe

2-Back > Rehearsal Control
left inferior parietal lobe

inference: left frontal = rehearsal control mechanism
left inferior parietal = storage

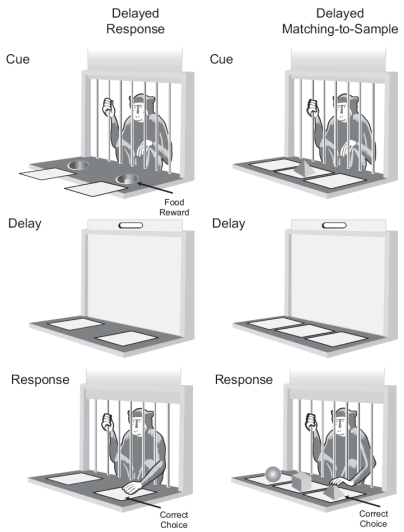
Tripartite Model of WM

(Baddeley & Hitch, 1974)



Visual WM for
"What" and "Where"?

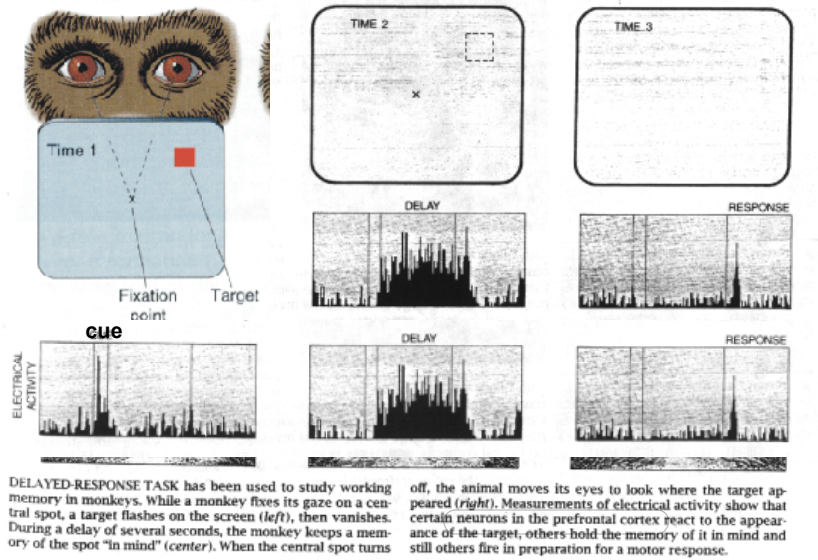
Prefrontal Cortex is Necessary for Object and Spatial WM



monkeys with PFC lesions show impaired performance

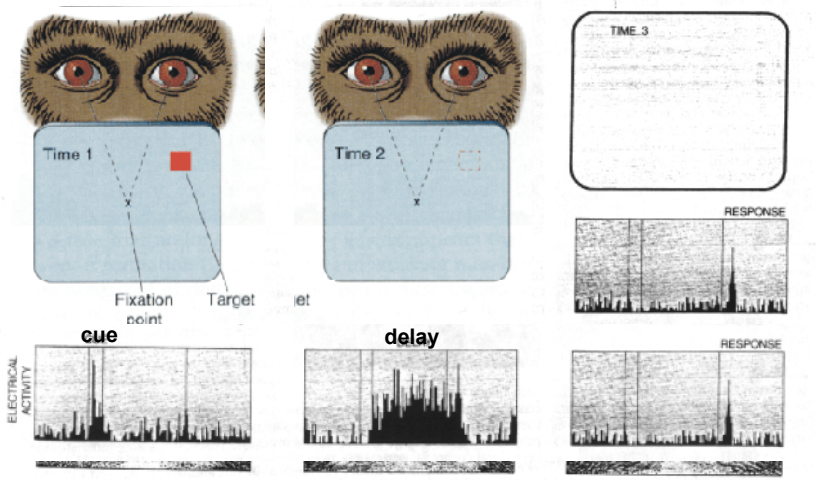
however, turn out the lights during the delay period and performance improves (though may not be normal)

Jacobson et al. 1935



DELAYED-RESPONSE TASK has been used to study working memory in monkeys. While a monkey fixes its gaze on a central spot, a target flashes on the screen (*left*), then vanishes. During a delay of several seconds, the monkey keeps a memory of the spot "in mind" (*center*). When the central spot turns off, the animal moves its eyes to look where the target appeared (*right*). Measurements of electrical activity show that certain neurons in the prefrontal cortex react to the appearance of the target, others hold the memory of it in mind and still others fire in preparation for a motor response.

(Goldman-Rakic and colleagues)



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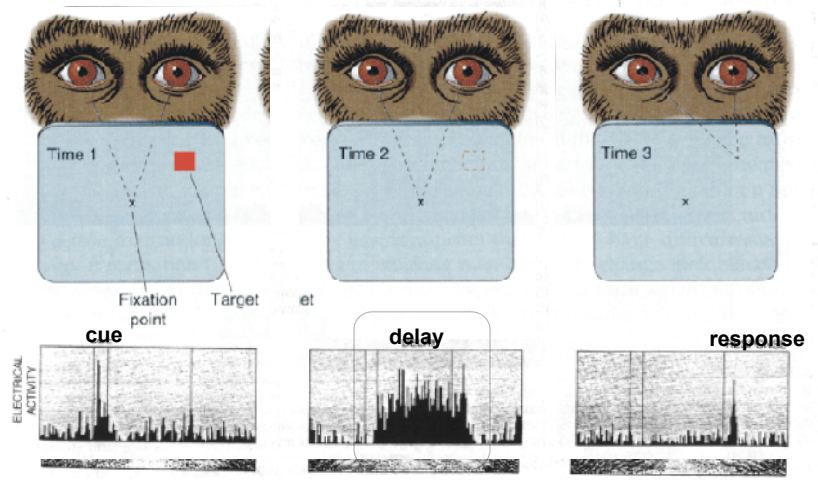

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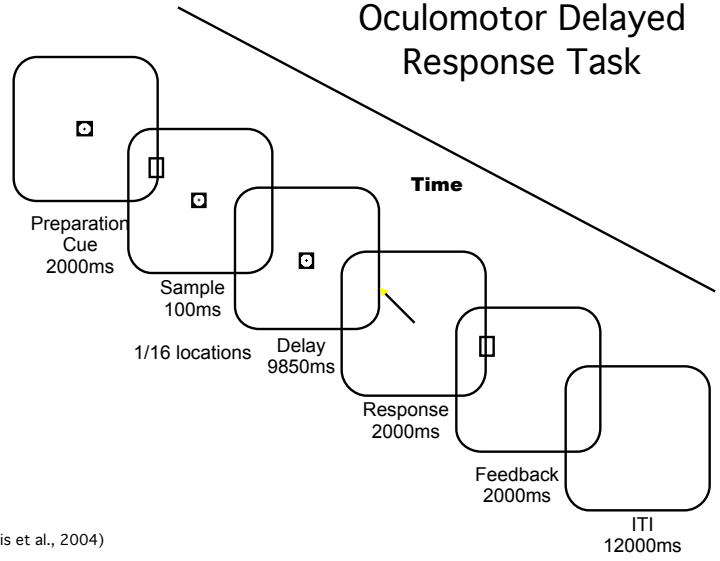
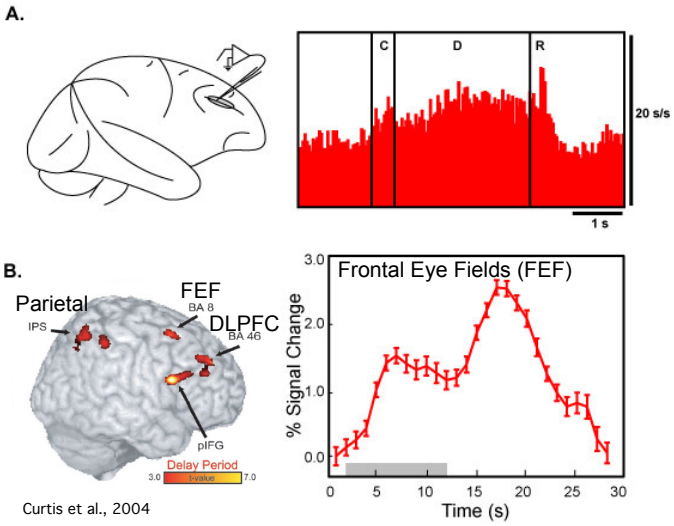
Oculomotor Delayed Response Task



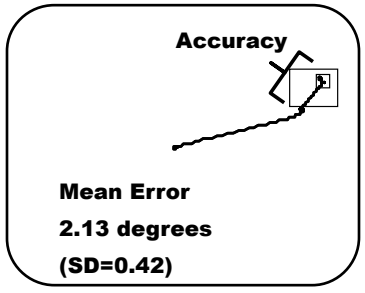
(Curtis et al., 2004)

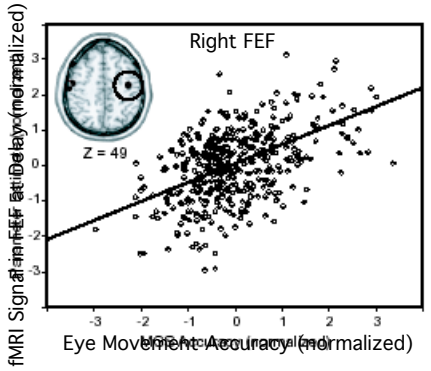
Prefrontal and Parietal Cortices: Oculomotor Delayed Response Task



Curtis et al., 2004

Prefrontal and Parietal Cortices: Oculomotor Delayed Response Task

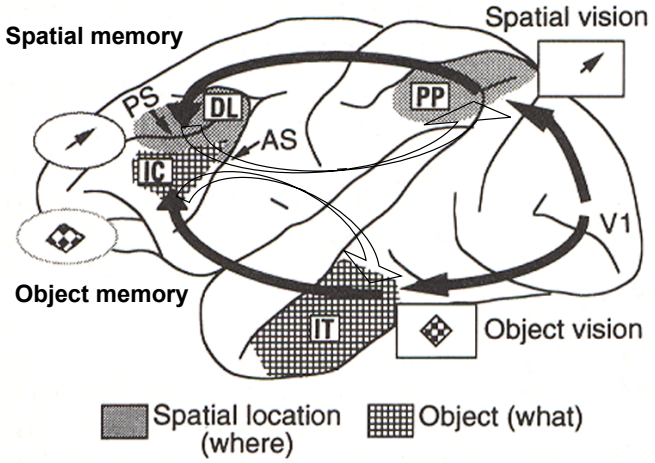




(Curtis et al., 2004)

WM delay periods
– prefrontal cortex neural firing rates increase
– disrupt delay period activity and performance declines (causation)
– firing rates in posterior cortical regions also increase

WM and Cortical Circuits: Reverberating Activity

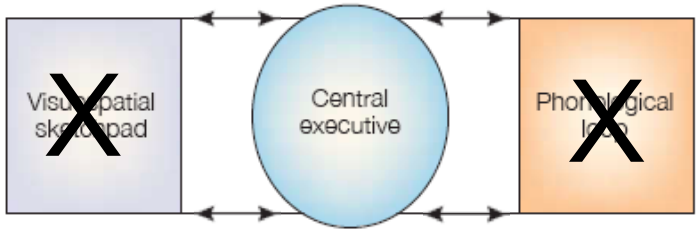


maintenance in WM occurs through the reverberation of activity through frontal-posterior circuits

(Wilson et al., 1993)

Tripartite Model of WM?

(Baddeley & Hitch, 1974)



Visuo-Object

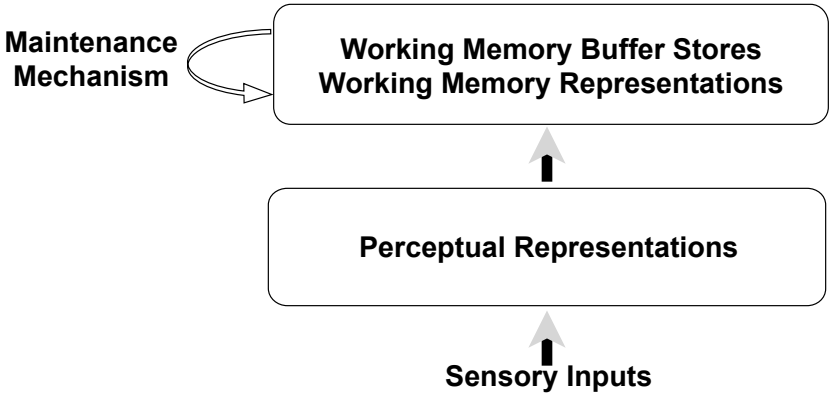
Spatial

Phonological loop

Semantic

Is WM a System or an Emergent Property?

Systems Hypothesis of WM



Emergent Hypothesis of WM

Hypothesis

WM emerges when attention is directed towards stimulus representations

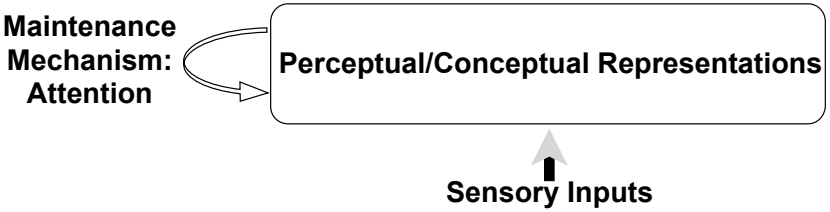
- WM buffers do not exist
- Information in WM resides in the perceptual/conceptual systems that represent that class of information

Prediction

The contents of visual WM reside in visual/perceptual cortex

- Should be able to decode the contents of WM from visual cortex

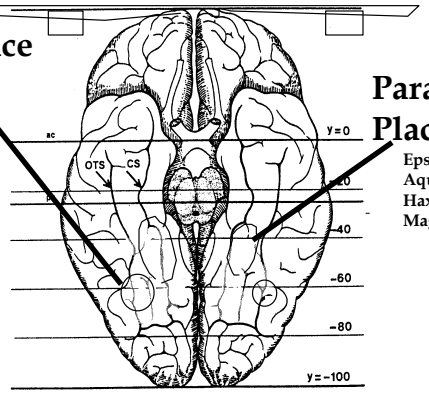
Emergent Hypothesis of WM



Perceptual Responses in Temporal Cortex

Fusiform Face Area (FFA)

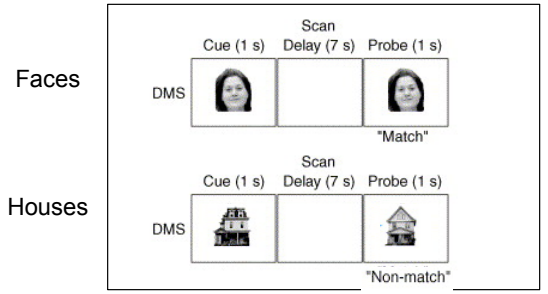
Kanwisher et al (97-00)
Tong et al (in press)
Sergent et al (92)
Haxby et al (91, 94, 99)
Puce et al (95, 96)
McCarthy et al (97)
Halgren et al (99)
And many others



Parahippocampal Place Area (PPA)

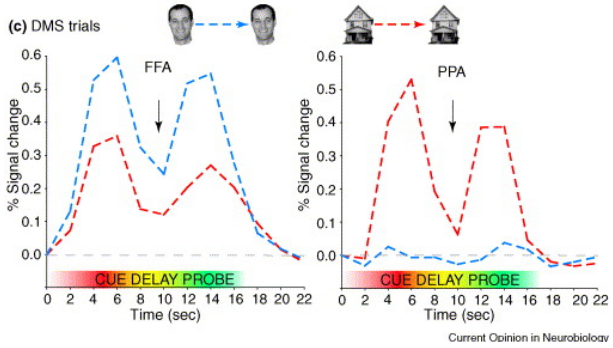
Epstein & Kanwisher (98, 00)
Aquirre et al (98, 99)
Haxby et al (99)
Maguire et al (96, 97, 98)

Temporal Cortex: Category-Specific Activation during WM Maintenance?



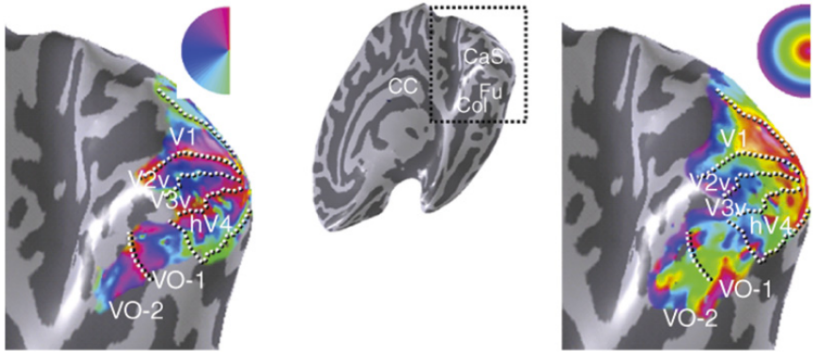
(Ranganath et al., 2004)

Temporal Cortex: Category-Specific Activation during WM Maintenance



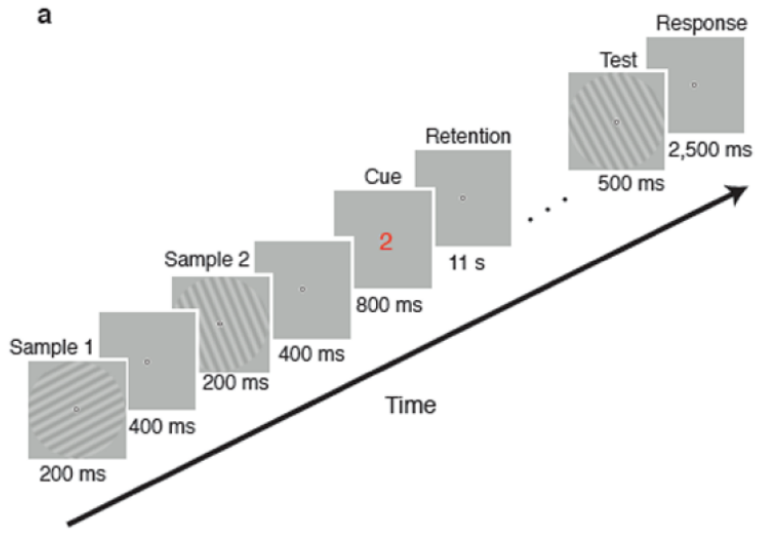
(Ranganath et al., 2004)

Testing the Emergent Hypothesis of WM



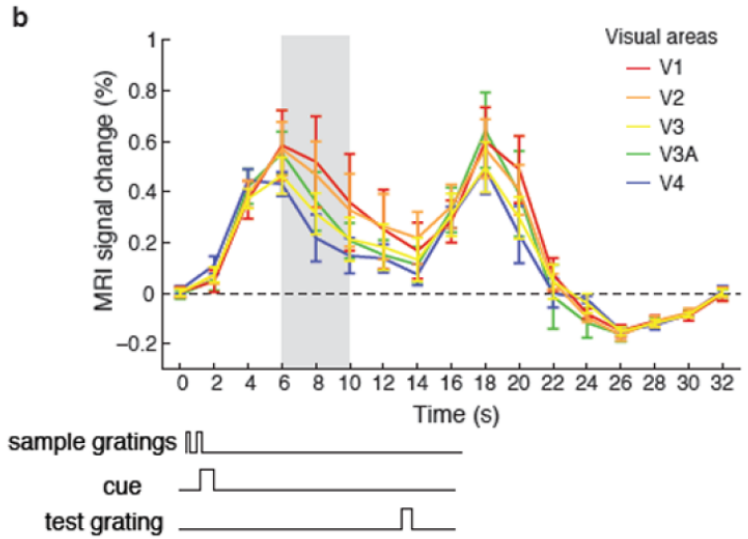
(Wandell et al., 2007)

Testing the Emergent Hypothesis of WM



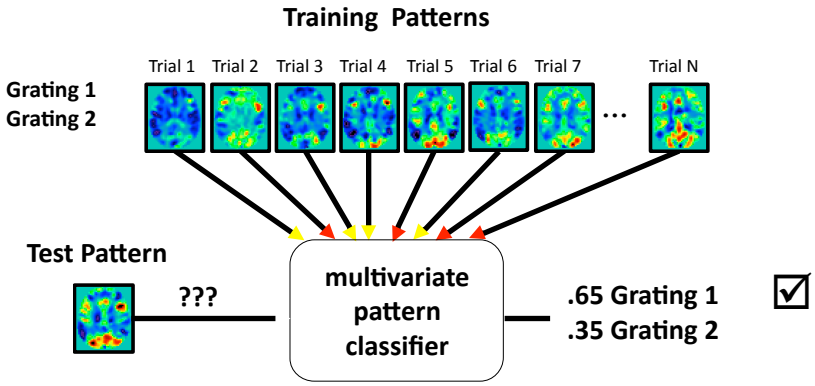
(Harrison & Tong, 2009)

Testing the Emergent Hypothesis of WM



(Harrison & Tong, 2009)

fMRI Data Analysis Approach



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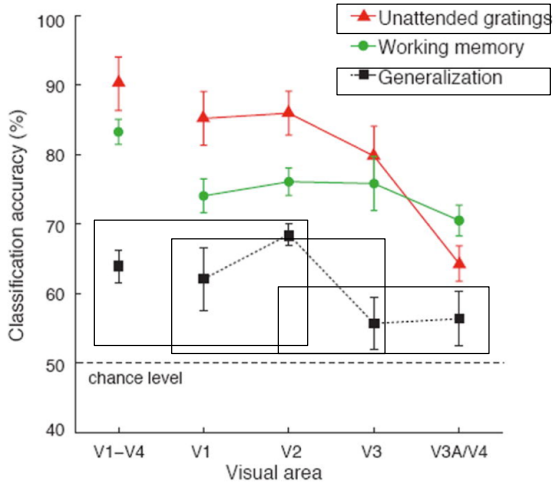


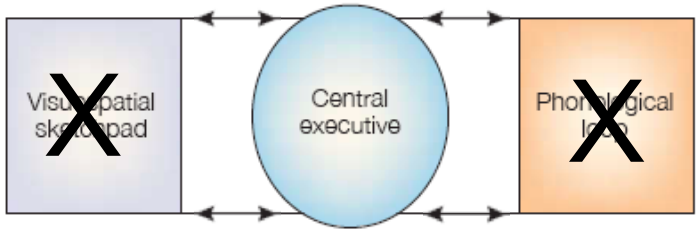
Unattended viewing (central letter detection task, while gratings flashed in background)

Patterns of activity even in the very earliest sensory cortical regions (V1) carry information about what (the item) is maintained in WM

(Harrison & Tong, 2009)

Tripartite Model of WM?

(Baddeley & Hitch, 1974)



Visuo-Object

Spatial

Phonological loop

Semantic

WM is an Emergent Property / NOT a system