Reading in the brain

2. Masking, subliminal reading, and the mechanisms of conscious access

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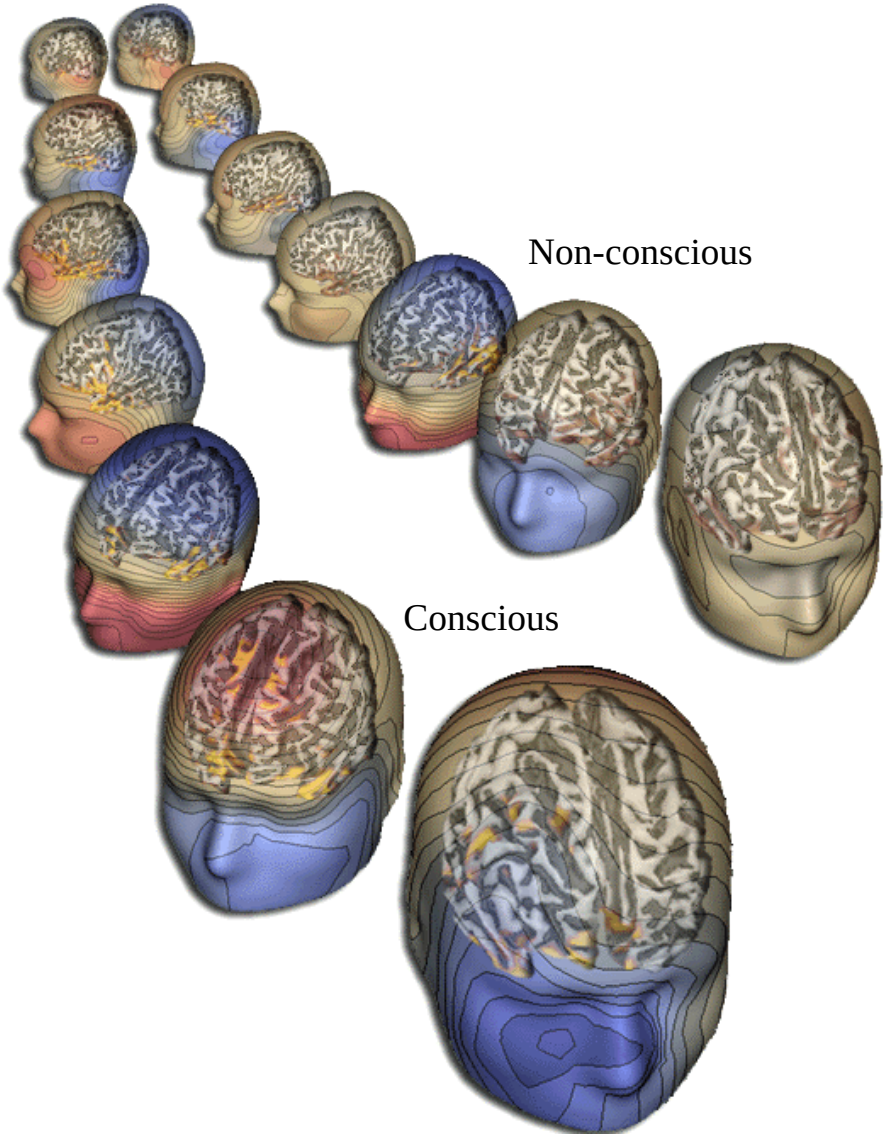
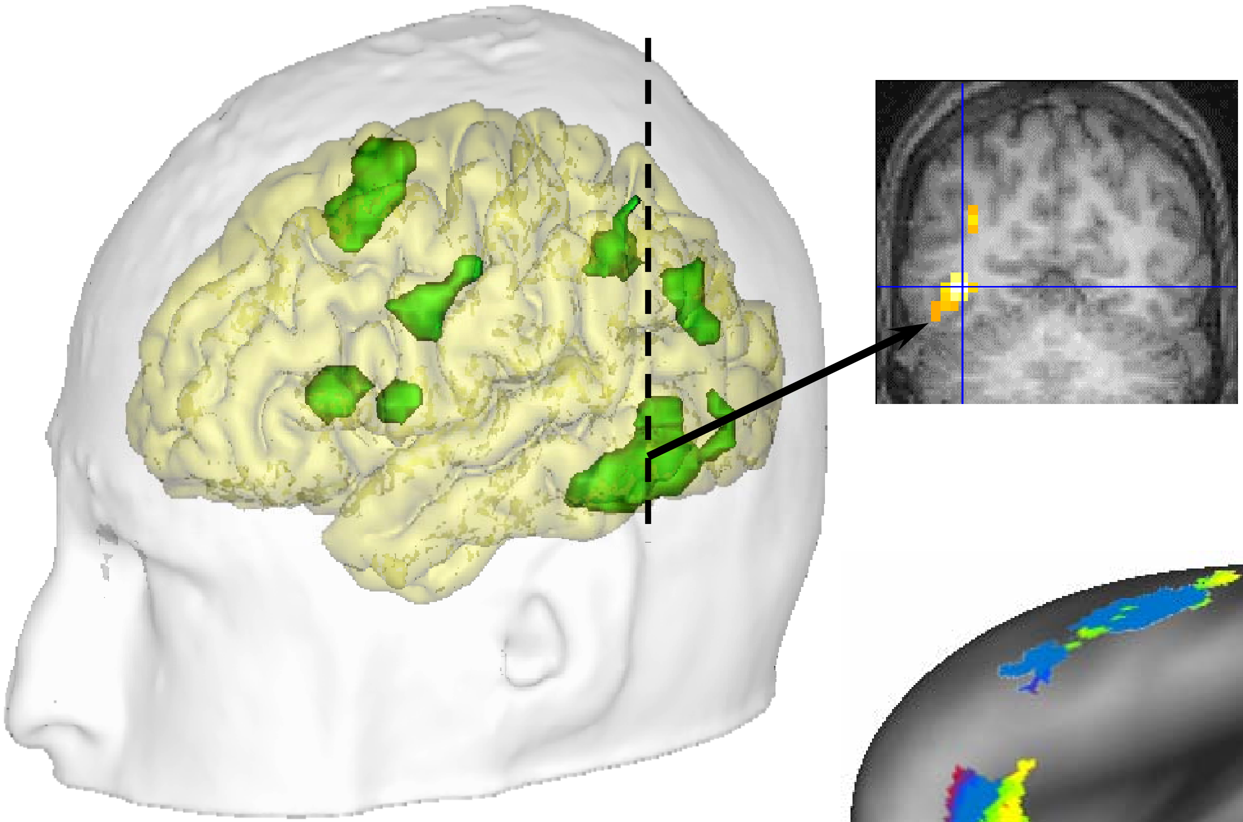
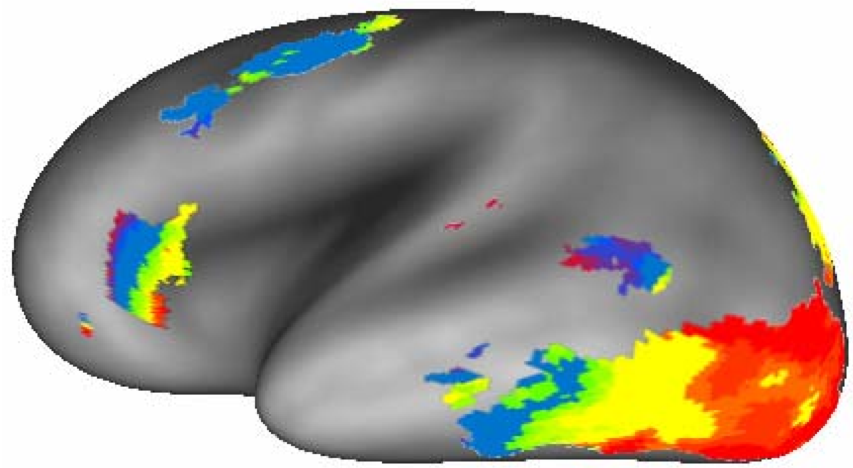


Image by Claire Sergent

The visual word form area



A subpart of the occipito-temporal visual system that systematically responds to written words.



A hierarchically organized region

False Font	Infrequent Letters	Frequent Letters	Frequent Bigrams	Frequent Quadrigrams	Words
[illegible]	JZWYWK	QOADTQ	QUMBSS	AVONIL	MOUTON

A short demonstration of digit masking

Two central issues in consciousness research

1. The depth of subliminal processing

- How deeply can subliminal stimuli be processed into the visual system?

2. The nature of conscious access

- What prevents subliminal stimuli from becoming conscious?
- What processes occur when a stimulus is consciously accessed, and when do conscious and non-conscious processing diverge?

Our research strategy

- The contrastive method: « … contrasting pairs of similar events, where one is conscious but the other is not. » (Baars, 1989)
- The primacy of the subjective: « …the first crucial step is *to take seriously introspective phenomenological reports*. (…) They constitute primary data that need to be measured and recorded along with other psychophysiological observations » (Dehaene & Naccache, 2001)

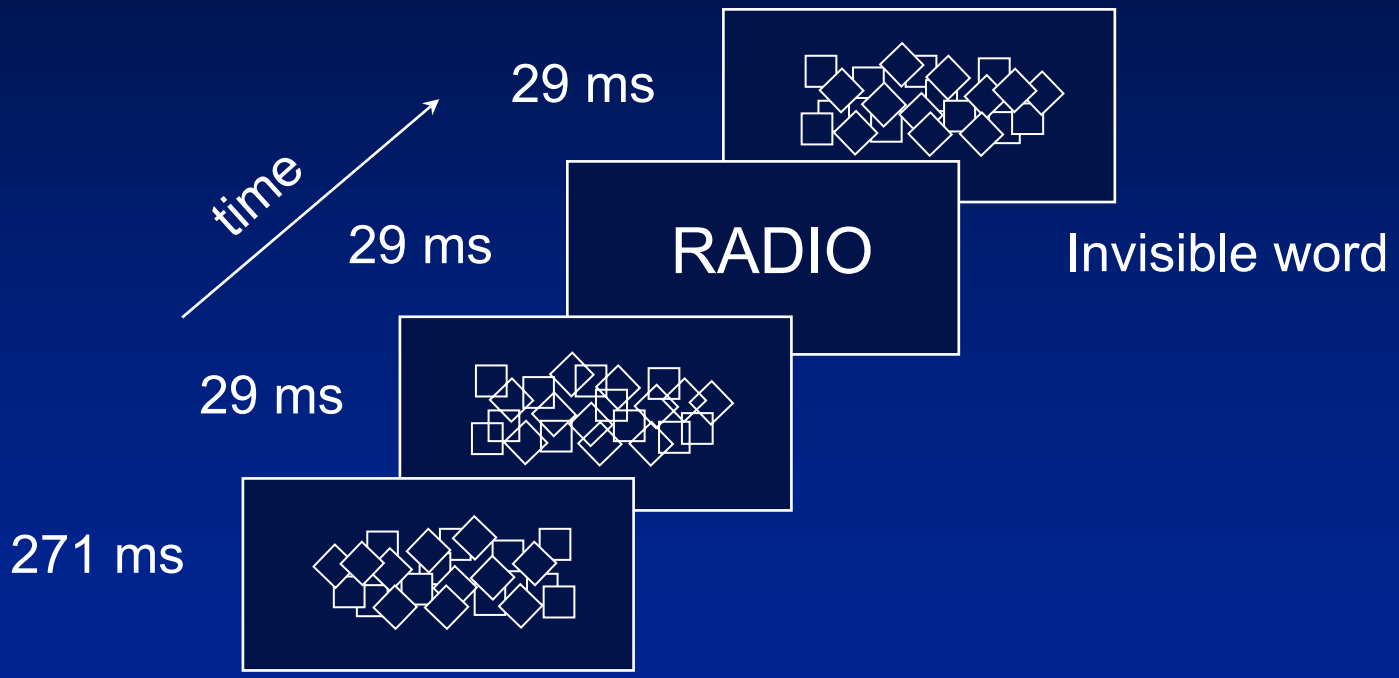
In summary, look for:
objective neurobiological correlates of *subjective* processes

Part I. The fate of a non-conscious stimulus

- **Masked words and digits elicit activity at a series of hierarchical levels, including visual, semantic and motor stages.**

- **fMRI priming can help decipher how information is coded in a given region.**

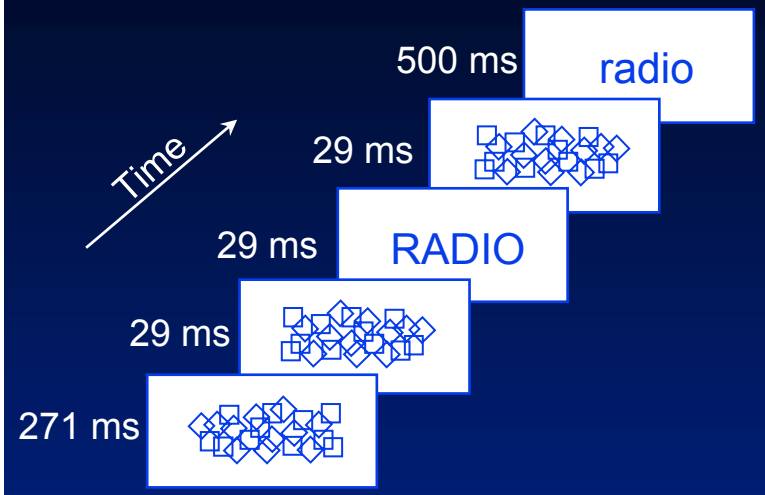
Making a word invisible: the masking paradigm

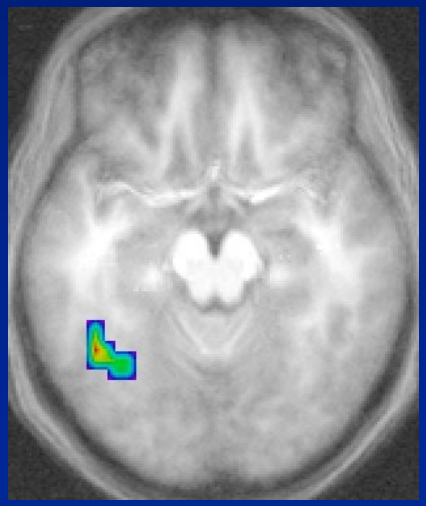


Dehaene et al., *Nature Neuroscience*, 2001

Invariance for case in the visual word form area

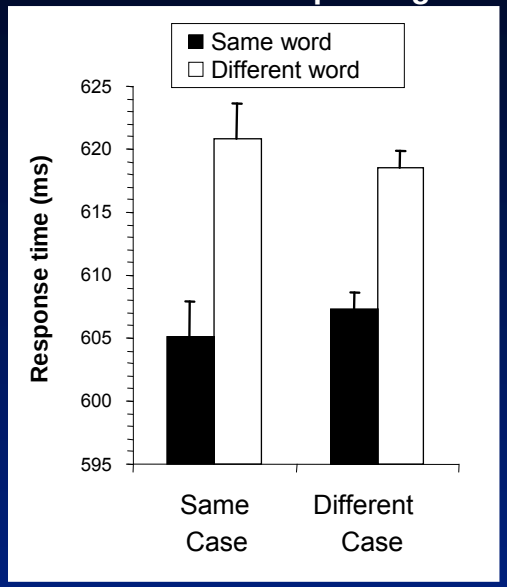
Dehaene et al, *Nature Neuroscience*, 2001; *Psychological Science*, 2004



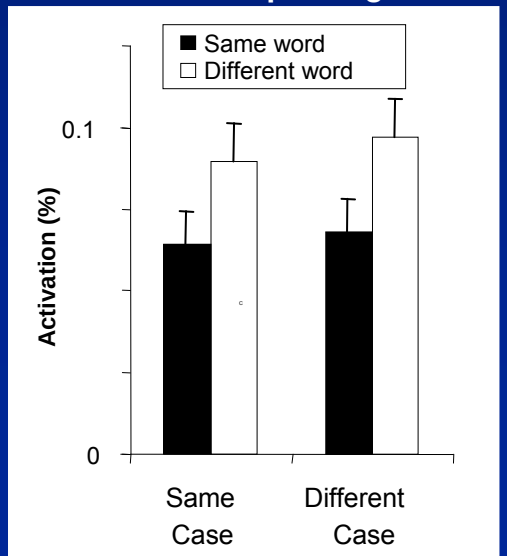


Left fusiform
(-44, -52, -20)

Behavioral priming

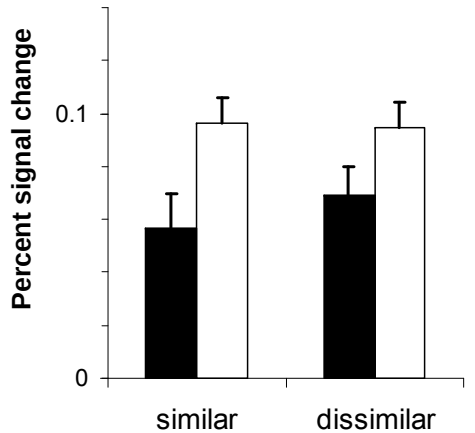


fMRI priming



Case-invariant priming independent of letter similarity

Left fusiform
-48, -52, -12



e.g. COUP-coup vs RAGE-rage

What are the coding units underlying orthographic priming?

Single letter?

Bigram?

Morpheme or whole word?

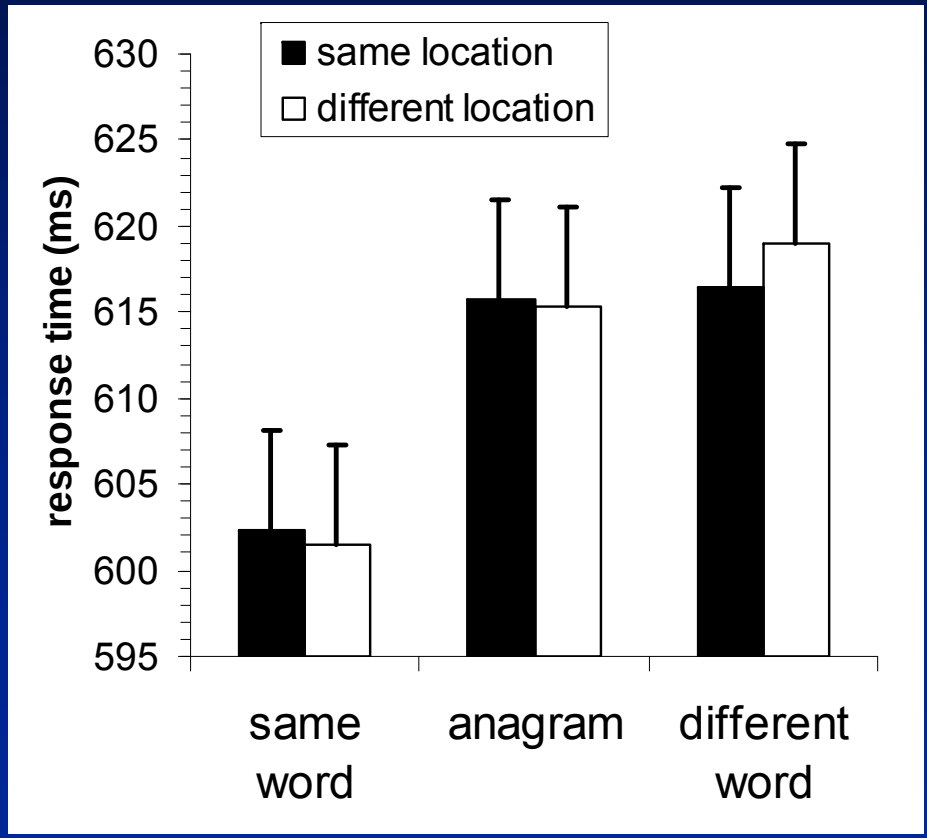
Prime-Target Relation

word location	**same word**	**anagram**	**different word**
same	#REFLET #reflet	#TREFLE #reflet	#PATERE #reflet
different	REFLET# #reflet	TREFLE# #reflet	EPATER# #reflet

Dehaene et al., *Psychological Science*, 2004

Prime-Target Relation			
word locations	same word	anagram	different word
same	#REFLET #reflet	#TREFLE #reflet	#PATERE #reflet
different	REFLET# #reflet	TREFLE# #reflet	EPATER# #reflet

Behavior



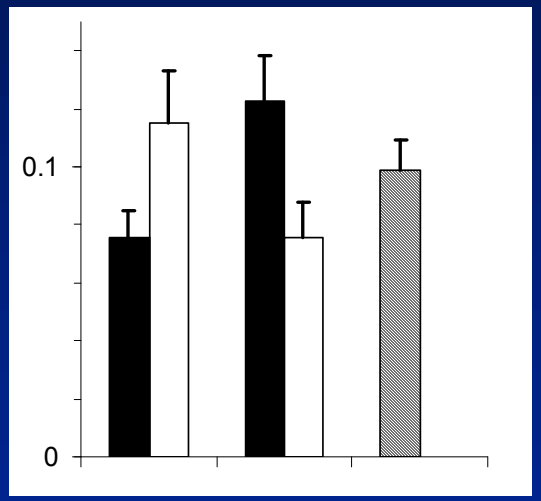
Dehaene et al., *Psychological Science*, 2004

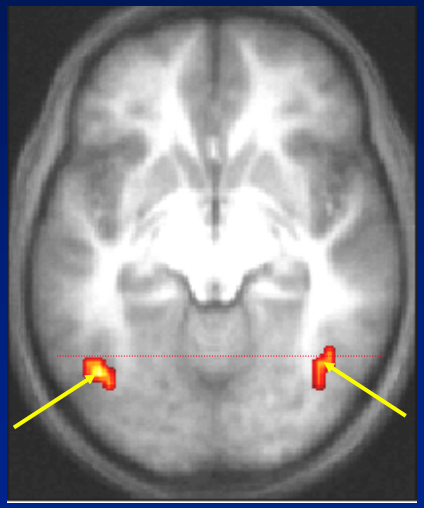
fMRI : location-specific priming

word locations	same word	anagram	different word
same	#REFLET #reflet	#TREFLE #reflet	#PATERE #reflet
different	REFLET# #reflet	TREFLE# #reflet	EPATER# #reflet

Prime-Target Relation

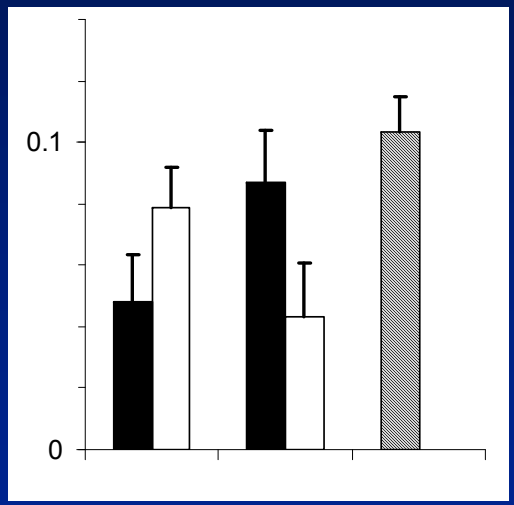
Left posterior fusiform





same location
different location
both locations

right posterior fusiform



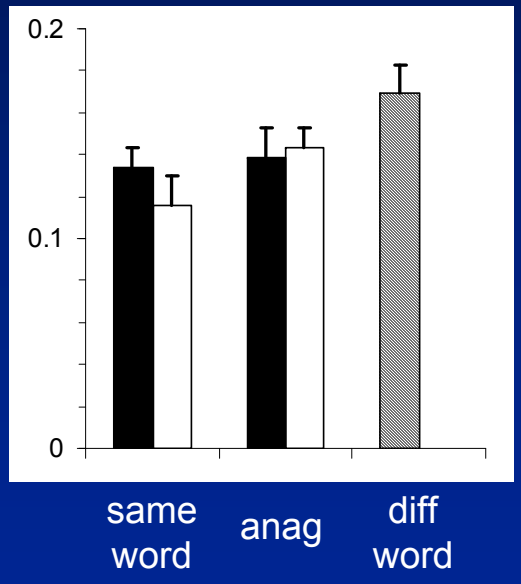
LETTERS AT THE SAME LOCATION

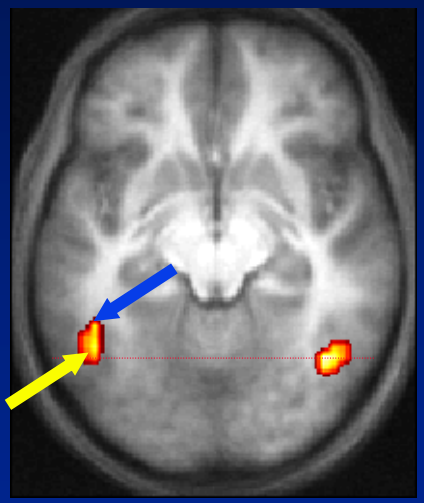
Dehaene et al., *Psychological Science*, 2004

Prime-Target Relation			
word locations	same word	anagram	different word
same	#REFLET #reflet	#TREFLE #reflet	#PATERE #reflet
different	REFLET# #reflet	TREFLE# #reflet	EPATER# #reflet

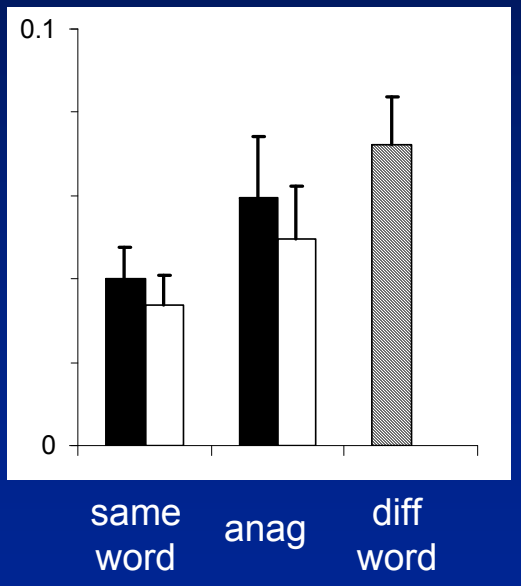
fMRI : location-independent priming

Left middle fusiform (y=-56)





Left middle fusiform (y=-48)

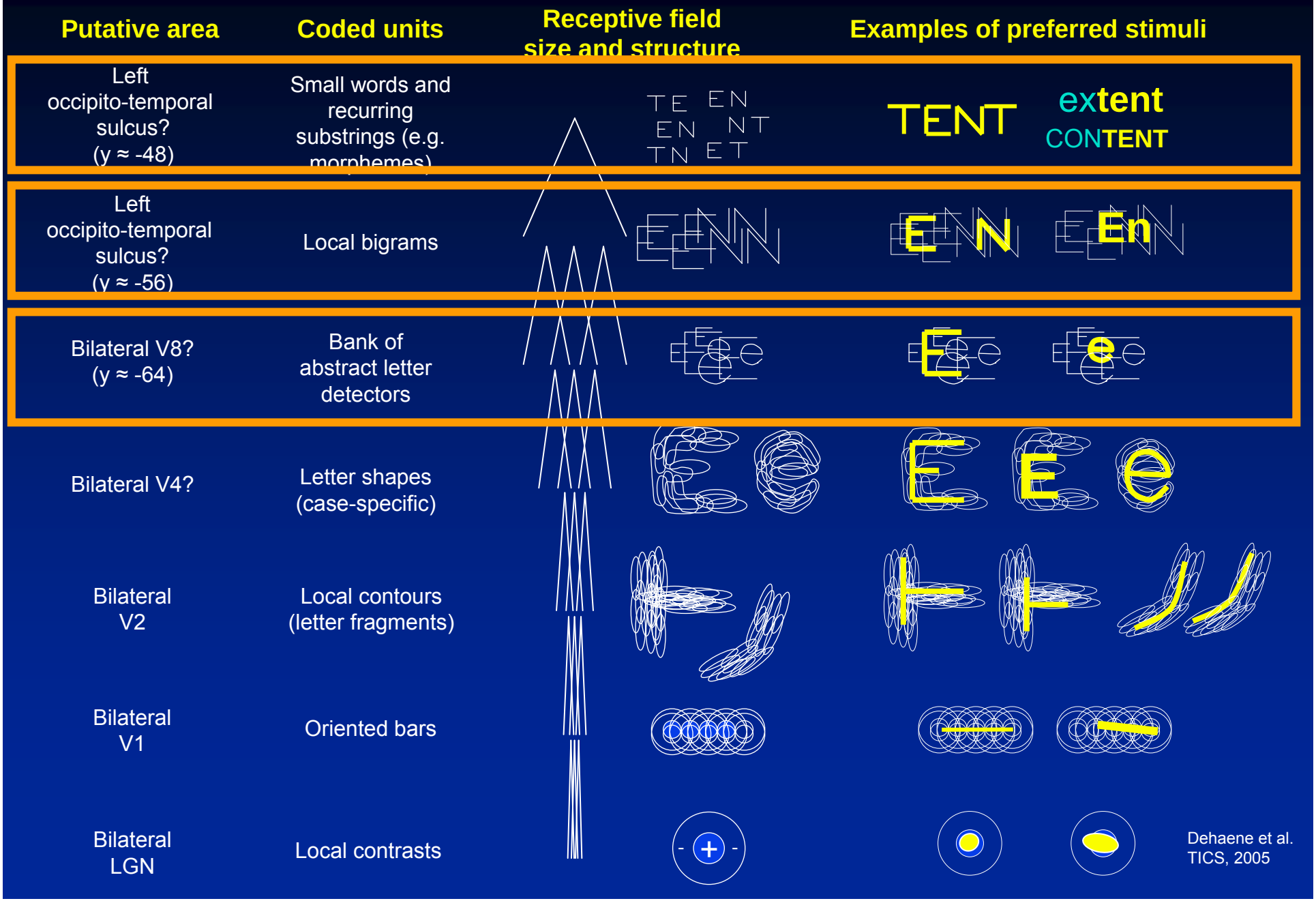


LETTERS AT ANY LOCATION

LARGER UNIT (WHOLE WORD?)

Dehaene et al., *Psychological Science*, 2004

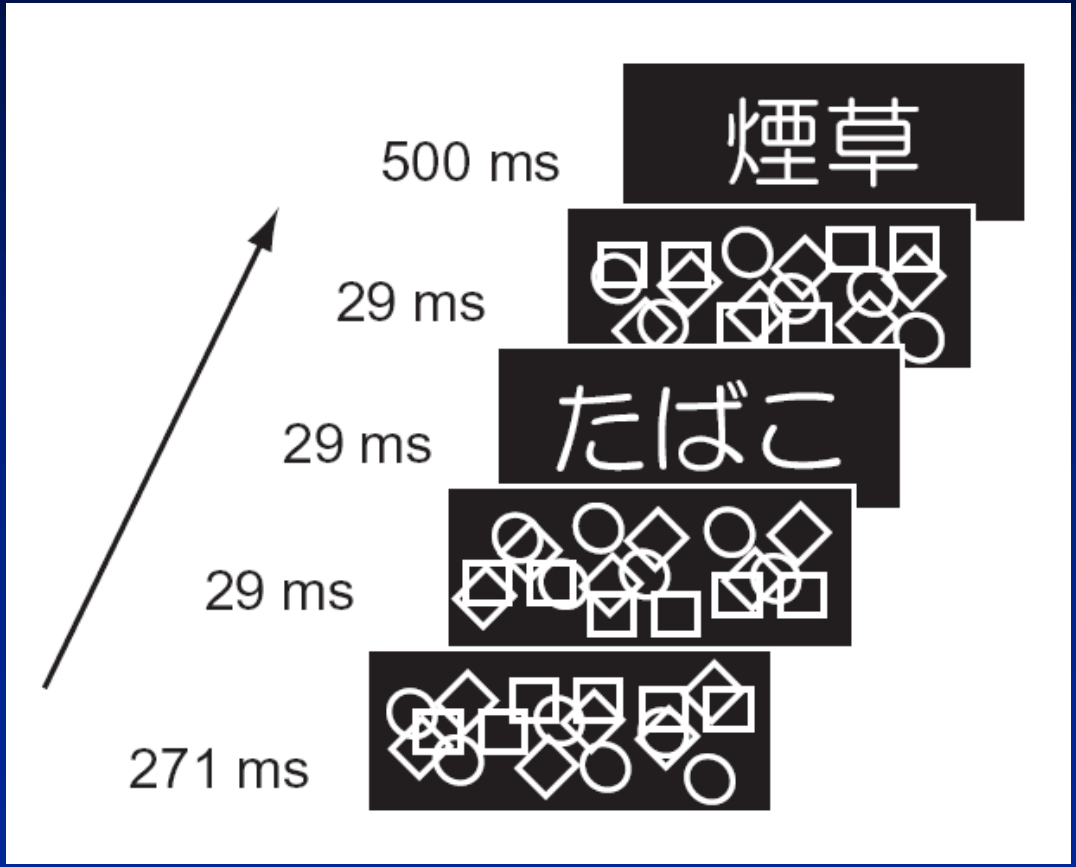
Local combination detectors: A model of invariant visual word recognition



Priming within and across scripts in Japanese subjects

Design:

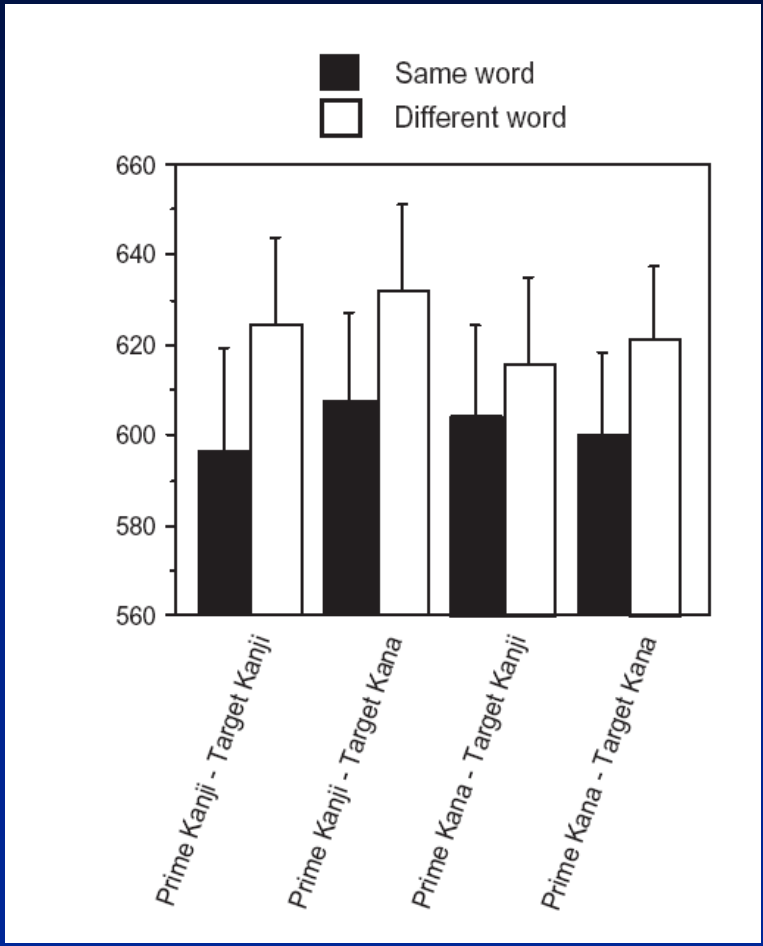
- Targets and primes can appear in Kanji or in Kana
- Task = semantic classification (natural/man-made)



Nakamura, Dehaene et al., JOCN, 2005

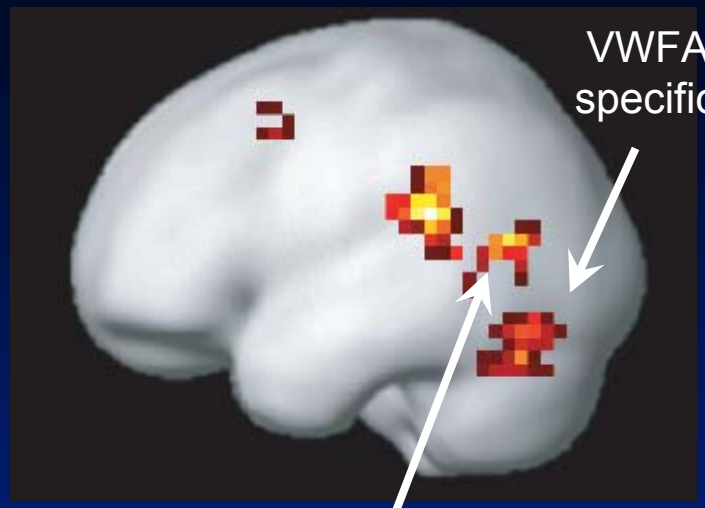
Repetition priming in Japanese

Within and cross-script priming in response times



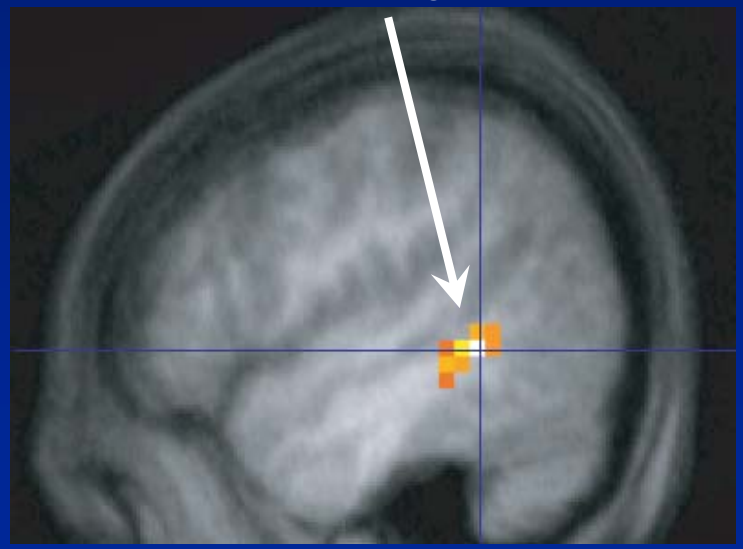
Nakamura, Dehaene et al., JOCN, 2005

Repetition priming with Kanji primes and Kanji targets



VWFA: Script-specific priming

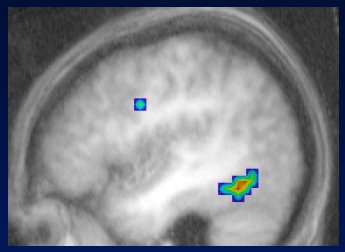
Left middle temporal region: Cross-script priming (semantic?)



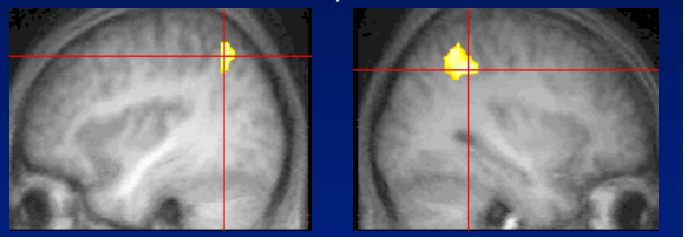
Evidence for extensive subliminal processing using fMRI priming

- Orthographic priming
  - Left fusiform gyrus (Dehaene et al, 2001; Devlin et al, 2004)
- Semantic priming
  - Numerical proximity in bilateral intraparietal sulci (Naccache and Dehaene, 2001)
  - Semantic proximity of words in left middle temporal gyrus (Devlin et al, 2004; Nakamura, Dehaene et al, 2005)
  - Amygdala activation by masked emotional words (Naccache et al, 2005)
- Motor priming
  - Bilateral motor areas (Dehaene et al., 1998)

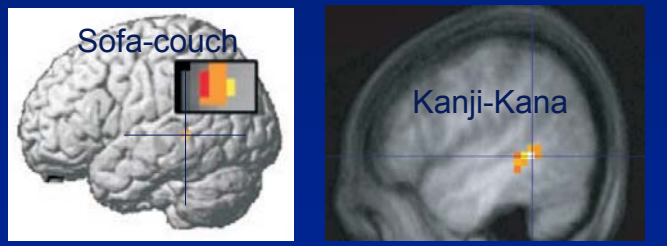
Visual word form area



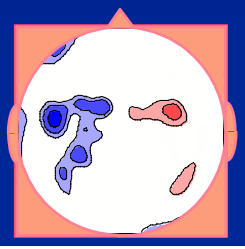
bilateral intraparietal sulci



Left middle temporal gyrus



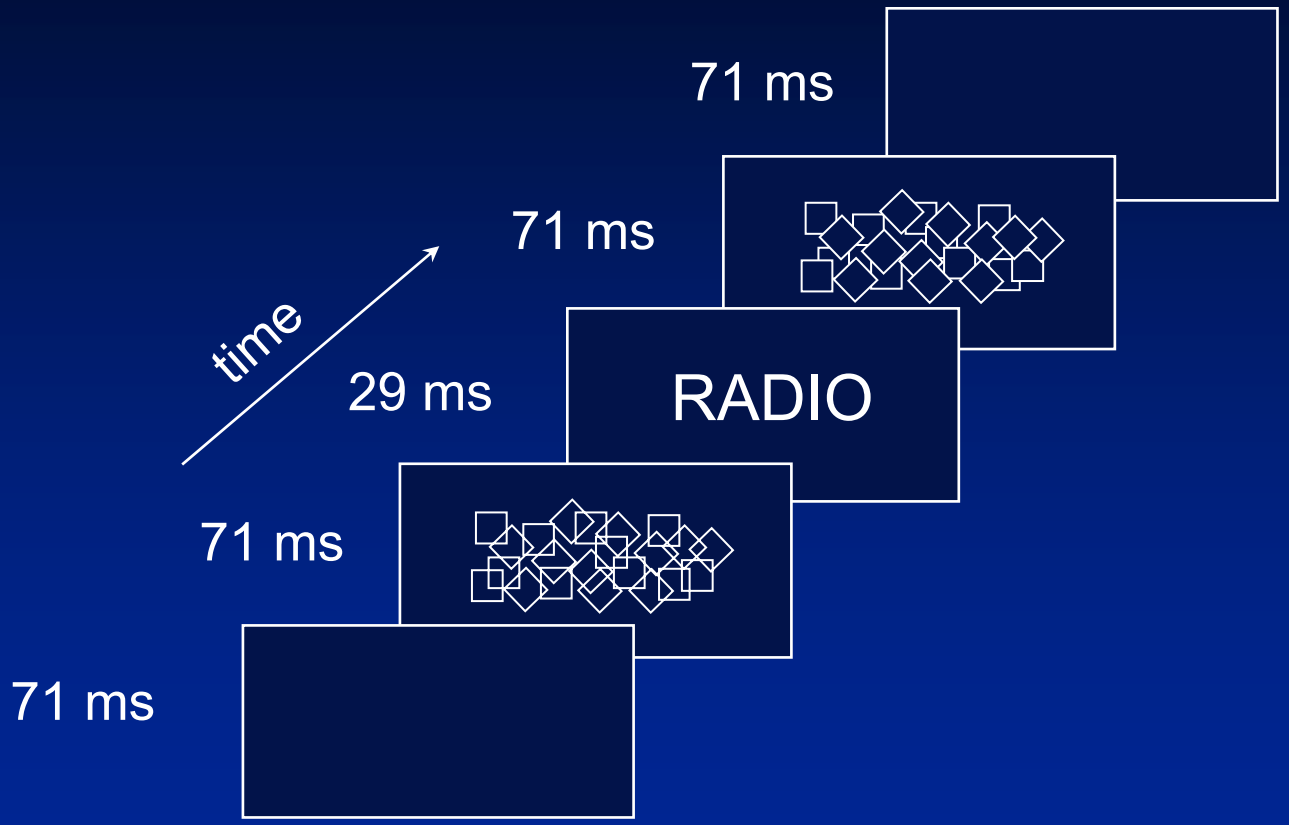
Motor lateralized readiness potential



Part II. The nature of conscious access

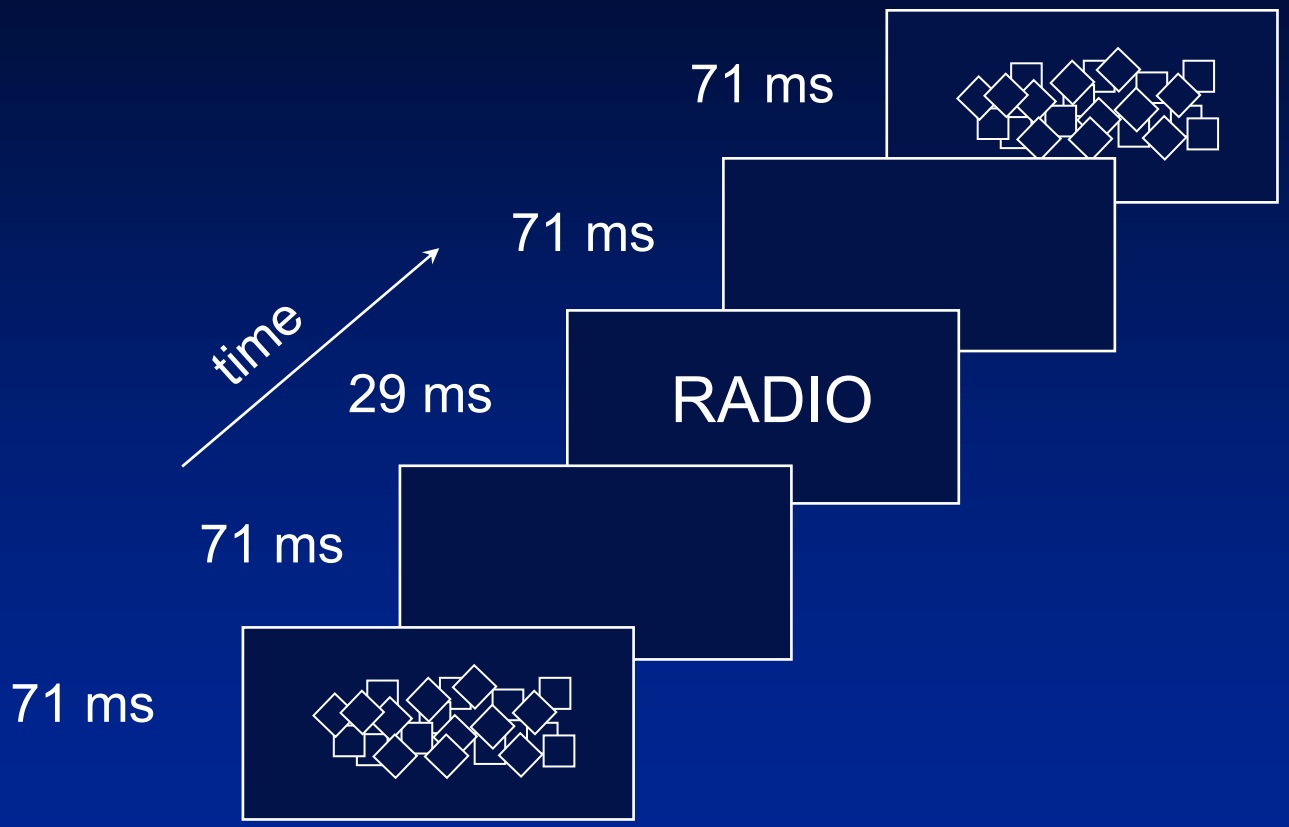
- **Conscious access is associated with a sudden activation of a distributed parieto-prefrontal network**

Making a word visible again



Dehaene et al., *Nature Neuroscience*, 2001

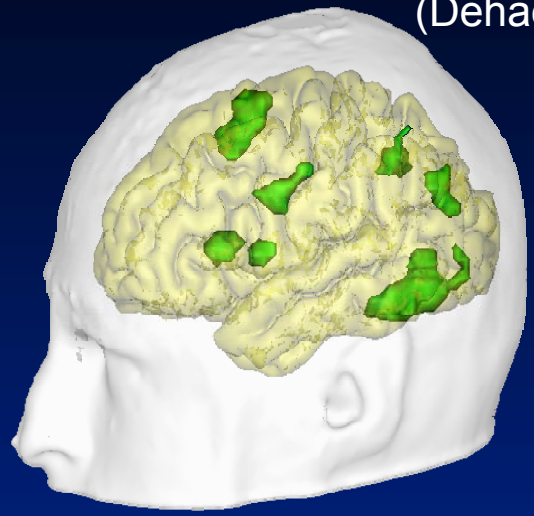
Making a word visible again

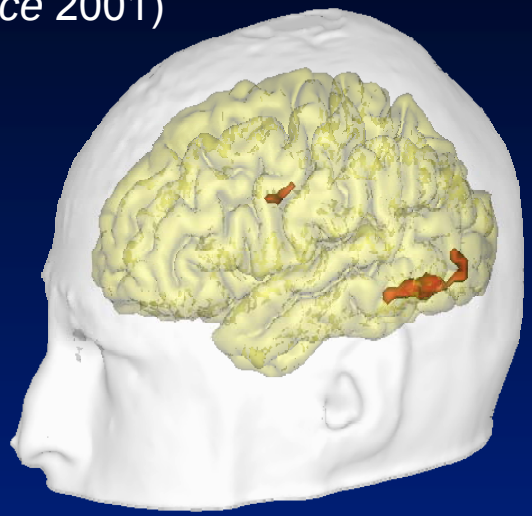


Dehaene et al., *Nature Neuroscience*, 2001

Consciousness correlates with
-Local amplification in the relevant processors
-Global parieto-frontal activity

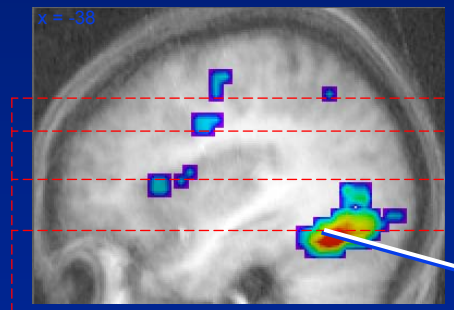
(Dehaene et al, *Nature Neuroscience* 2001)

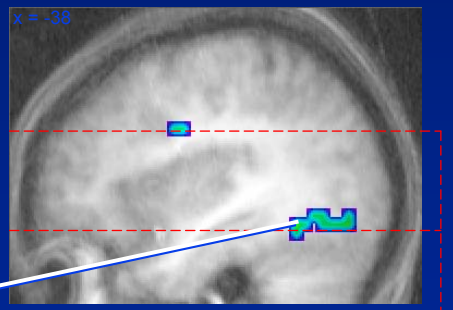


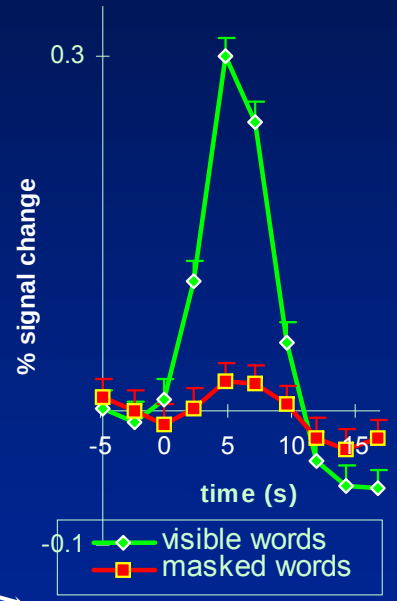


visible words

masked words

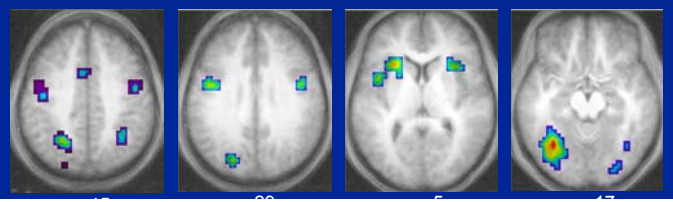


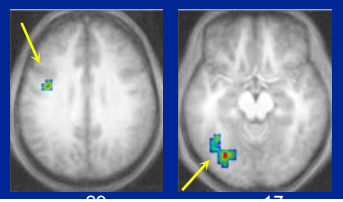




left fusiform gyrus

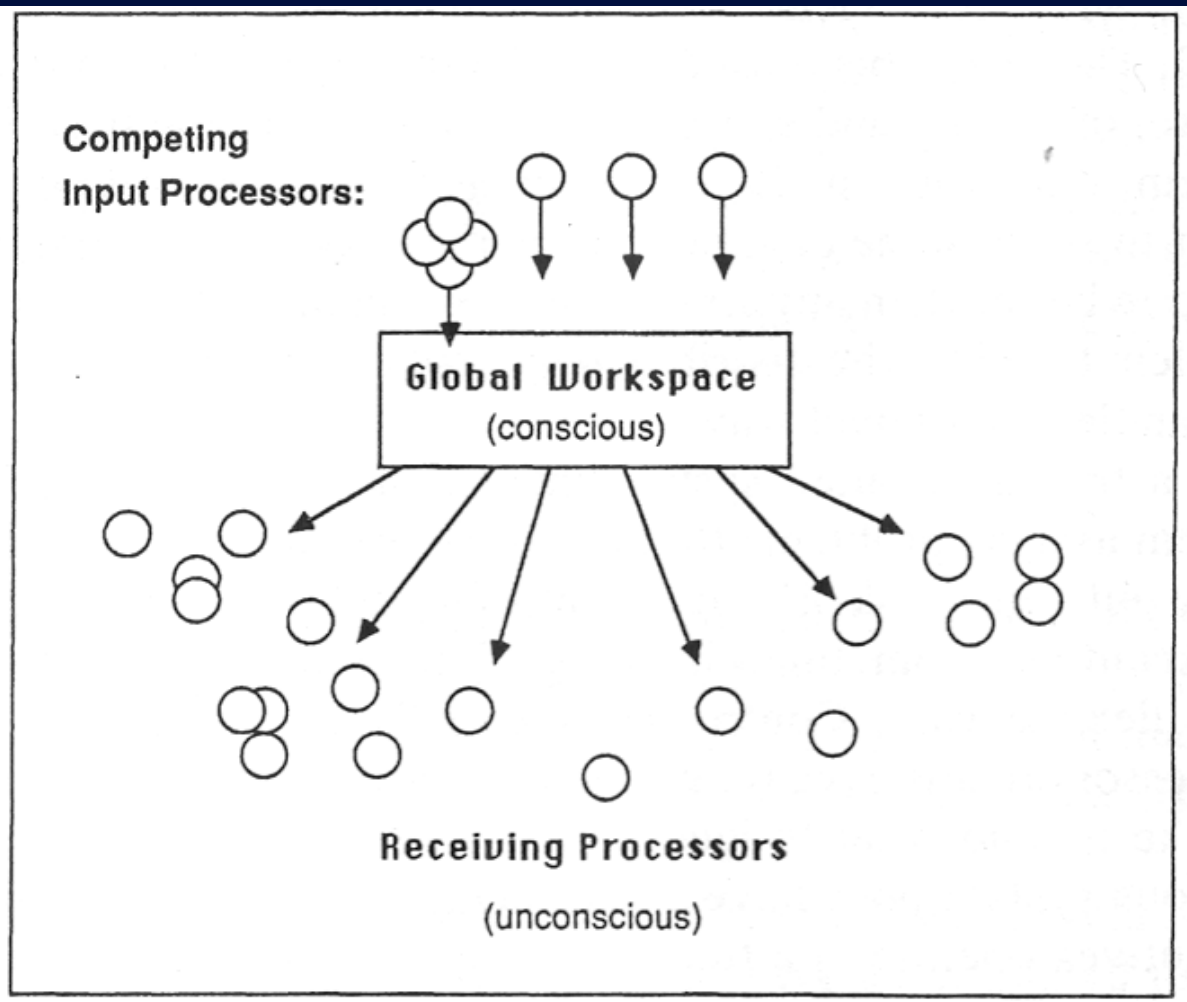
(-48, -60, -12)





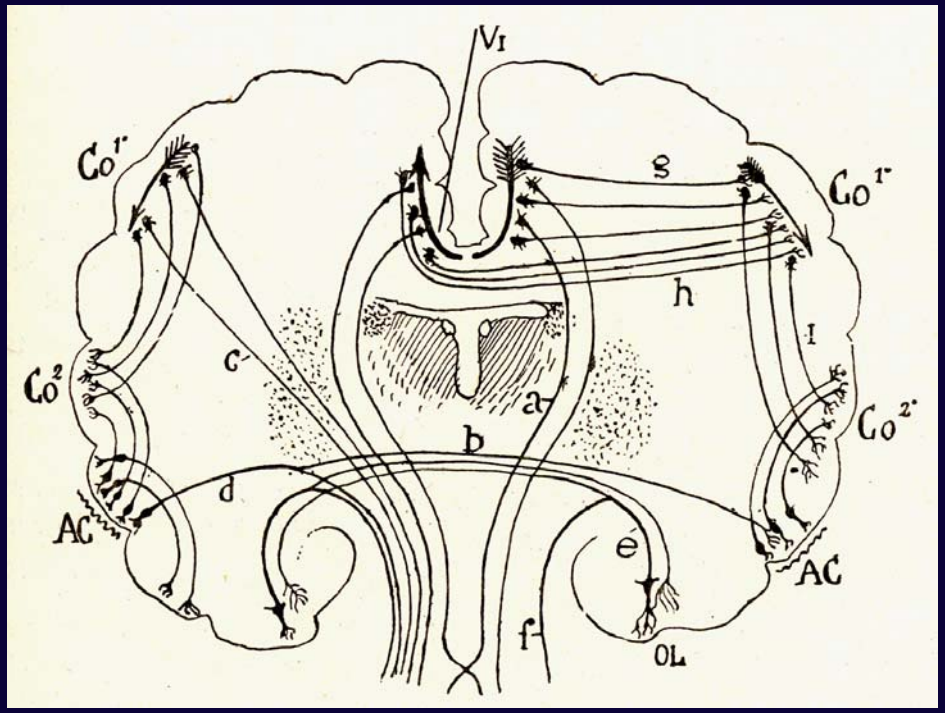
Baar's (1989) theory of a conscious global workspace:

An architecture mixing parallel and serial processing



Model 1. A global workspace in a distributed system.

What is the neural basis of the global workspace?

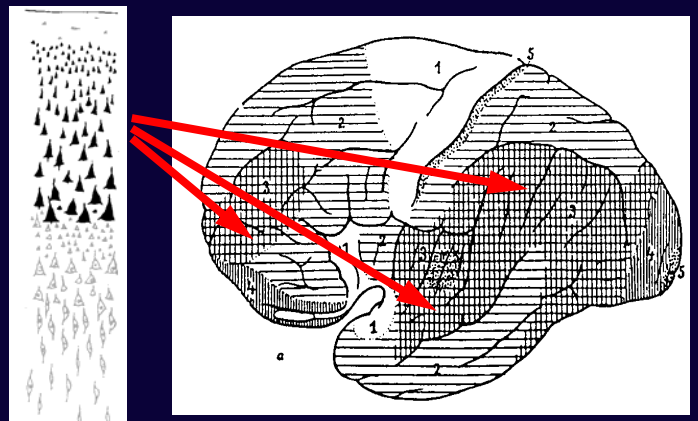


…the intellectual activity, the will and self-consciousness…
are the result of a combined action of a large number of mnemonic spheres

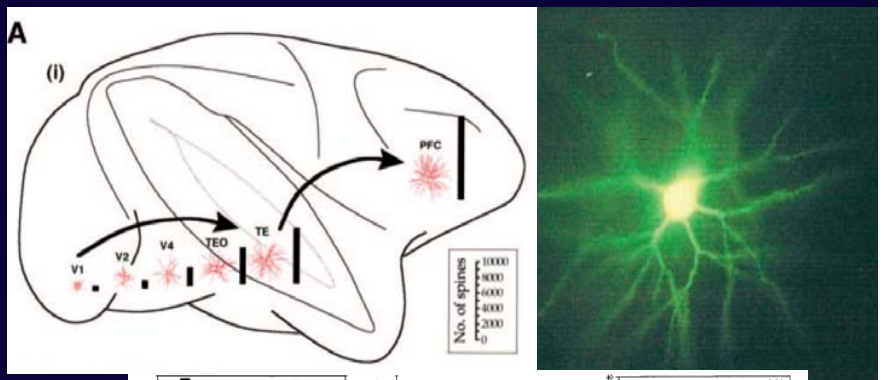
(Ramon y CAJAL, *Histologie*, p.878)

Prefrontal cortex and temporo-parietal association areas form long-distance networks

Von Economo (1929):
Greater layer II/III thickness



Guy Elston (2000)
Greater arborizations and spine density



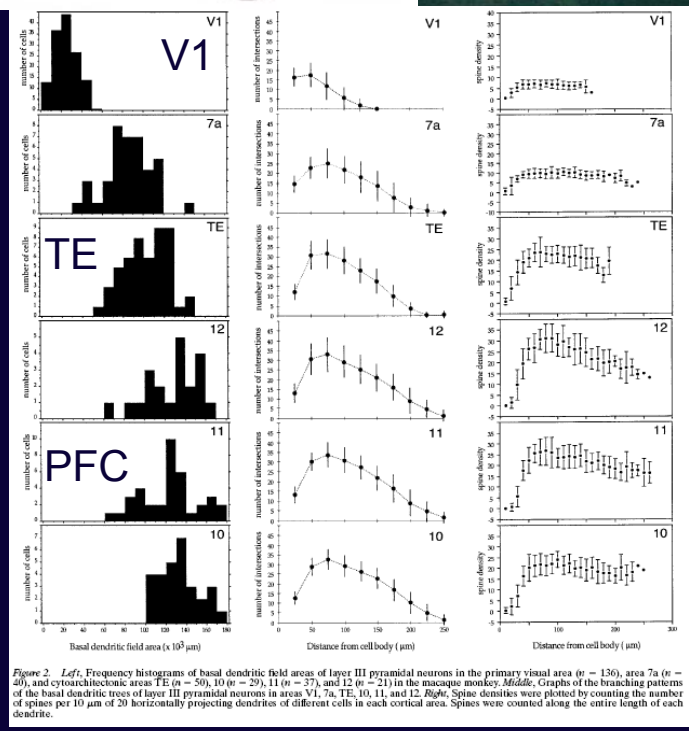
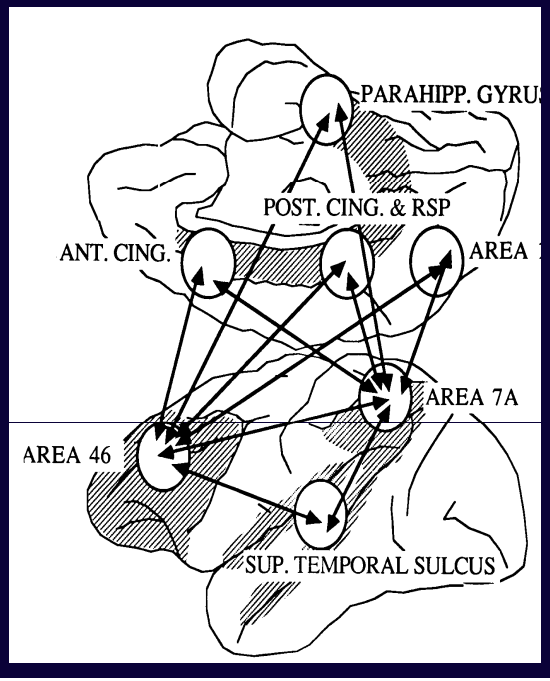
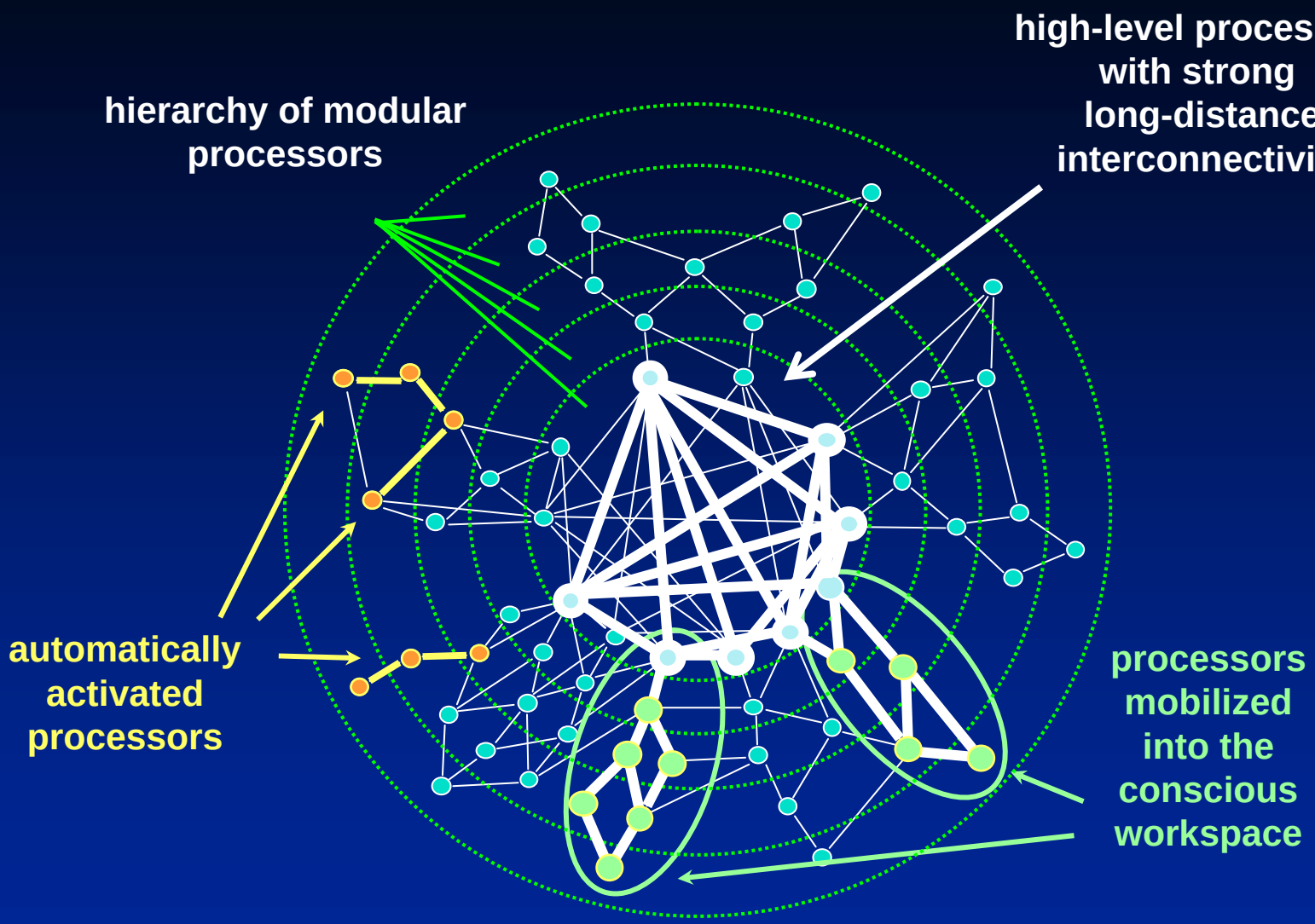


Figure 2. *Left*, Frequency histograms of basal dendritic field areas of layer III pyramidal neurons in the primary visual area ($n = 136$), area 7a ($n = 40$), and cytoarchitectonic areas TE ($n = 50$), 10 ($n = 29$), 11 ($n = 37$), and 12 ($n = 21$) in the macaque monkey. *Middle*, Graphs of the branching patterns of the basal dendritic trees of layer III pyramidal neurons in areas V1, 7a, TE, 10, 11, and 12. *Right*, Spine densities were plotted by counting the number of spines per 10 μm of 20 horizontally projecting dendrites of different cells in each cortical area. Spines were counted along the entire length of each dendrite.

Pat Goldman-Rakic (1980s):
long-distance connectivity of dorso-lateral prefrontal cortex



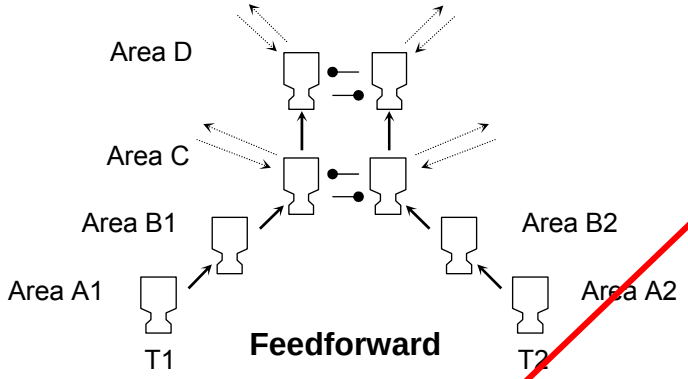
The global neuronal workspace model

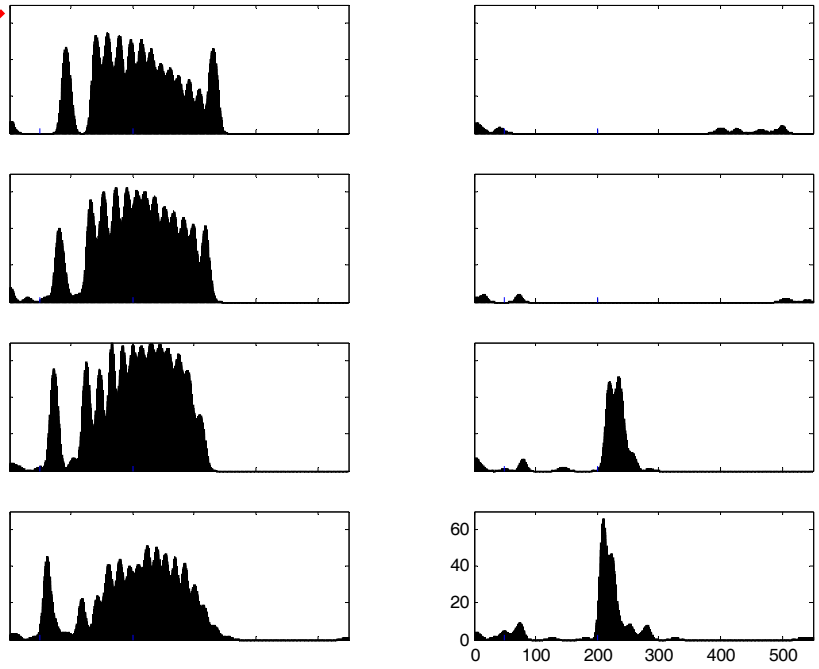


Dehaene, Kerszberg & Changeux, *PNAS,* 1998
Dehaene & Changeux, *PNAS,* 2003; PLOS, 2005
inspired by Mesulam, Brain, 1998

Detailed simulations of the global neuronal workspace using a semi-realistic network of spiking neurons

(Dehaene et al., *PNAS* 2003, *PLOS Biology*, *2005*)

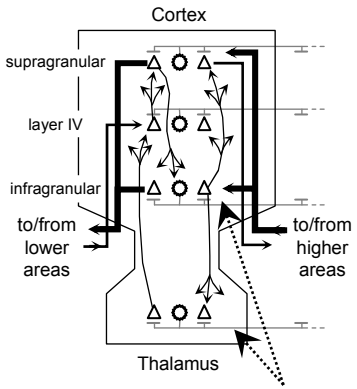




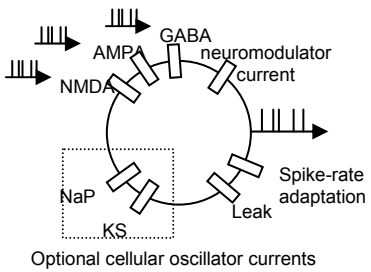
« Ignition » of the global workspace by target T1

Failure of ignition by target T2

Thalamocortical column



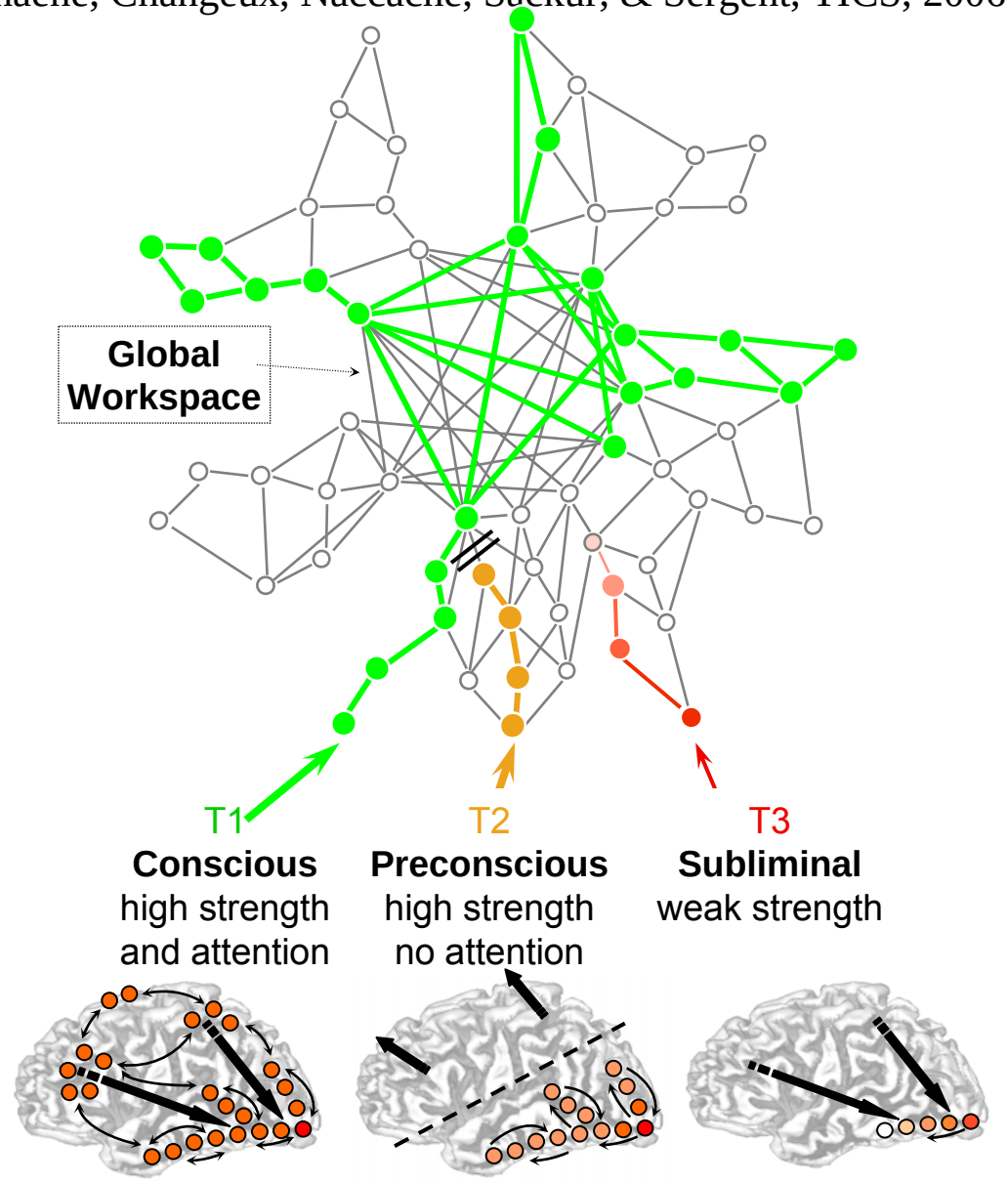
Spiking neurons



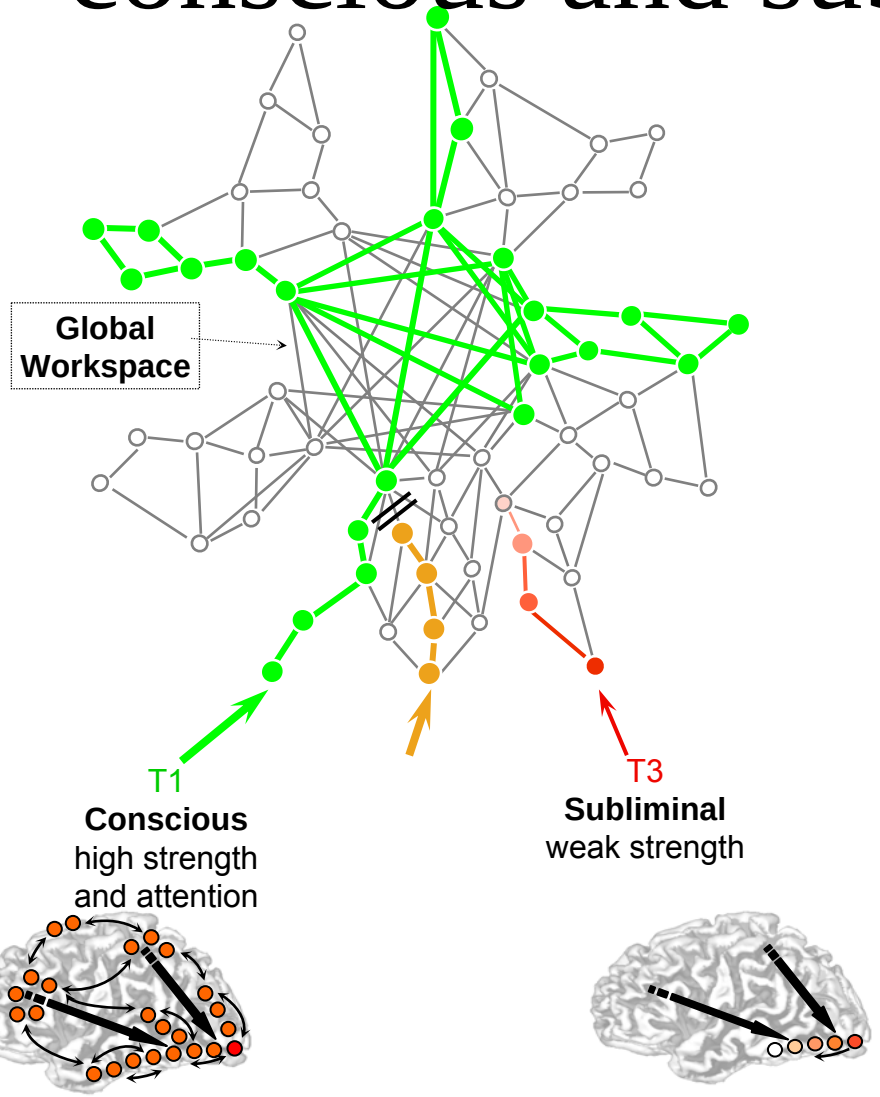
Dehaene, Sergent, & Changeux, *PNAS*, 2003

Three distinguishable states of **subliminal**, **preconscious** and **conscious** processing

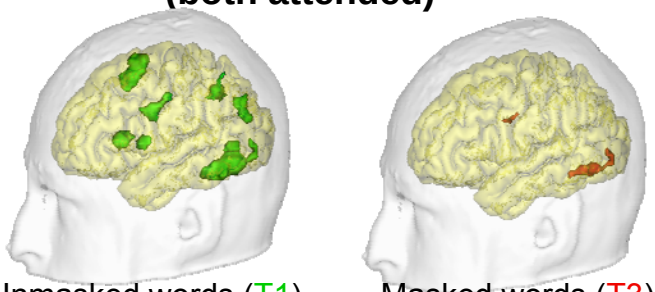
Dehaene, Changeux, Naccache, Sackur, & Sergent, TICS, 2006[2]



Contrast between conscious and subliminal processing



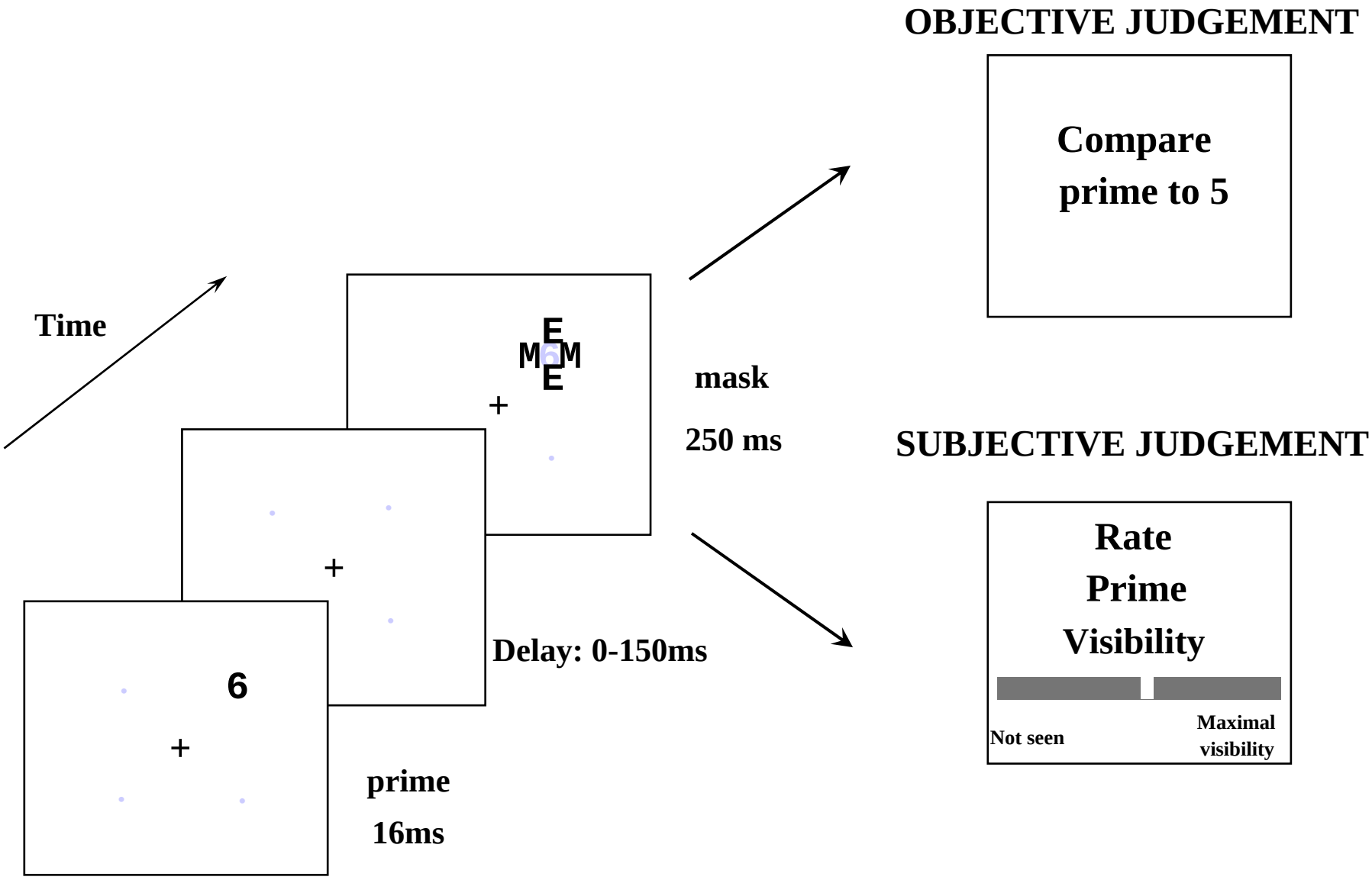
T1 versus T3 : unmasked versus masked stimuli (both attended)



Unmasked words (T1)

Masked words (T3)

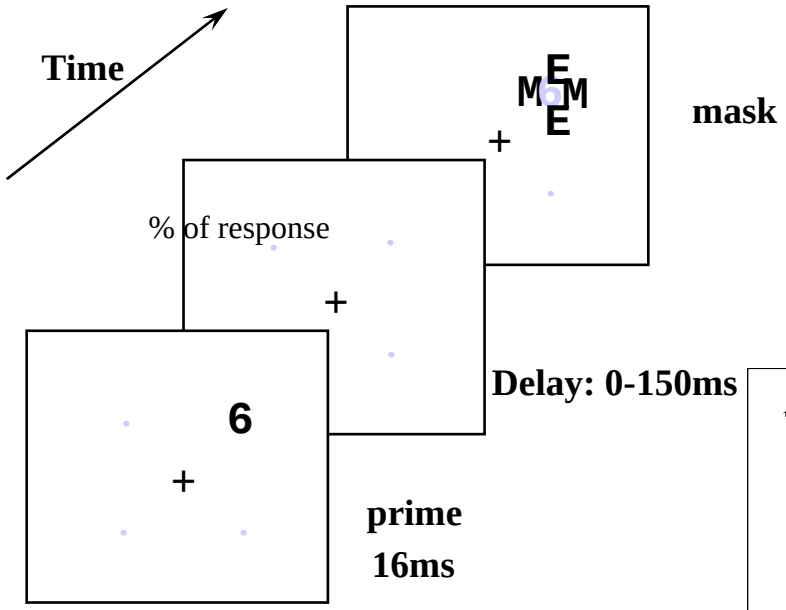
DIGIT MASKING PARADIGM

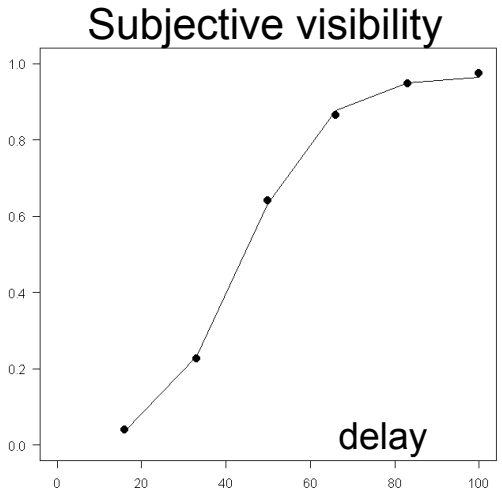


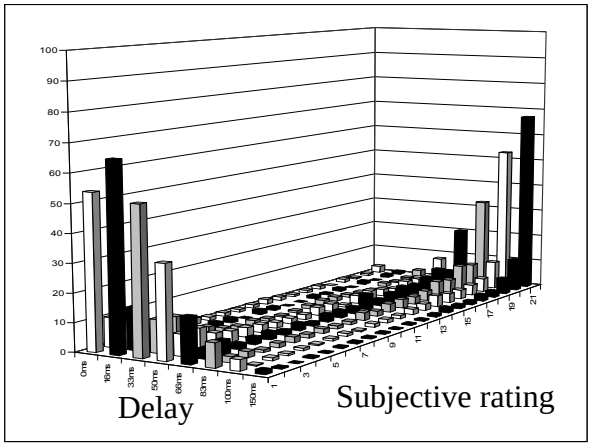
Antoine Delcul

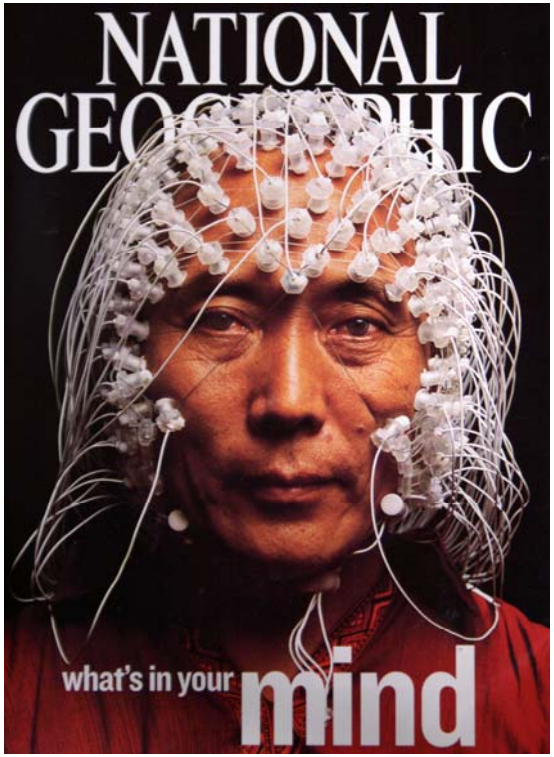
Exploring the cerebral mechanisms of the non-linear threshold in conscious access

(Delcul and Dehaene, PLOS Biology 2007)



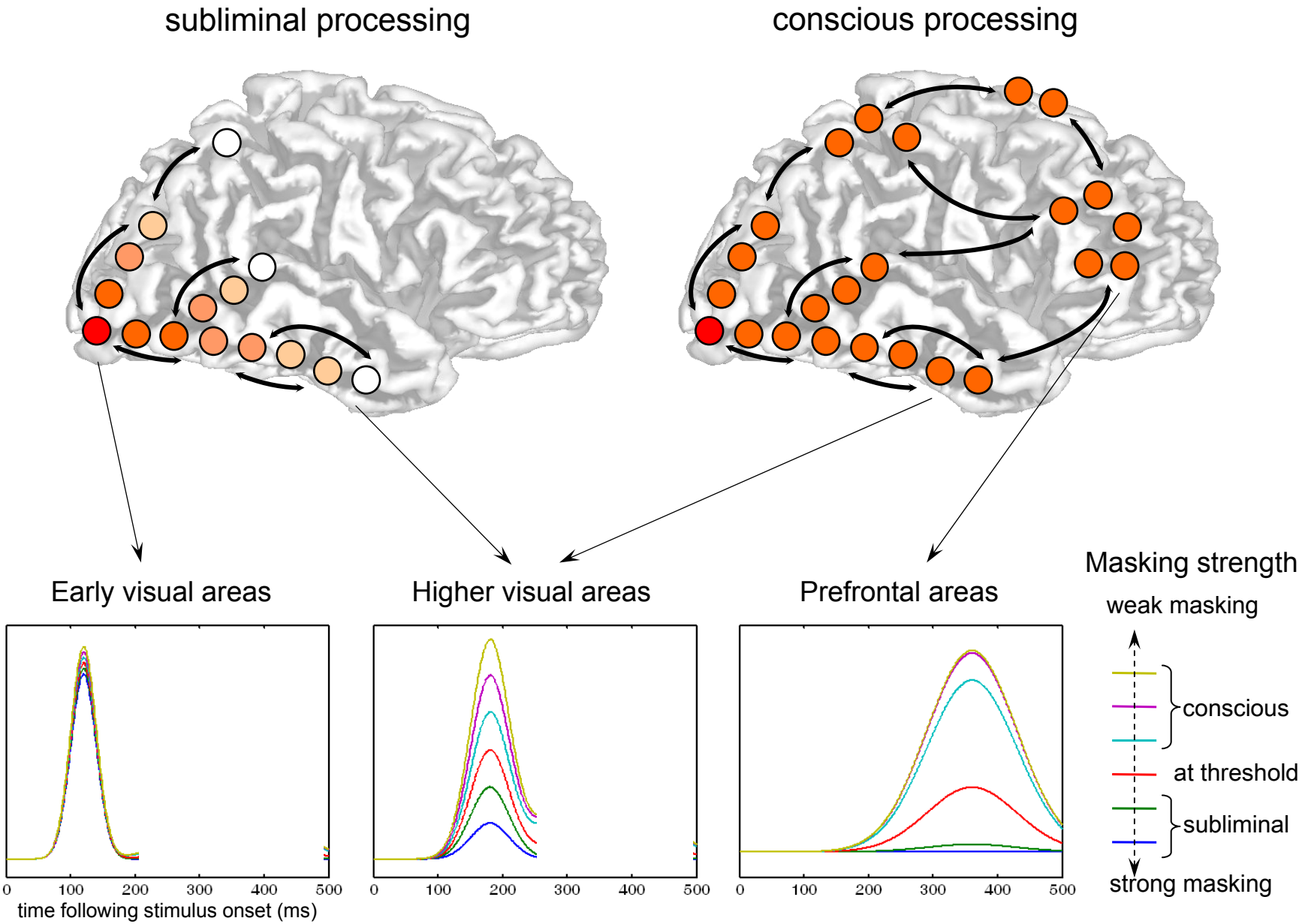






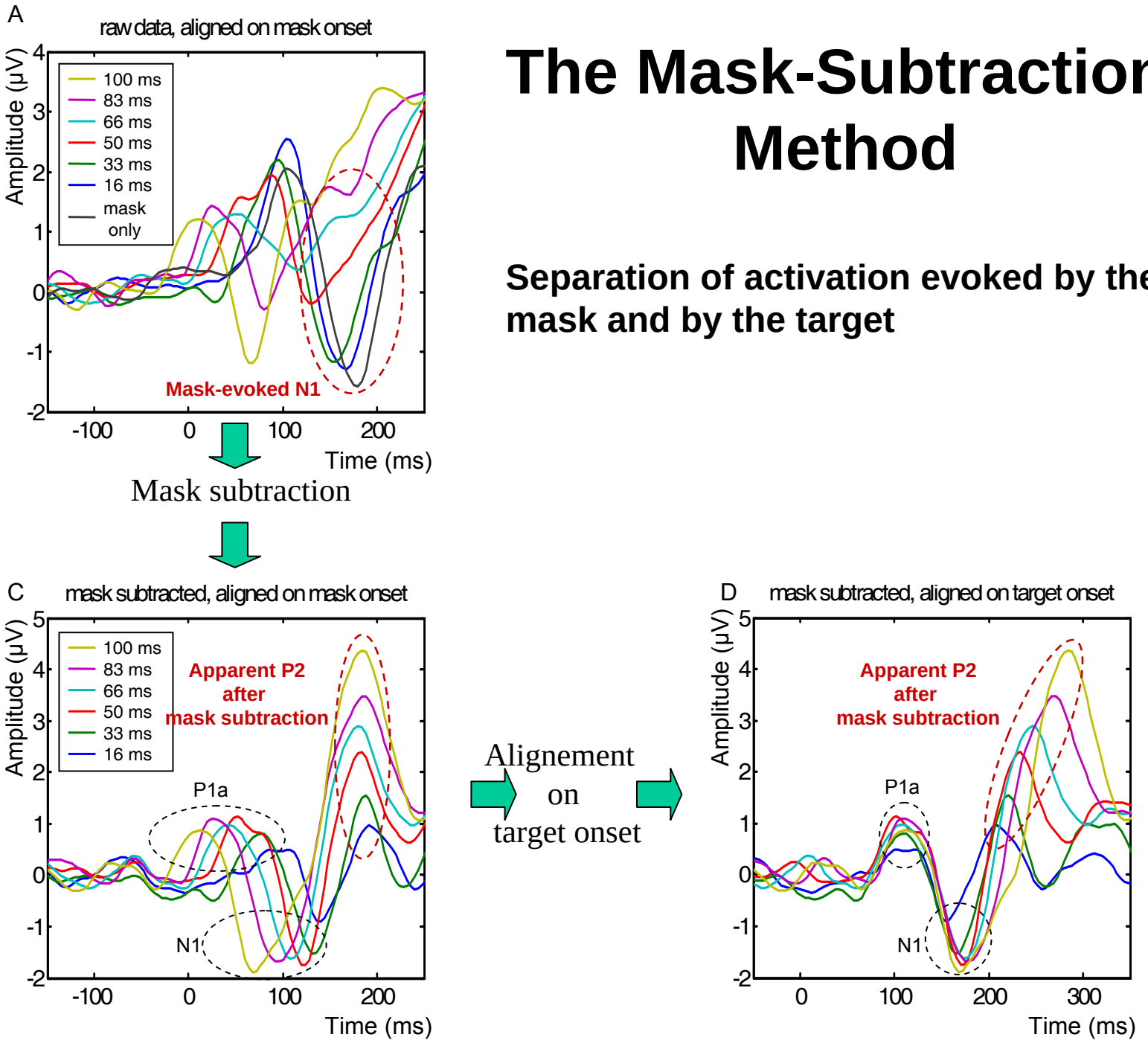
Logic = Use this sigmoidal profile as a « signature » of conscious access. Which ERP components show this profile?

Predictions of the global neuronal workspace model

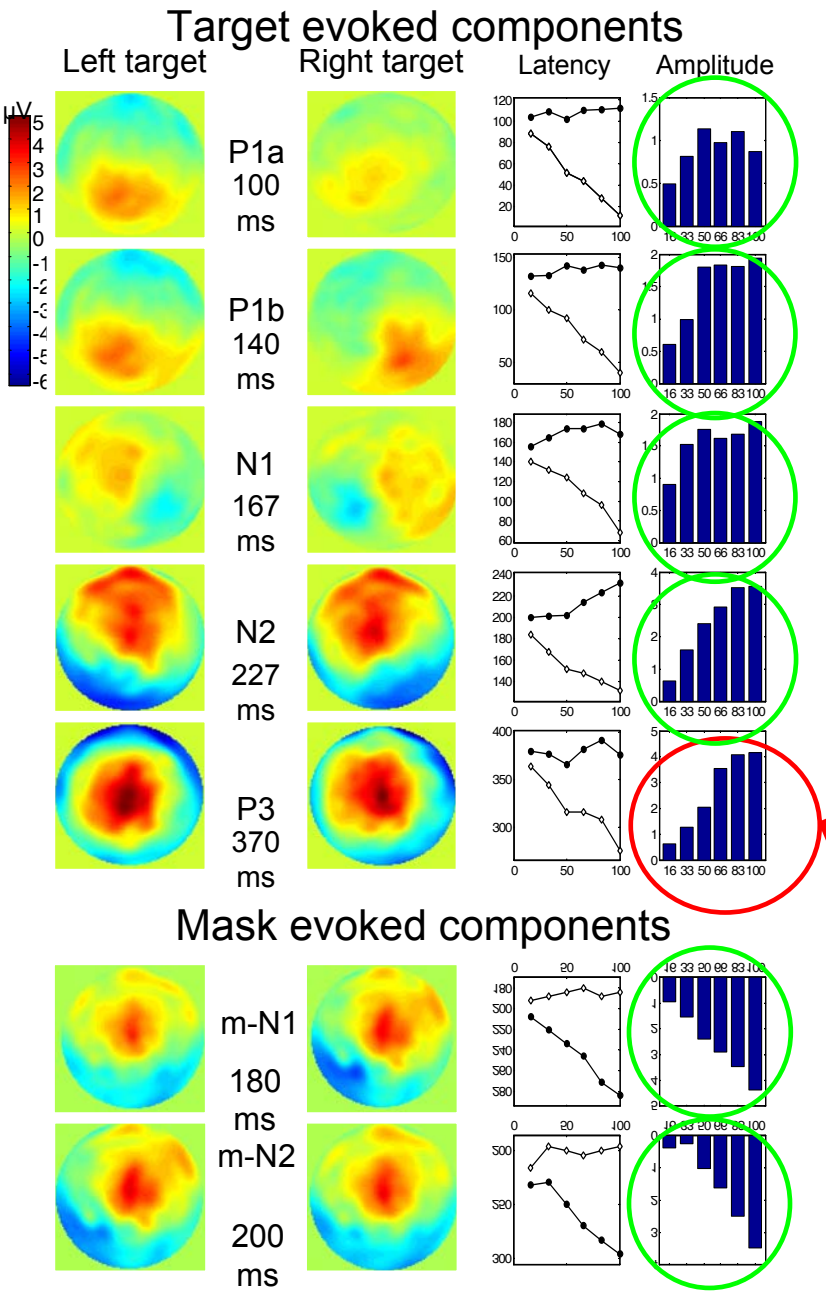


The Mask-Subtraction Method

Separation of activation evoked by the mask and by the target



Brain mechanisms of masking



Conclusions:

-Masking leaves the P1a and N1 essentially intact (except at the shortest SOA)

-Masking reduces the P1b (less inter-hemispheric transfer)

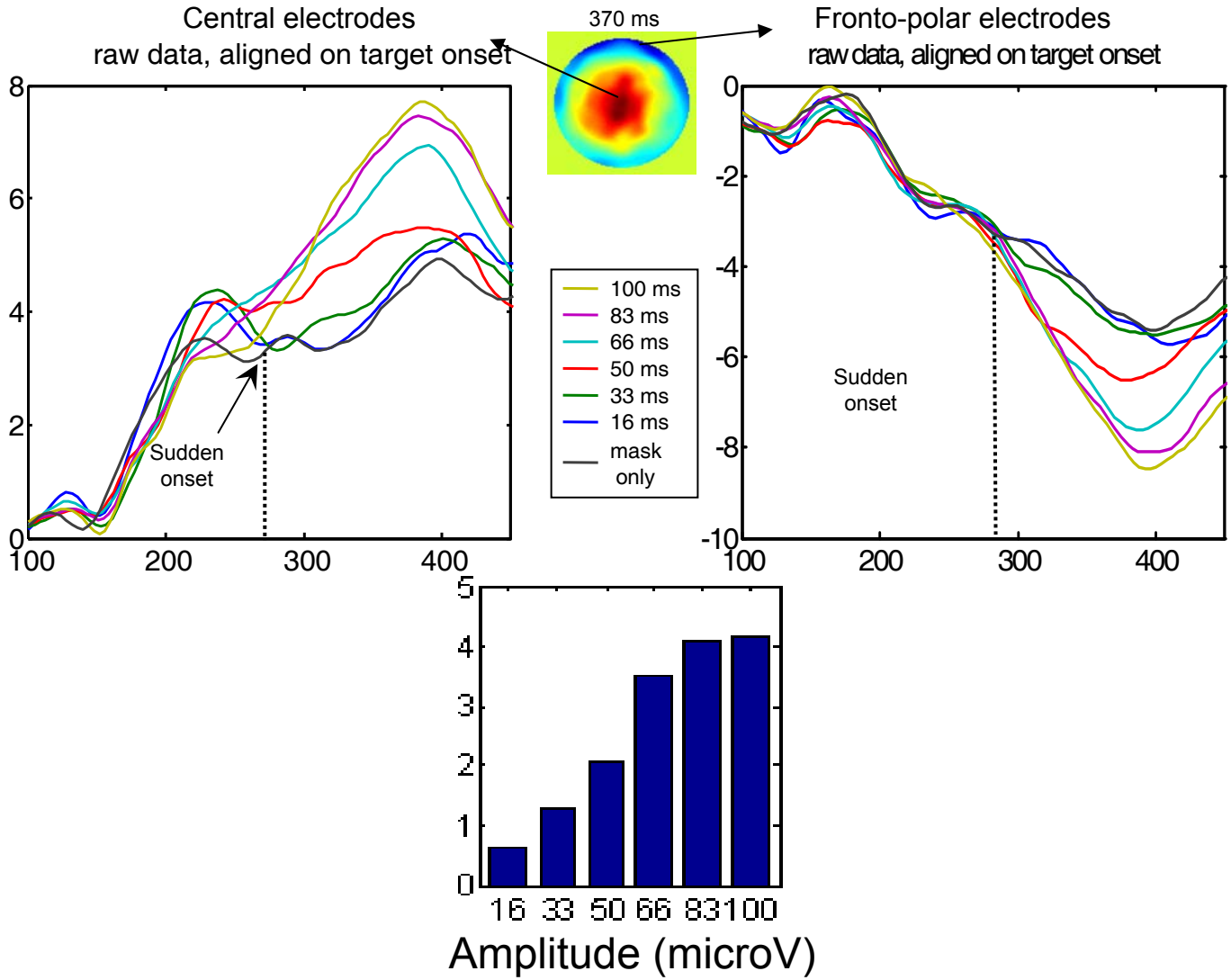
-Masking interrupts the N2

-As the masking delay increases

- -target activation become increasingly stronger and longer lasting
- -Mask activation decreases correspondingly

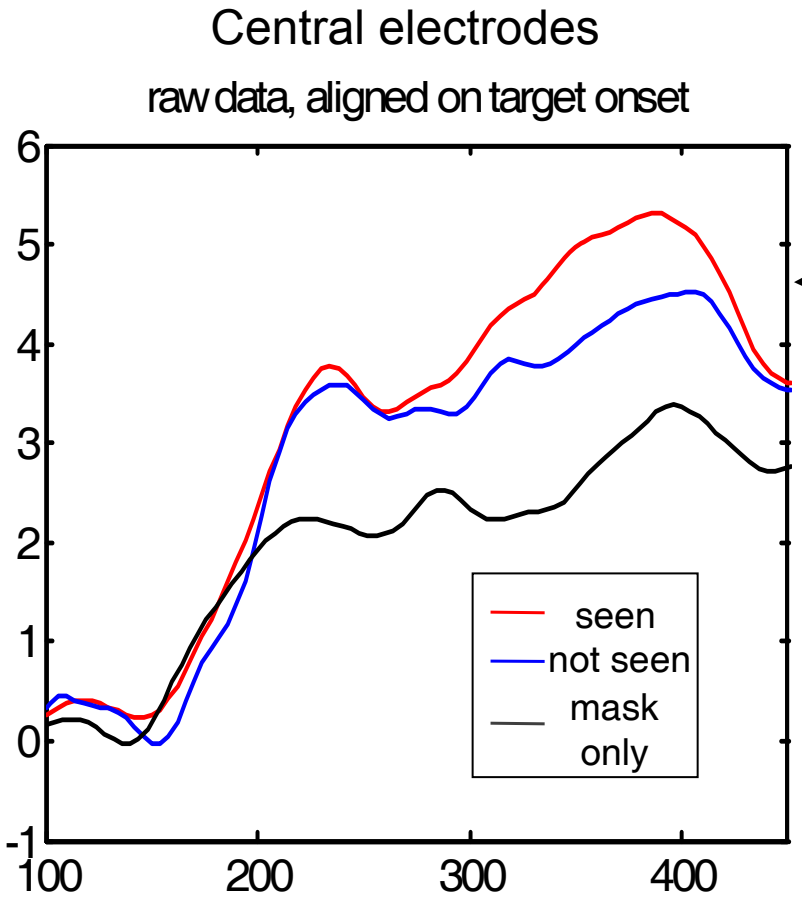
- Only the P3 shows a non-linearity similar to behavioral report

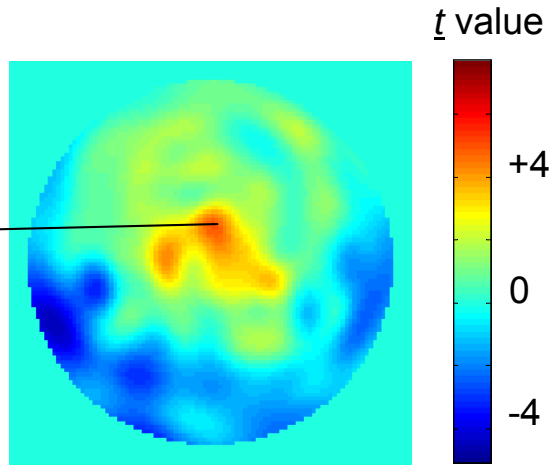
P3: sudden non linear divergence around 270 ms



A **second independent criterion** for conscious access: Only the amplitude of the P3 distinguishes **seen versus not-seen trials** at a fixed delay (50 ms)

(9 subjects only)





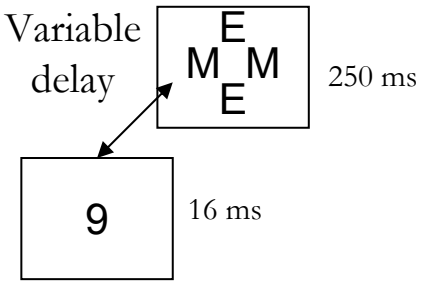
t-test at t=341 ms post target

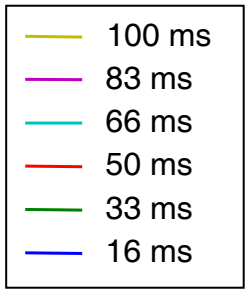
→Note, however, that the unseen stimuli evoke strong activation at SOA=50 ms.

→ All components showed a significant difference: Not-seen > mask-only

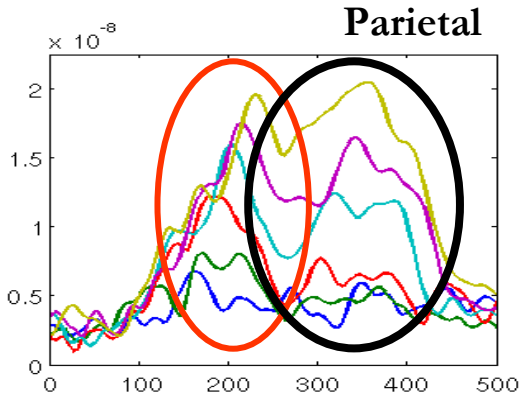
A late non-linearity underlying conscious access during masking

(Delcul et Dehaene, PLOS Biology 2007)

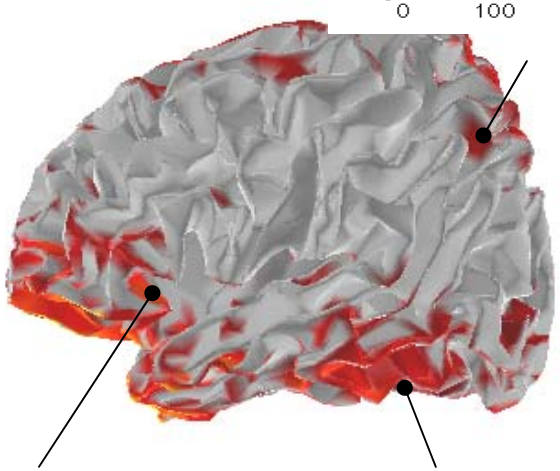




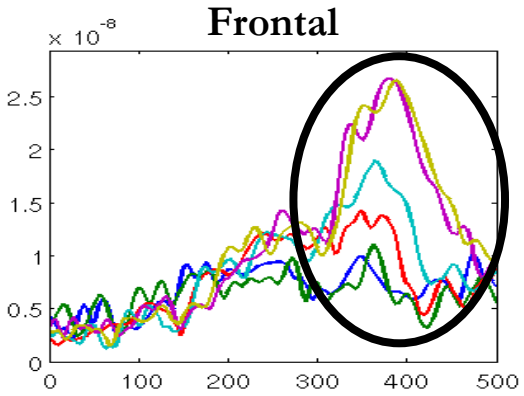
First phase: local and linear

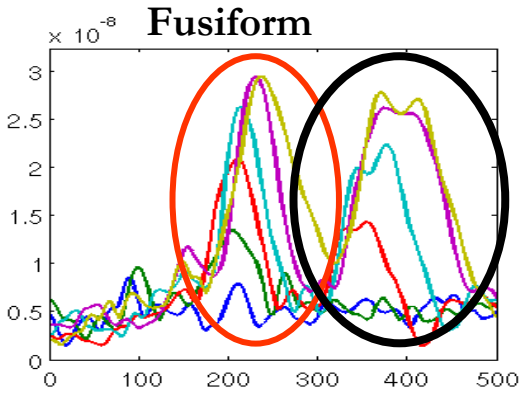


Distributed visual, parietal and prefrontal activity at the peak of the P3 (conscious trials)

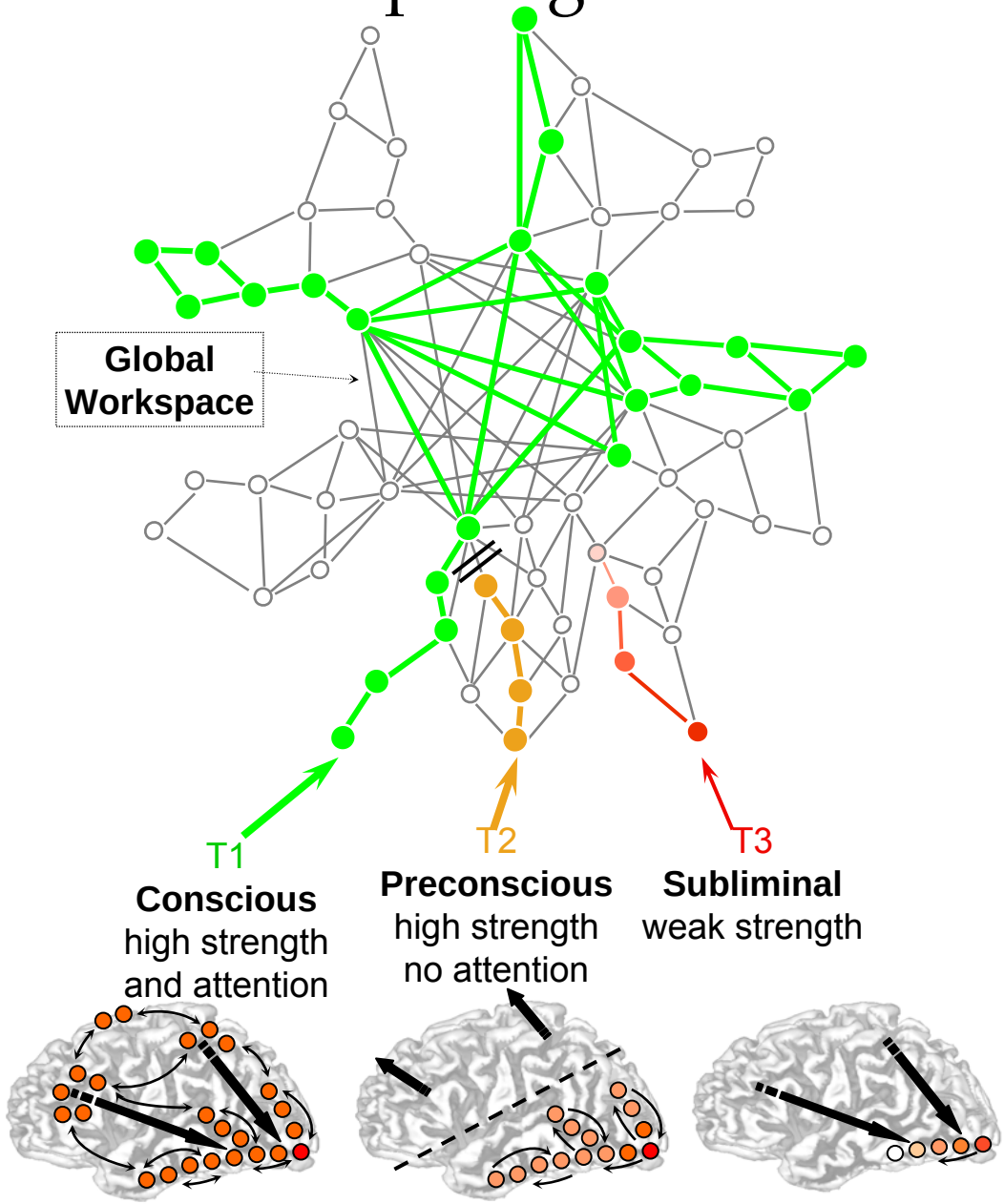


Second phase: global and non-linear (amplification)

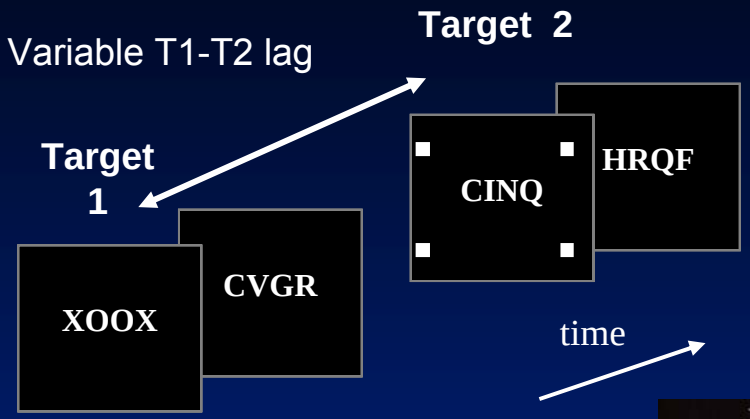


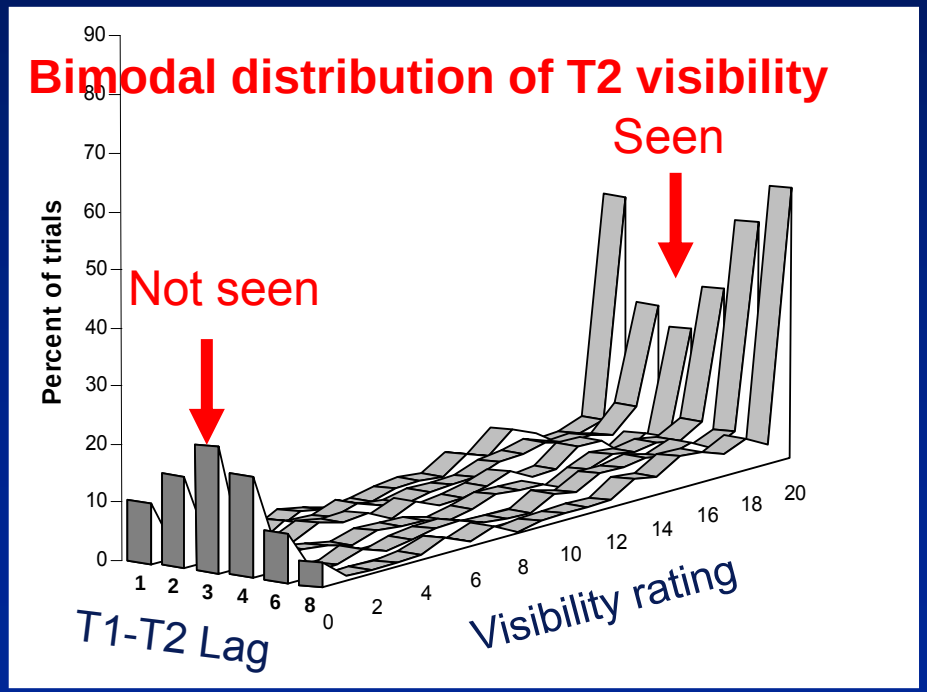


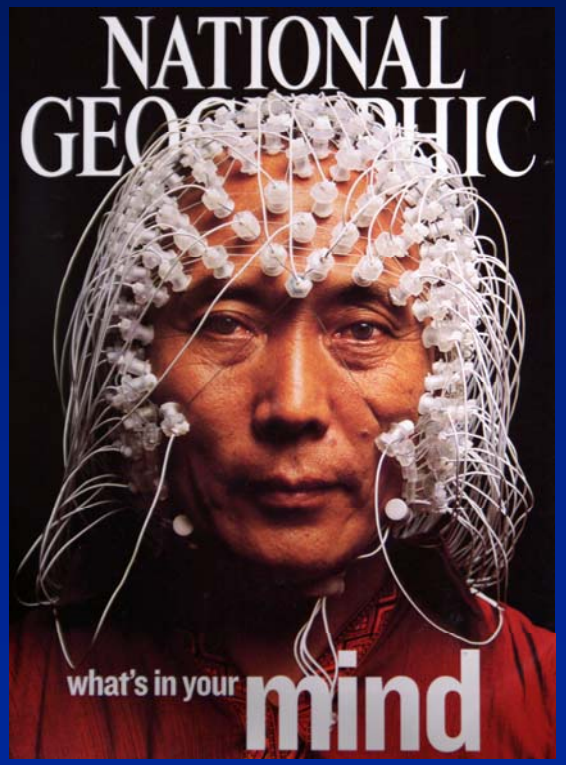
Test of the theory
2. with two competing stimuli during AB



Conscious access and non-conscious processing during the attentional blink







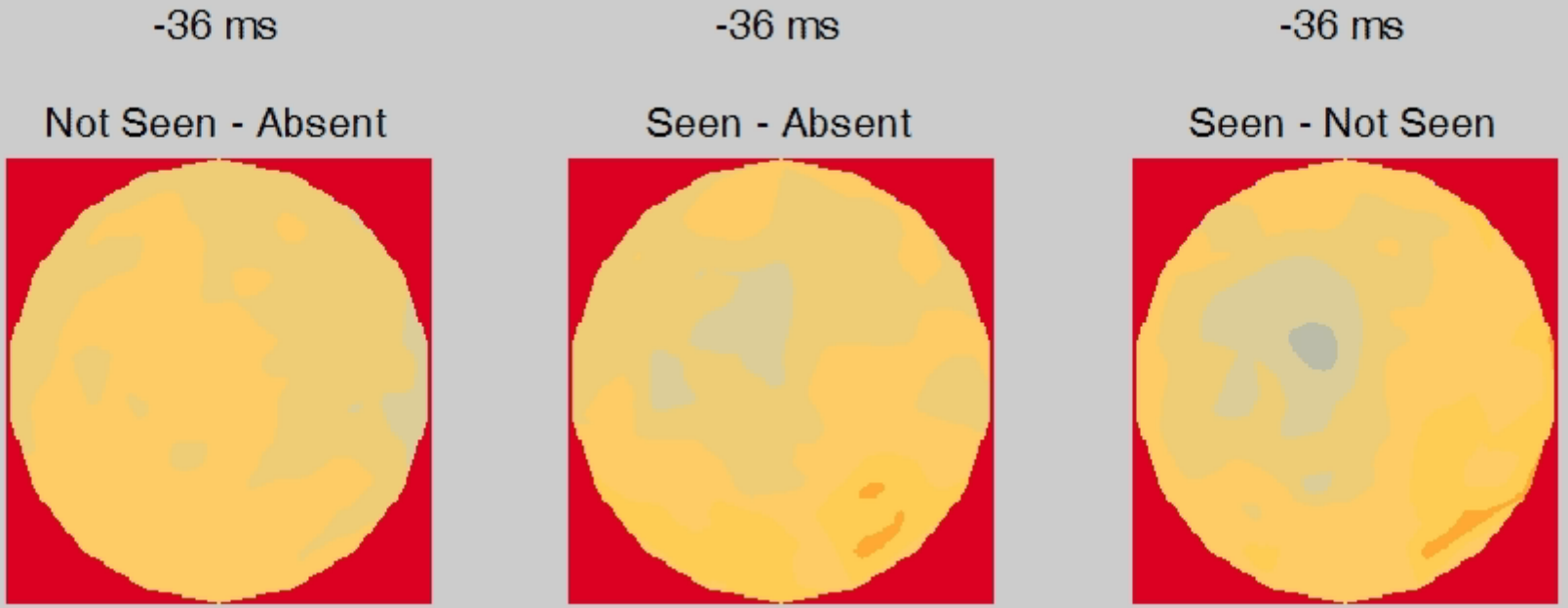
Sergent, Baillet & Dehaene, *Nature Neuroscience*, 2005

Time course of scalp-recorded potentials during the attentional blink

UNSEEN T2
(minus T2-absent trials)

SEEN T2
(minus T2-absent trials)

DIFFERENCE

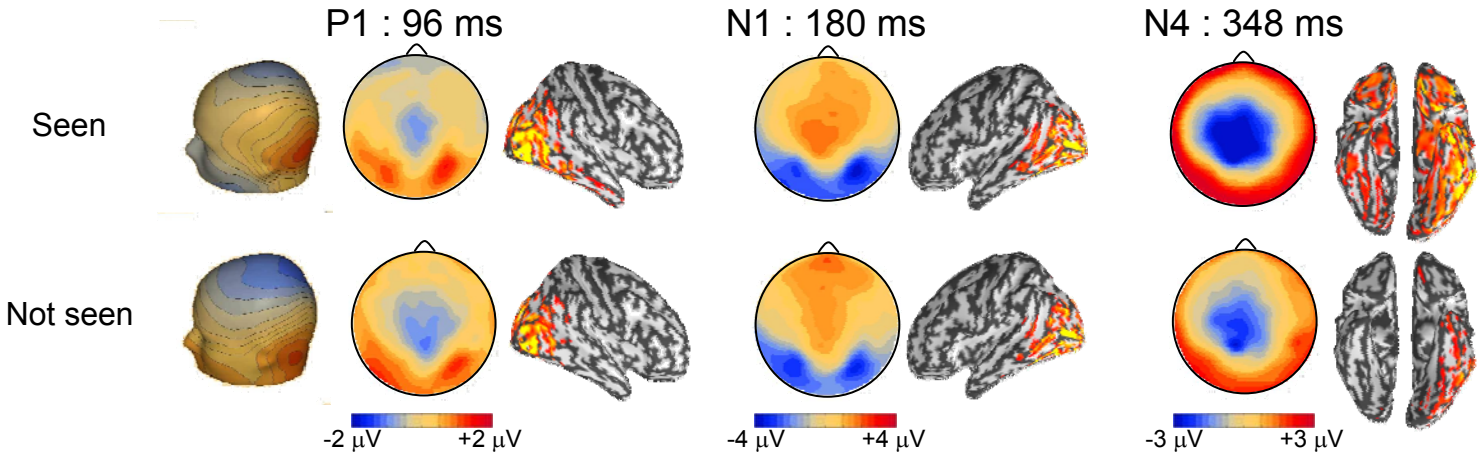


Sergent et al., *Nature Neuroscience*, 2005

Timing the divergence between seen and not-seen trials in the attentional blink (Sergent et al., *Nature Neuroscience* 2005)

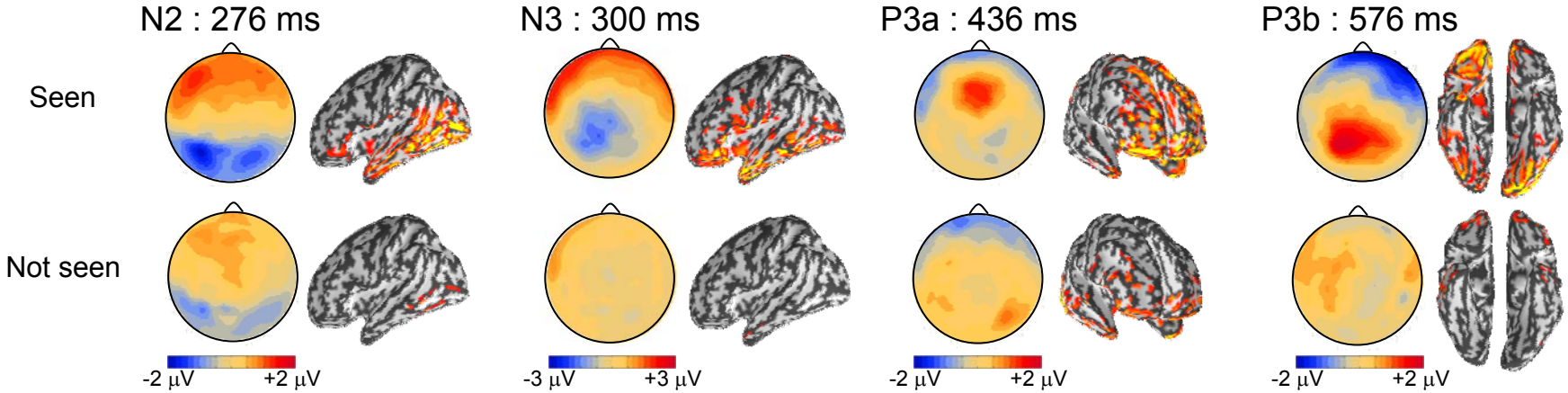
Unchanged initial processing

Late non-conscious processing



Abrupt divergence around 270 ms…

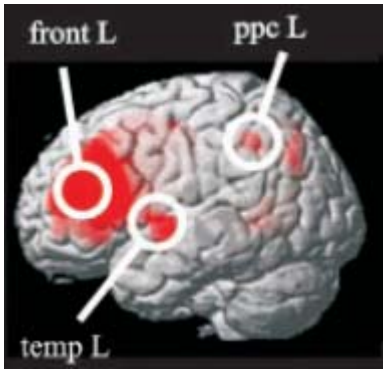
All-or-none ignition

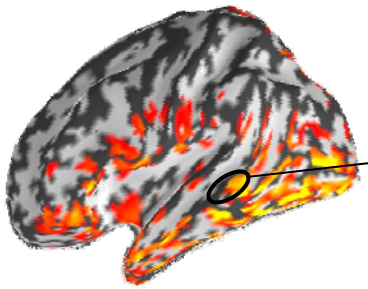


Difference between seen and not seen trials

Recording of ‘virtual sources’ at various cortical locations

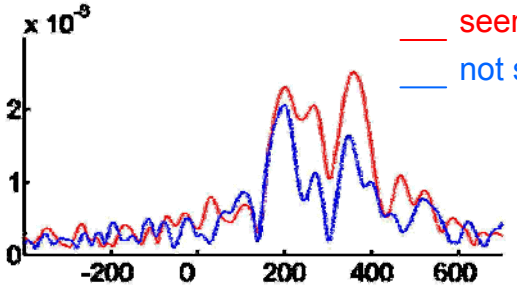
MEG:
Gross et al,
PNAS 2004



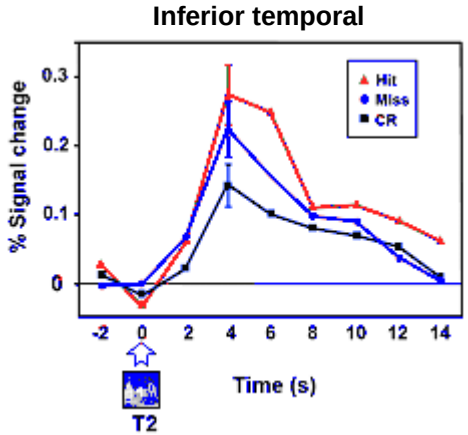


t = 300 ms

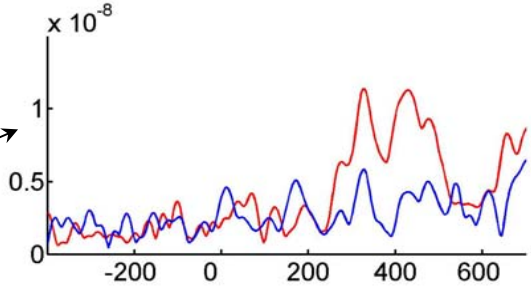
Middle temporal



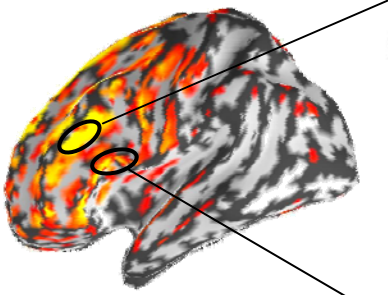
Inferior temporal



Dorsolateral prefrontal

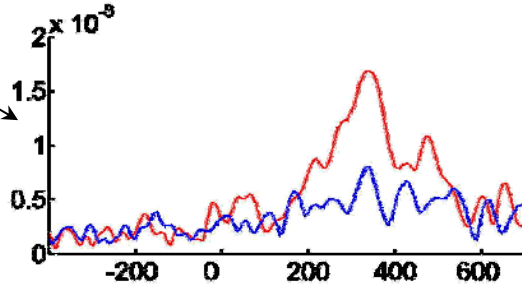


fMRI:
Marois et al,
Neuron 2004

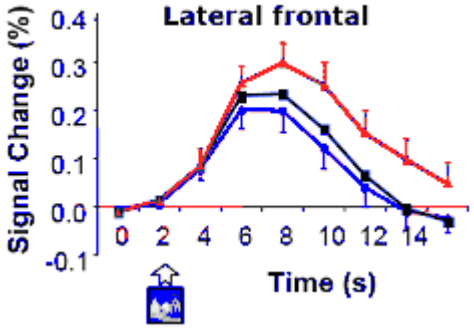


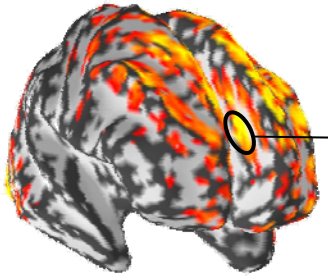
t = 436 ms

Inferior frontal



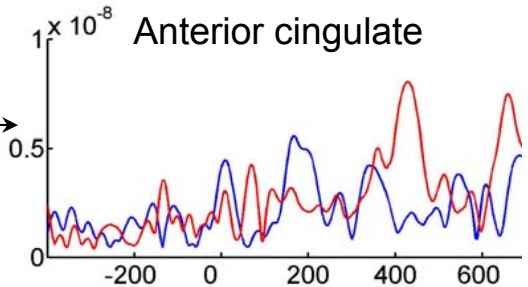
Lateral frontal



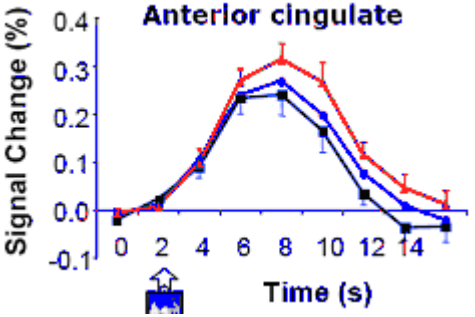


t = 436 ms

Anterior cingulate

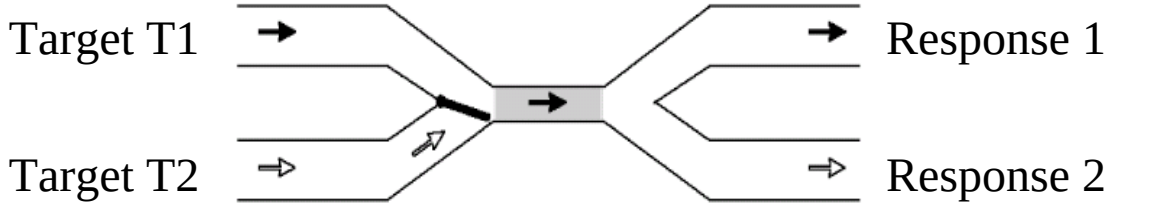


Anterior cingulate

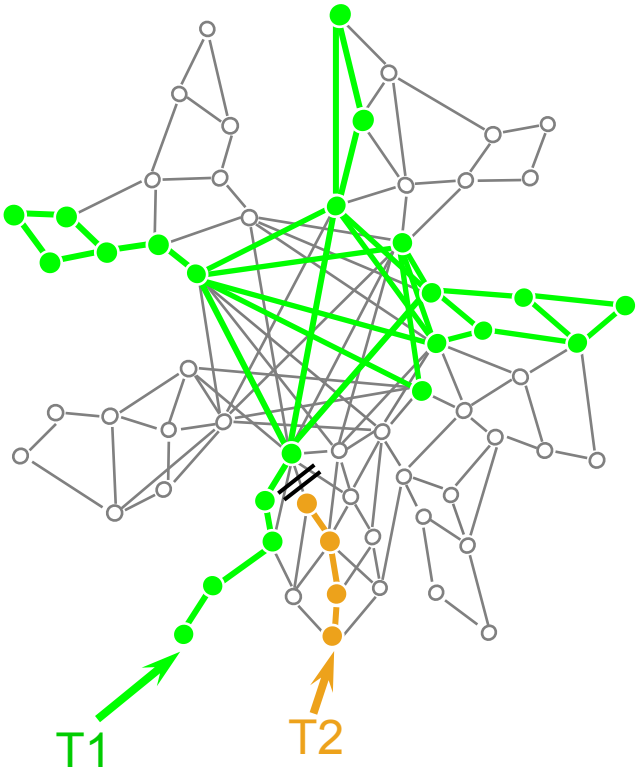


Test of the theory
3. with two competing stimuli during PRP

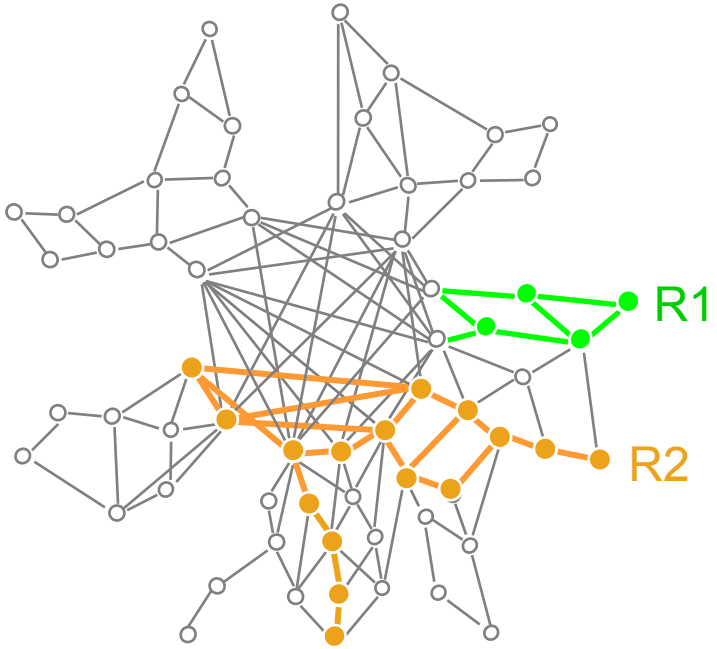
Pashler's « central bottleneck » model of the psychological refractory period



Workspace state for task 1

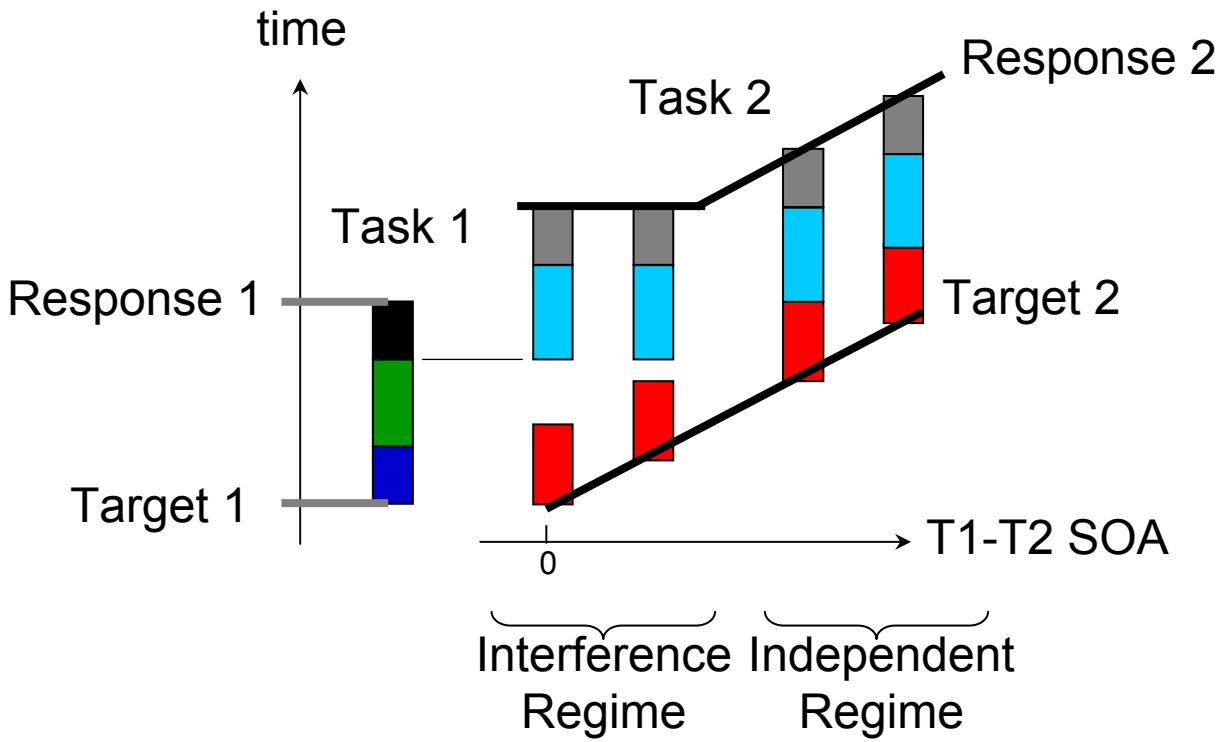


Workspace state for task 2



Sigman and Dehaene, PLOS Biology, 2005

Pashler's central bottleneck model

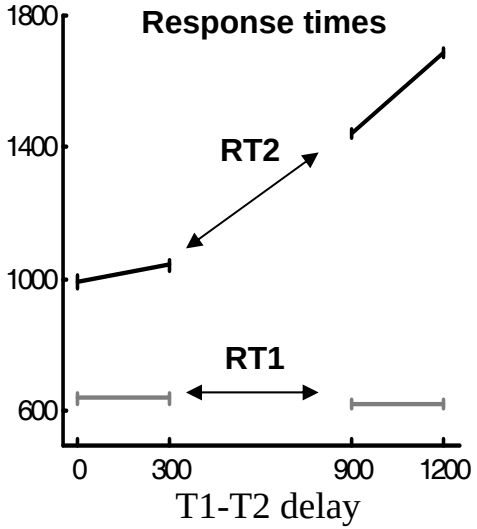


Event-related potentials dissociate parallel and serial stages during dual-task processing

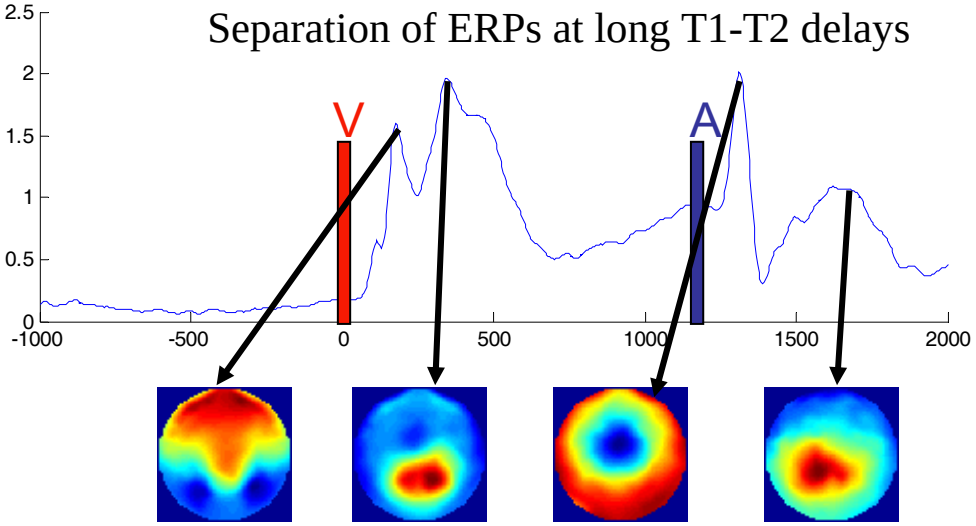
Task 1: number comparison of a visual Arabic numeral with 45, respond with right hand

Task 2: pitch judgment on an auditory tone, respond with left hand

- 300 ms delay in or outside of the interference regime

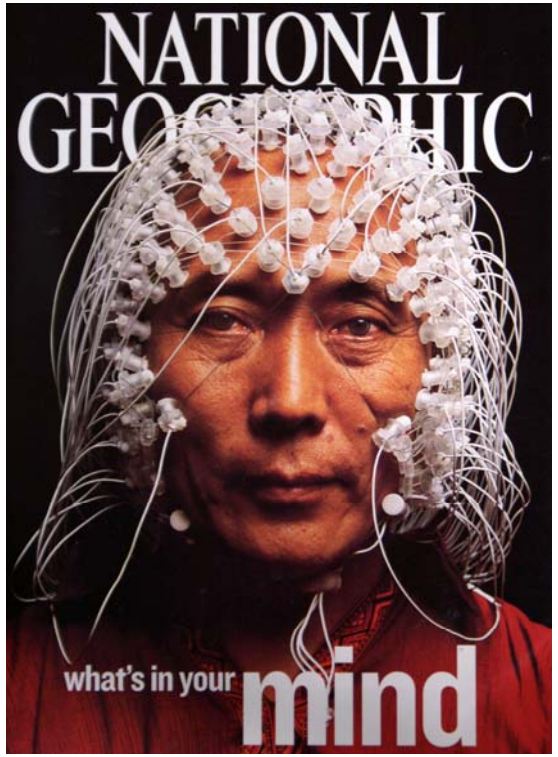


Separation of ERPs at long T1-T2 delays



N1 P3 N1 P3

Visual events Auditory events



Sigman and Dehaene, submitted

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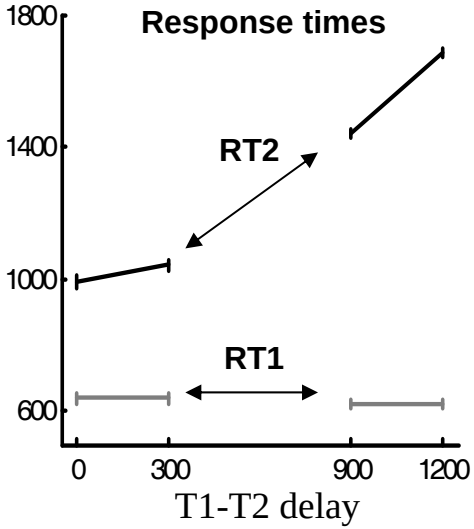
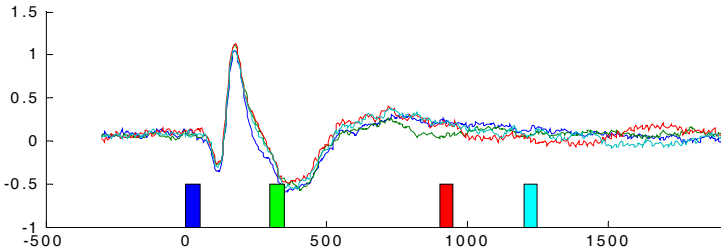
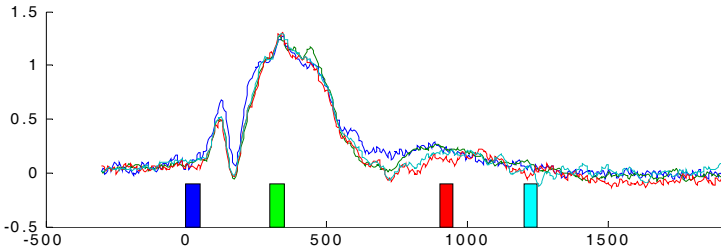


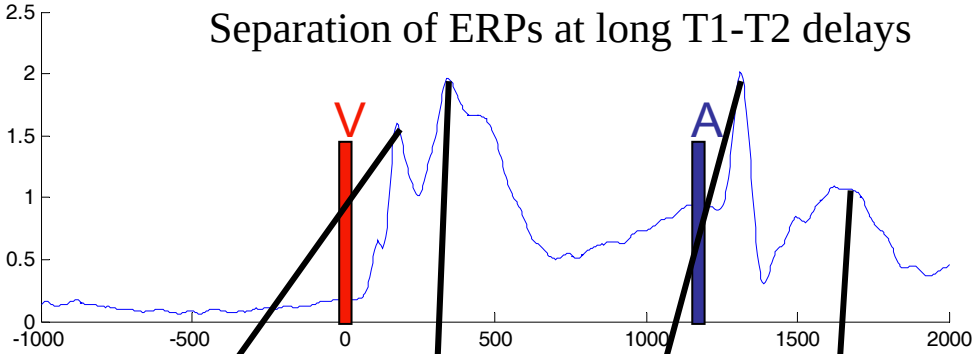

N1

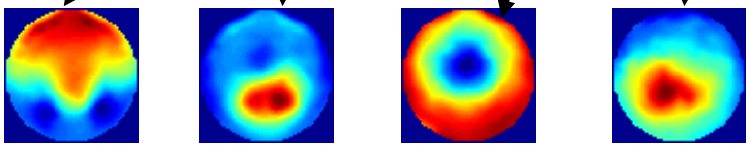



P3



Separation of ERPs at long T1-T2 delays

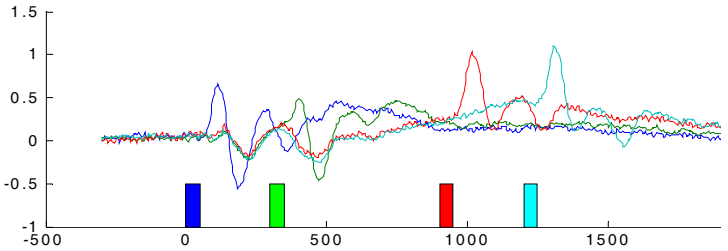




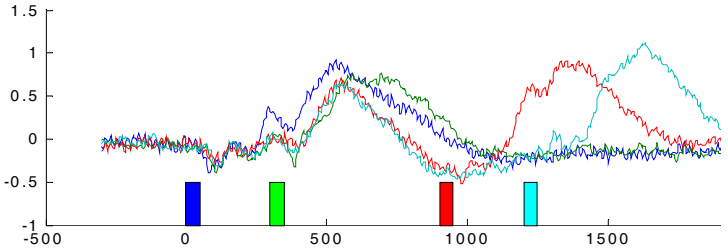
N1 P3 N1 P3

Visual events Auditory events


N1



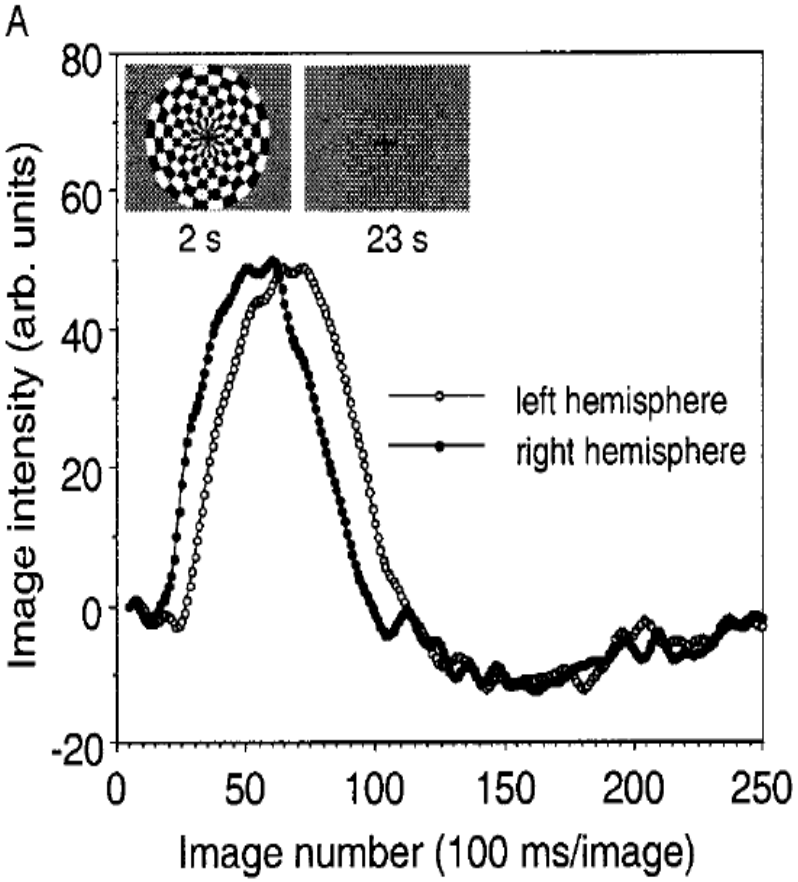

P3



Sigman and Dehaene, submitted

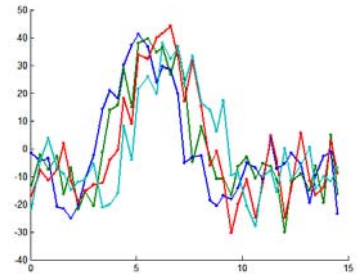
Functional MRI can be sensitive to small delays, in the order of a few hundreds of milliseconds

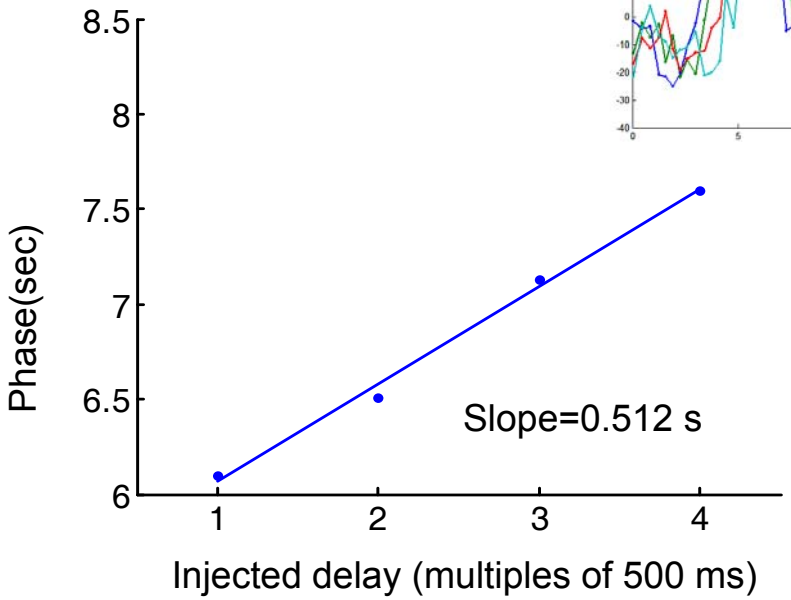
Sigman, M., Jobert, A., LeBihan, D., & Dehaene, S. (2006). Parsing a sequence of brain activations at psychological times using fMRI. *NeuroImage, 2006*



Menon et al, 1998

- The phase of the BOLD response can be estimated with high precision even when the TR exceeds 2 seconds
- Injected delays of ~200 ms can be distinguished *with whole-brain imaging*
- Changes in onset, duration or both can be separated





Separating parallel and serial stages during dual-task processing with high temporal resolution fMRI

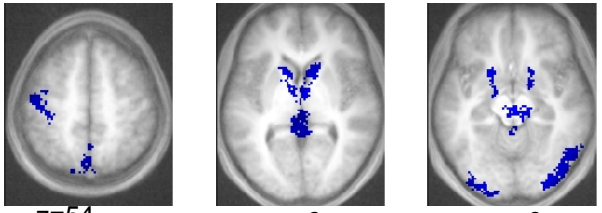
Task 1: number comparison of a visual Arabic numeral with 45, respond with right hand

Task 2: pitch judgment on an auditory tone, respond with left hand

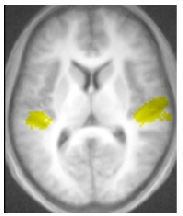
- 300 ms delay in or outside of the interference regime

- slow fMRI (one trial = 14.4 s)

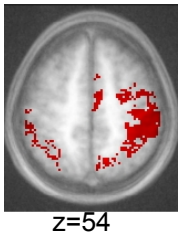
Task 1 network



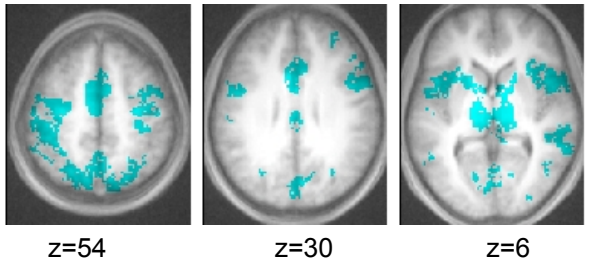
Task 2 perceptual



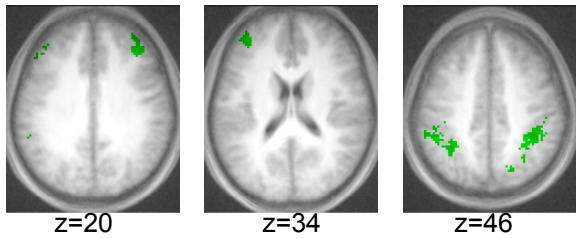
Task 2 Decision/motor

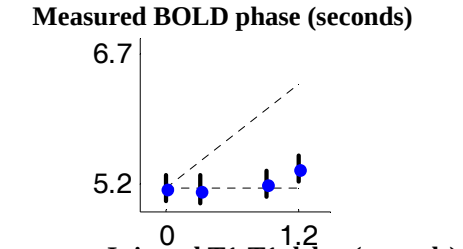


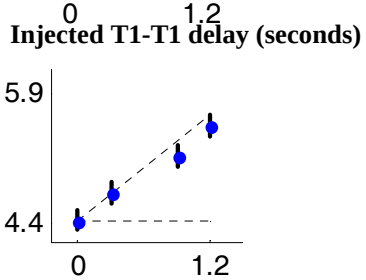
Shared between task 1 and task 2

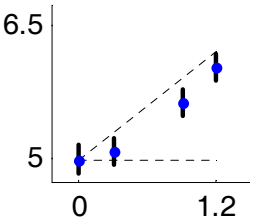


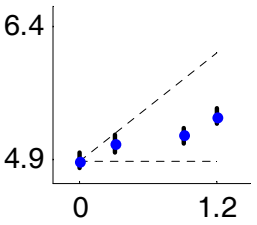
High-level control

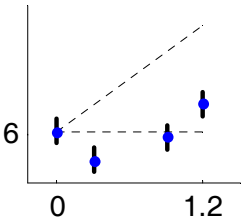






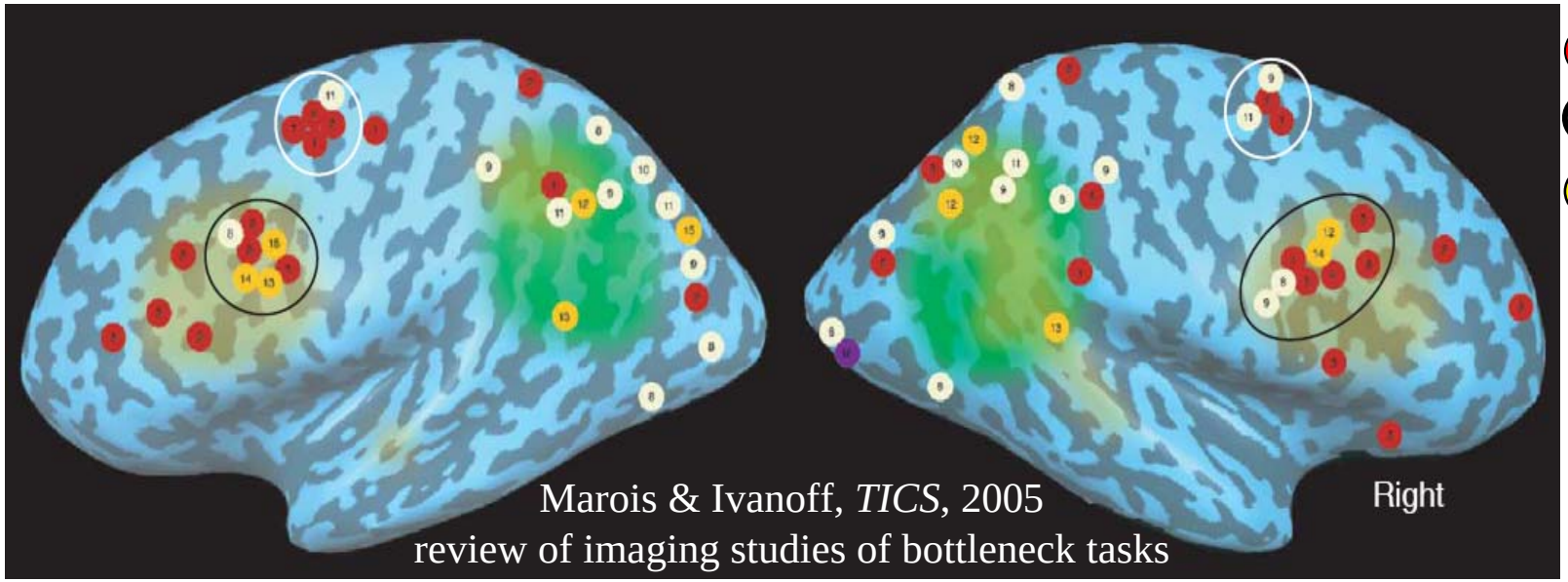






Sigman and Dehaene, submitted

Locating the sites of processing bottlenecks: parieto-prefrontal networks

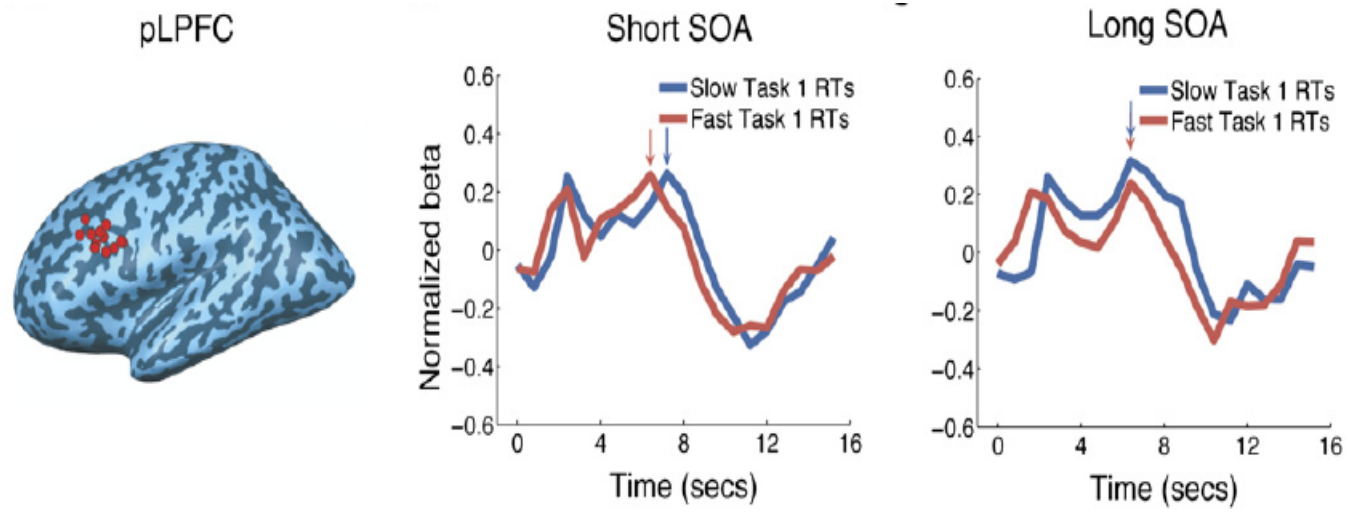


PRP

VSTM/MOT

Att. Blink

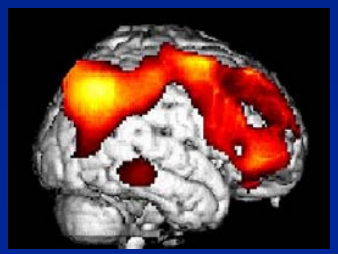
Marois & Ivanoff, *TICS*, 2005
review of imaging studies of bottleneck tasks



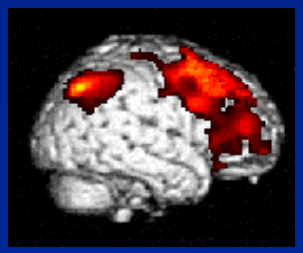
Dux, Ivanoff, Asplund & Marois, *Neuron*, 2007

Conclusion: Towards a neuronal understanding of consciousness

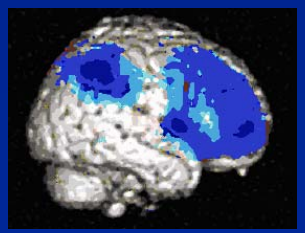
- Non-conscious processing is extensive in the human brain
- Brain activity can remain non-conscious for at least two reasons:
  - bottom-up strength is insufficient (e.g. masking)
  - Top-down attention is distracted (e.g. attentional blink)
- A representation becomes conscious whenever it wins the central competition and ignites a distributed, self-sustained assembly of neurons in prefrontal, cingulate and other cortical association areas
- Conscious access corresponds to a sharp and relatively late (~270 ms) dynamical phase transition in neural network activity.
- Although I have only talked about access to consciousness, changes in viligance (intransitive consciousness) relate to neuromodulation of the same network (S. Laureys, P. Maquet).



Vegetative state



Coma



Slow-wave sleep

General anesthesia