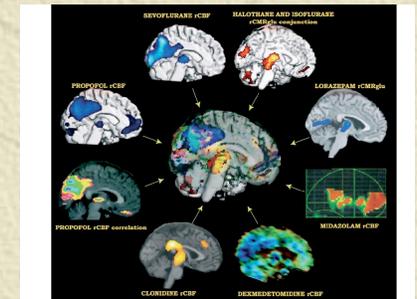
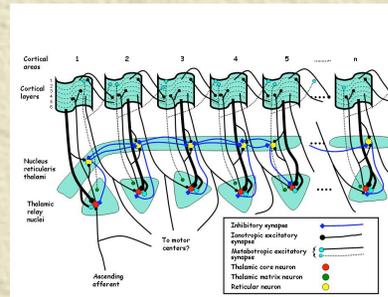
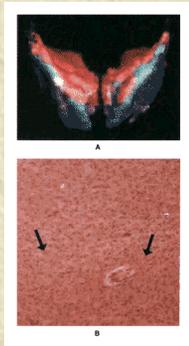


The Role of the Thalamus in Human Consciousness



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Funded by



Themes

- ✧ Primary consciousness
- ✧ The thalamic dynamic core
 - ◆ Synthetic construct: We experience results, not processes
 - ◆ Lesions, stimulation, and anesthesia
 - ◆ Anatomy and physiology of thalamus
 - ◆ Neural synchronization and consciousness
- ✧ Cortical and subcortical criteria for the definition of brain death

Primary consciousness

- ✦ Searle: how is it that a brain can give rise to experience at all?
- ✦ **Primary consciousness**: basic awake experience such as perceptions, feelings, memories, thoughts
 - ◆ Qualitativeness, subjectivity, unity
 - ◆ Not when deep sleep, coma, surgical anesthesia
- ✦ **Secondary consciousness**: consciousness of self (> 3 yrs), consciousness of being consciousness, recursive levels of consciousness
- ✦ Not Block or Lamme: no phenomenal vs reportable/access distinction

Views of brain generation of primary consciousness

- ✦ Mass action of brain (dynamical system theory - e.g., Nunez)
- ✦ Distributed but integrated activity of cerebral cortex (generally accepted)
- ✦ Distributed but integrated activity of thalamocortical loops (esp. Llinás & Ribary)
- ✦ **Diencephalic** (viz. thalamic) activity (esp. Penfield)

Thalamic dynamic core: Four evidential pillars

-
- ✦ I. **Consciousness is a synthetic construct**: we experience results (products) of computations, not the computations (processes) themselves (Lashley, Kinsbourne, Prinz, Rees, Koch, Baars)
 - ✦ II. Lesions, neurosurgery, and anesthetic action point to **thalamic "relay" nuclei** as **critical** (Penfield, Alkire, Jennett, et al)
 - ✦ III. **Anatomy and function of thalamus** and cortex (Mumford, Steriade, Llinás,...)
 - ✦ IV. **Neural synchronization is a NCC** => dynamic core (Kinsbourne, Dennett, Tononi & Edelman, Varela group)

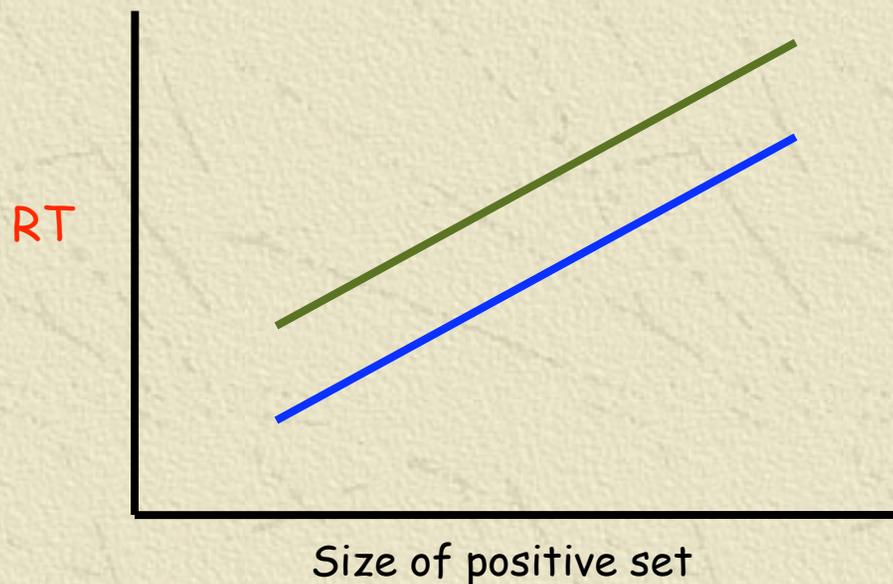
I. We experience products not processes...

-
- ✦ Crovitz: maximum rate of consciously following strobe light = 4 to 5 Hz (250 to 200 msec per cycle) => conscious processing is slow
 - ✦ **Sternberg STM scanning**: no awareness of process; 40 Hz (25 ms/item) scan rate => unconscious processing is fast
 - ✦ LTM search & Retrieval: no awareness of memory search codes, only of memories themselves (or retrieval failure)
 - ✦ Speech: not aware of composing utterances, phonemes, (co-)articulation, etc.
 - ✦ Perception: not aware of complex processing in visual, auditory, etc. systems that informs percepts; "Grand Illusion of Complete Perception"; **change blindness; inattentional blindness**
 - ✦ **Most cortical processing is unavailable to consciousness. Why does some cortical activity "appear" in consciousness and other not?**

Short term memory scanning (Sternberg, 1966)

Positive set: 3 5 1 9 6 $\xrightarrow{2 \text{ sec}}$ Test: 4 $\xrightarrow{\text{RT}}$ Answer: No

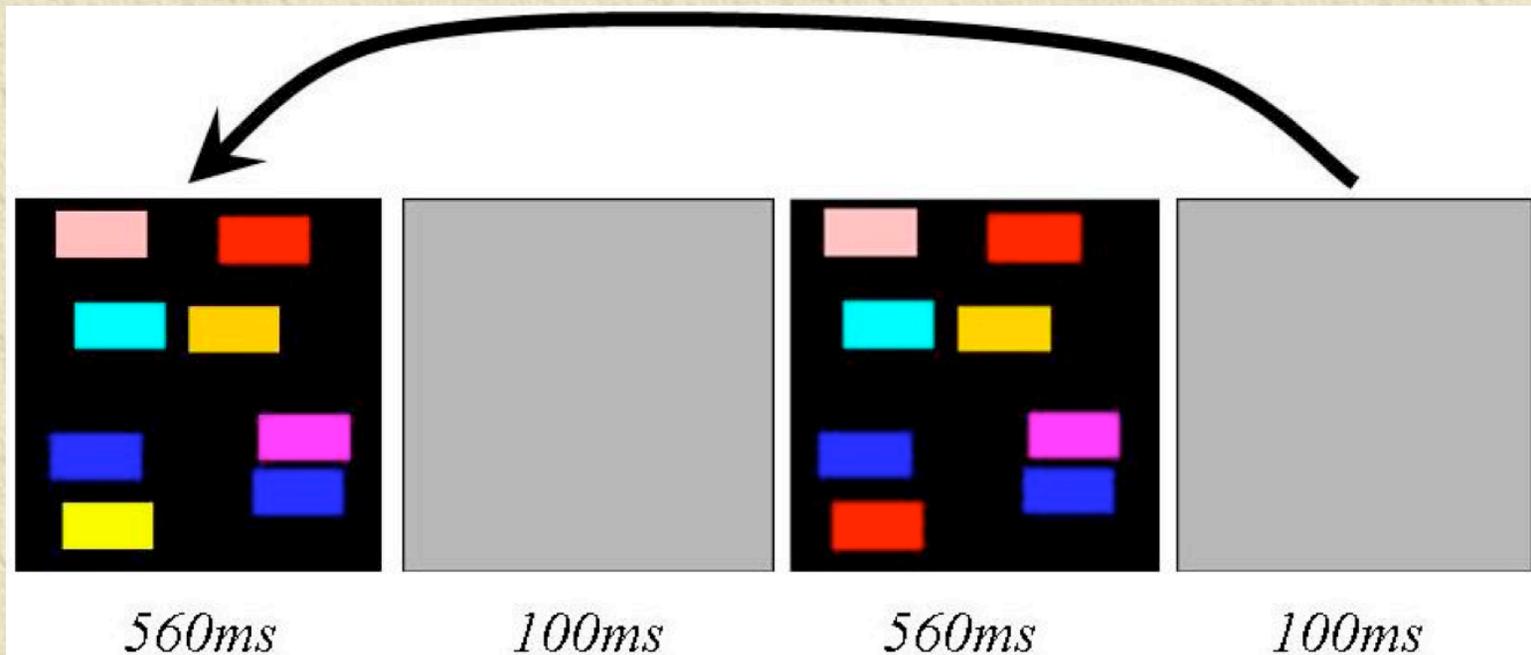
Positive set: 5 1 8 3 $\xrightarrow{2 \text{ sec}}$ Test: 1 $\xrightarrow{\text{RT}}$ Answer: Yes



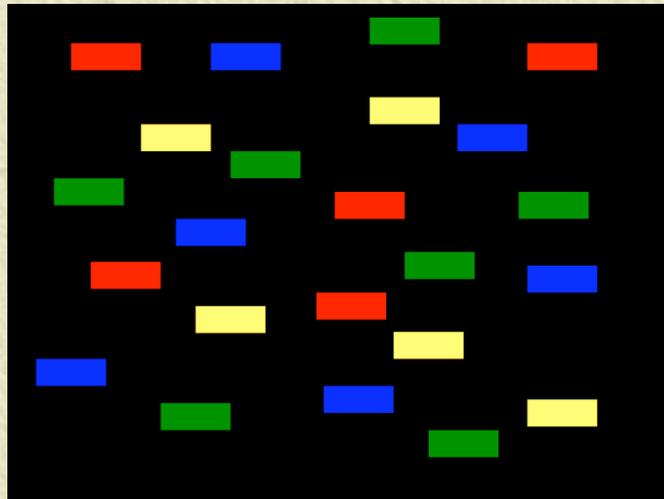
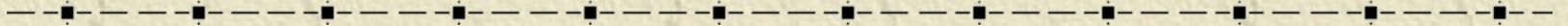
Slope =
25-35 ms per
item, yes or
no => serial
exhaustive
search

Change blindness (Simons, Rensink, O'Regan, Clark)

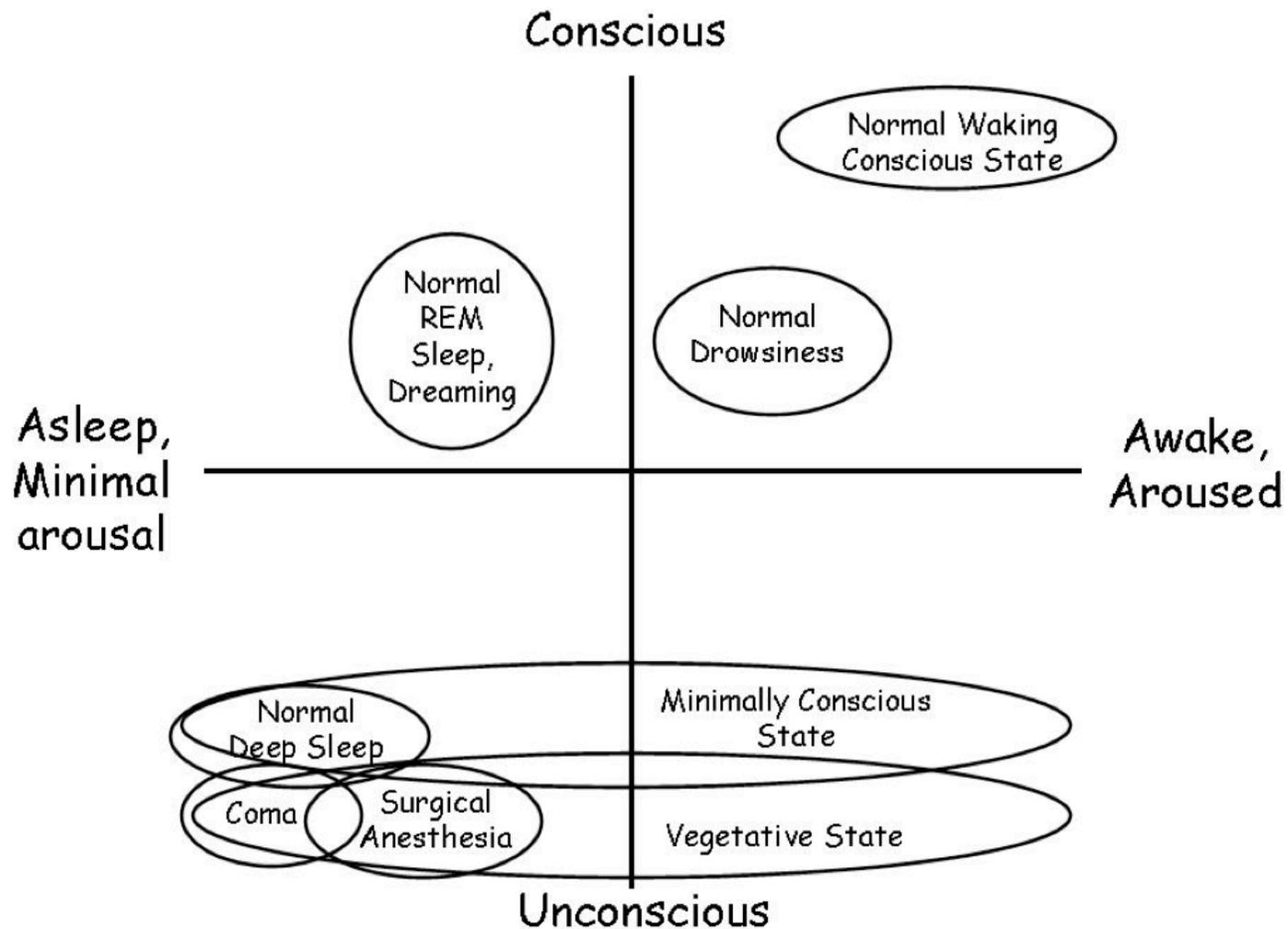
Bayless & Ward, 2009



- ✦ Usually natural scenes
- ✦ Impression of seeing everything
- ✦ Change not seen until precise object or part attended but is then obvious
- ✦ Blank masks transients that would reveal change



II. Vegetative state, lesions, and anesthetics

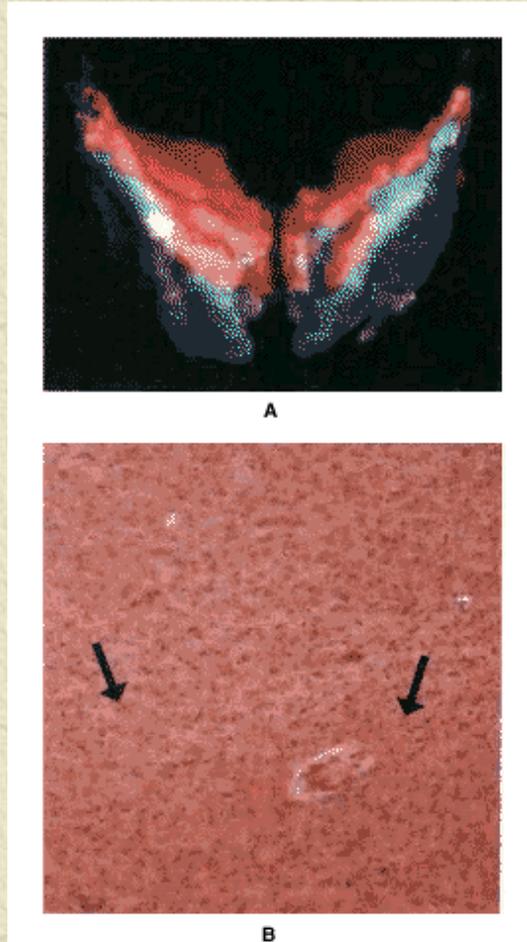
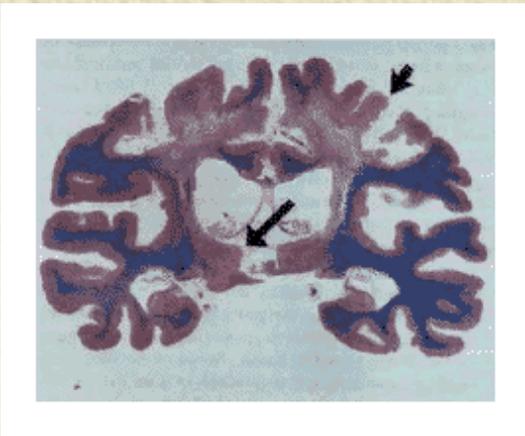


Vegetative state correlates

- ✦ Adams et al: (Brain, 2000)
 - ✦ Non-traumatic injury (hypoxia): damage to thalamus in 100% of cases
 - ✦ Traumatic injury: damage to *either* subcortical white matter or thalamus or both in 100% of cases
- ✦ Jennett et al, (Neurology, 2001)
 - ✦ VS associated with either severe DAI or thalamic damage or (usually) both, severe disability often neither ($\chi^2=16.5$, $p<0.0001$)
- ✦ Maxwell et al (2004): VS associated with extensive ($\approx 30\%$) loss of neurons in dorsomedial nucleus, moderate disability with $<5\%$ loss
- ✦ Highlight: VS cases of minimal cortical damage with extensive thalamic damage

Lesions: Karen Ann Quinlan

Karen Ann Quinlan's Brain at Autopsy (see Kinney et al 1994)



Thalamus-massive loss

Drug/alcohol reaction;
permanent vegetative
state for 14 years



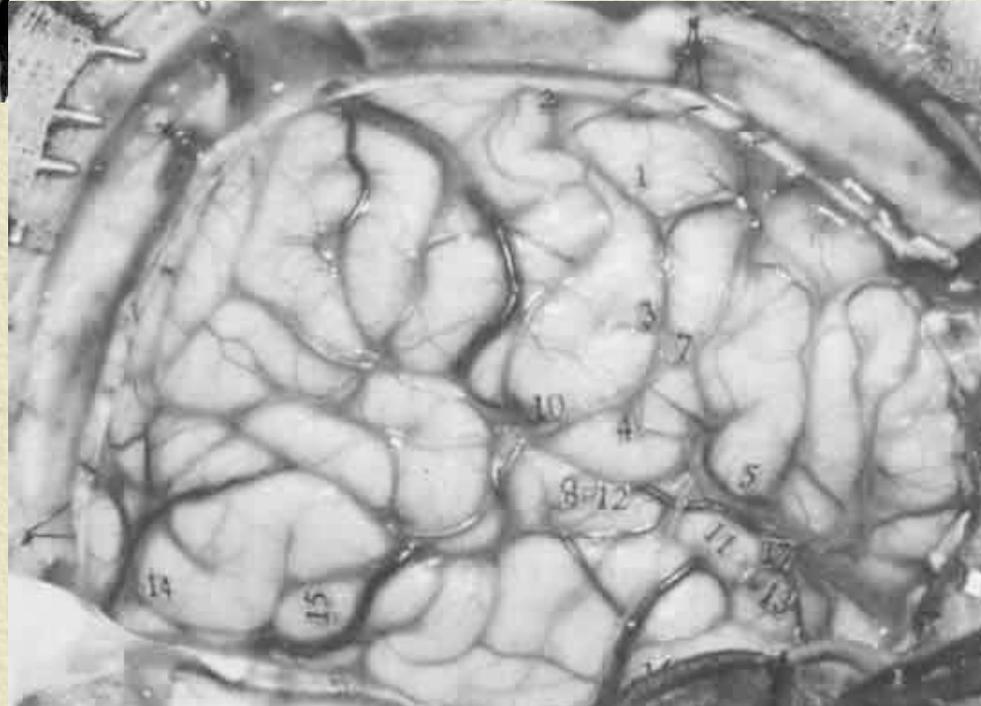
Cortex-little loss

Penfield's neurosurgery and stimulation mapping



Patient
M.M.
treated for
intractable
epilepsy

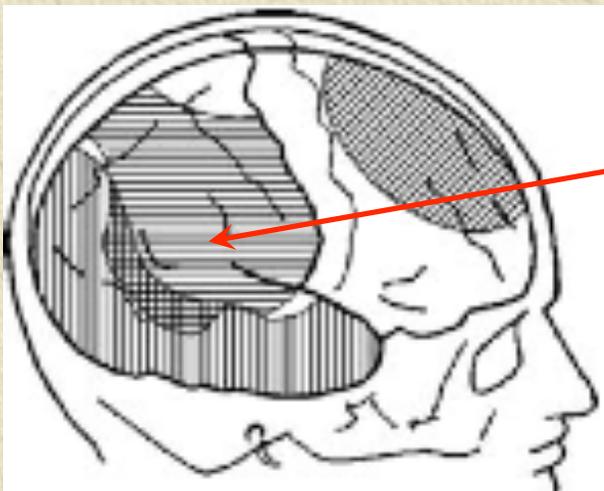
M.M.'s cerebral cortex mapped via
electrical stimulation by Penfield



Neurosurgery and stimulation mapping

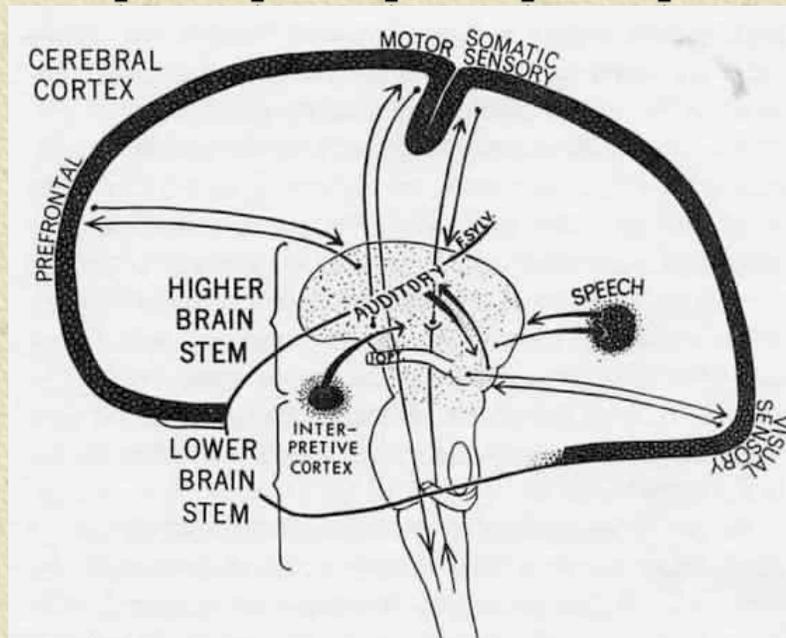
✧ Penfield (*The Mystery of the Mind*, 1975):

- ◆ The mechanisms of epilepsy and electrical stimulation mapping imply that "...there are two brain mechanisms that have strategically placed gray matter in the diencephalon ..., viz. (a) the *mind's mechanism* (or highest brain mechanism); and (b) the *computer* (or automatic sensory-motor mechanism)." (p. 40).

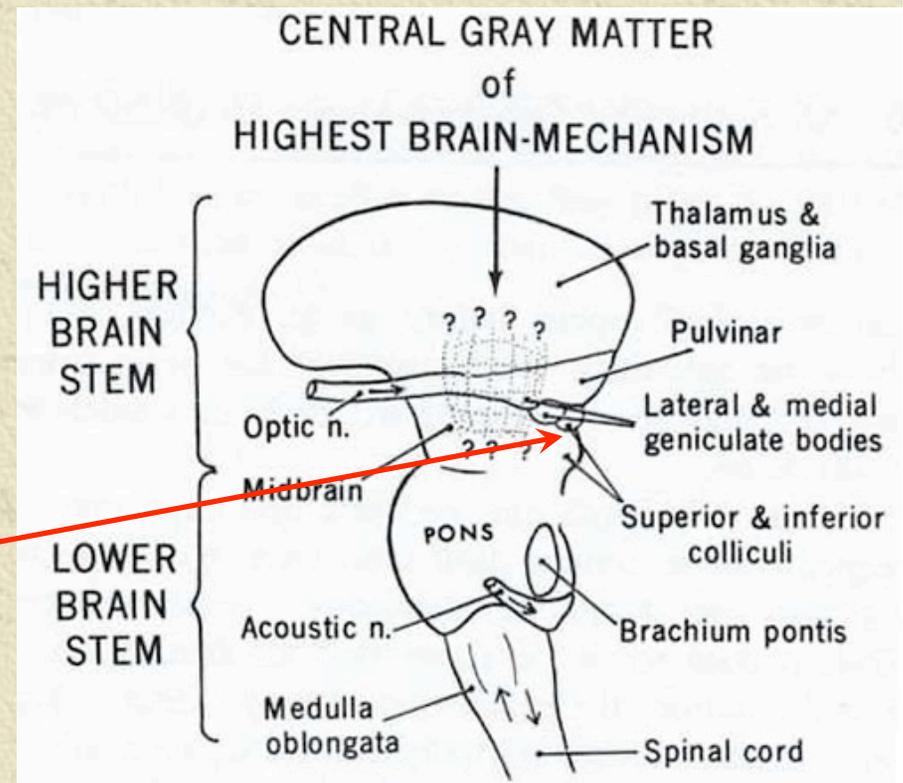


Excisions of massive amounts of cortex did not abolish consciousness

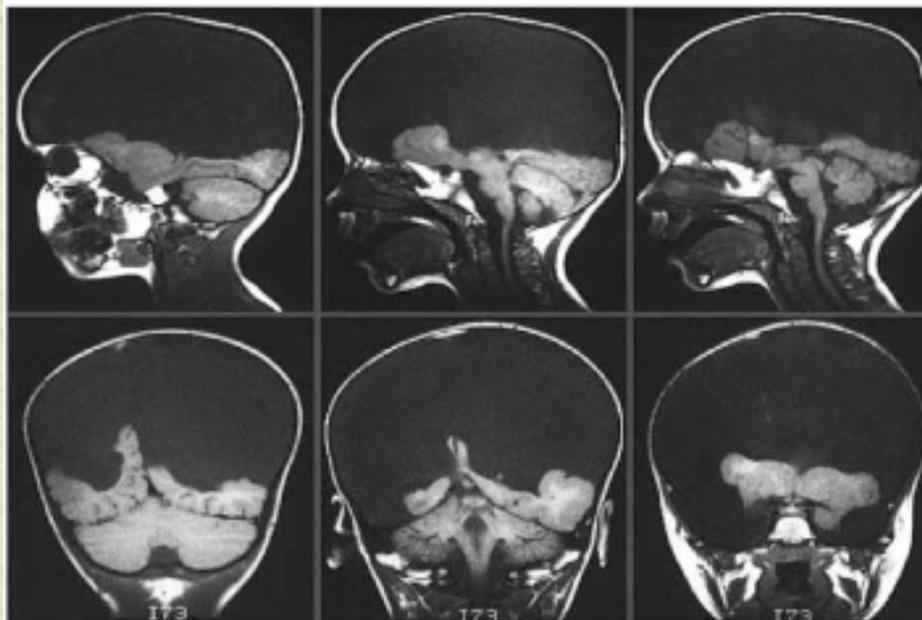
Penfield's "mind mechanism"



Merker (2006, BBS):
argued SC is locus of
conscious analog
simulation of world

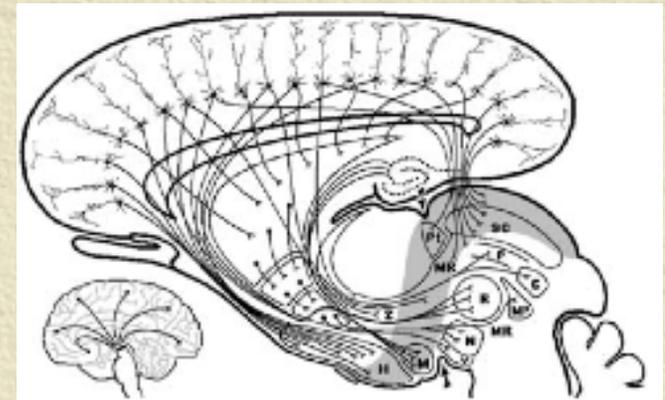


Merker's superior colliculus hypothesis of the substrate of consciousness in the absence of cortex: Hydranencephaly



Preserved thalamus; many subcortical inputs, esp auditory

Hydranencephalic child reacting to the presence of her brother



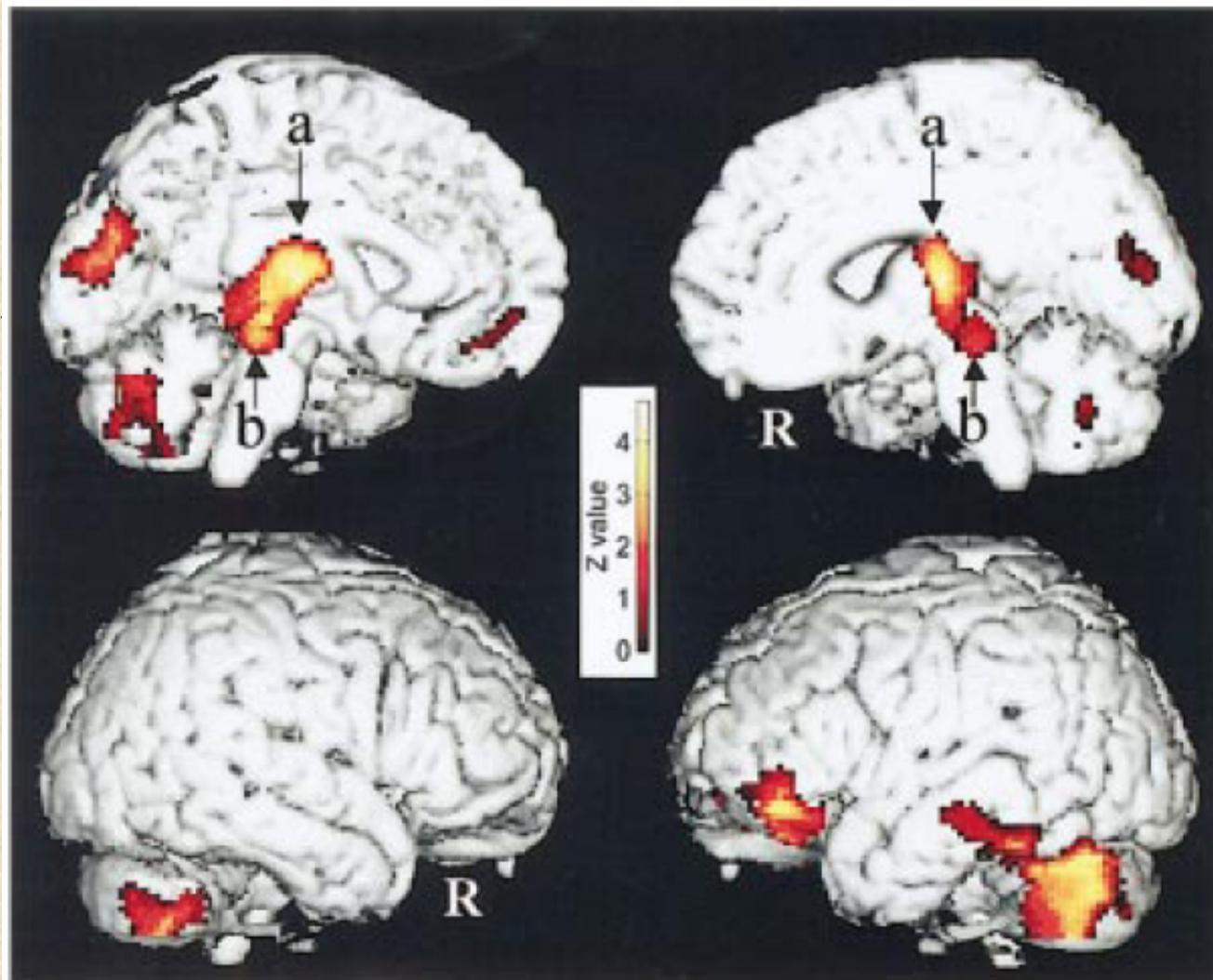
Convergence of brain circuitry in the di- and mesencephalon



General anesthesia

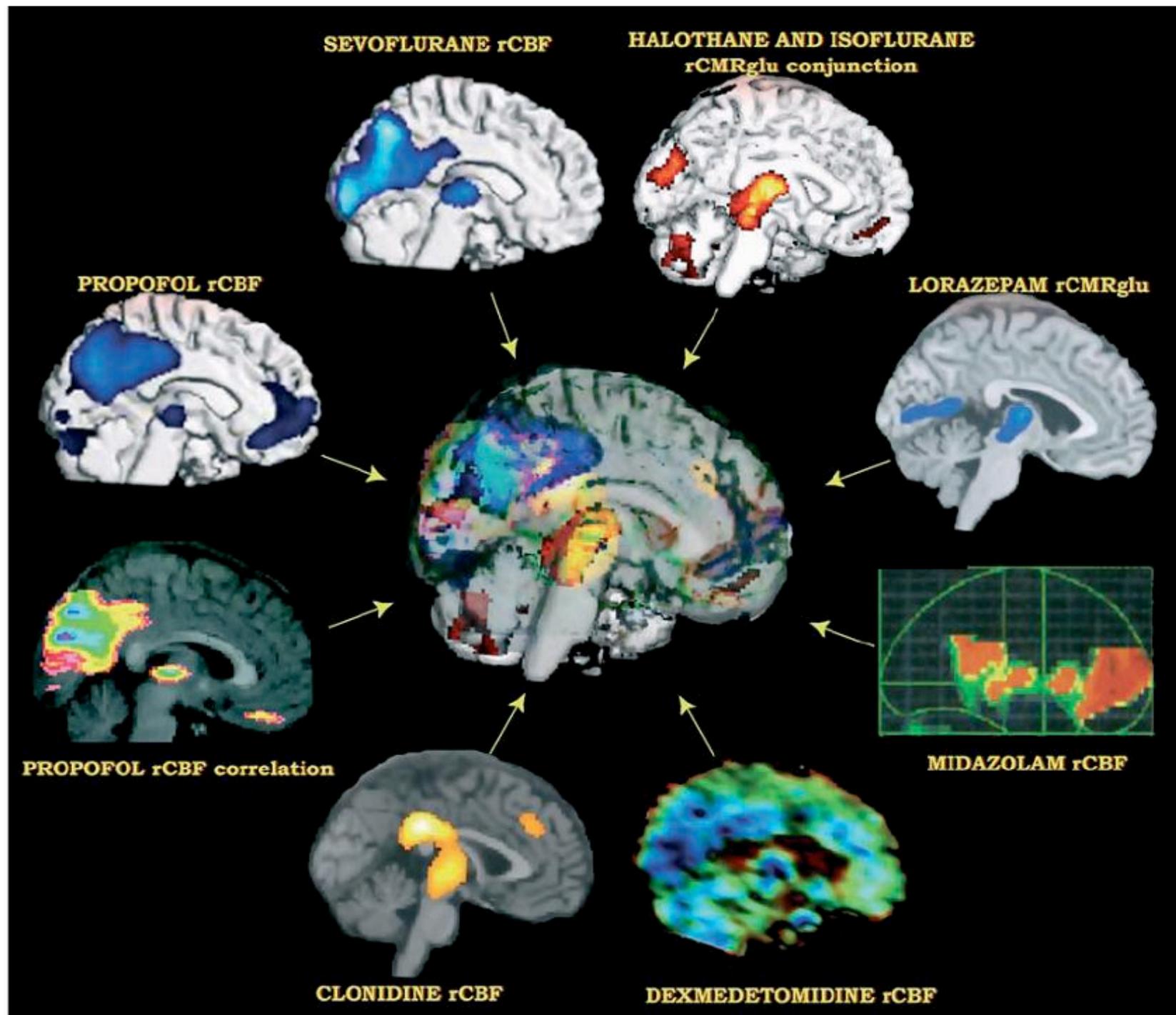
✧ Alkire et al (2000) *Consciousness & Cognition*:

- ◆ Common brain loci and mode of action of different general anesthetics imply that the critical mechanism of general anesthesia is a hyperpolarization block of the thalamic relay nuclei neurons



Common brain areas where halothane and isoflurane anesthesia significantly depresses activity; *a.* thalamus, *b.* midbrain reticular formation

Alkire et al (2000) *Consciousness & Cognition*

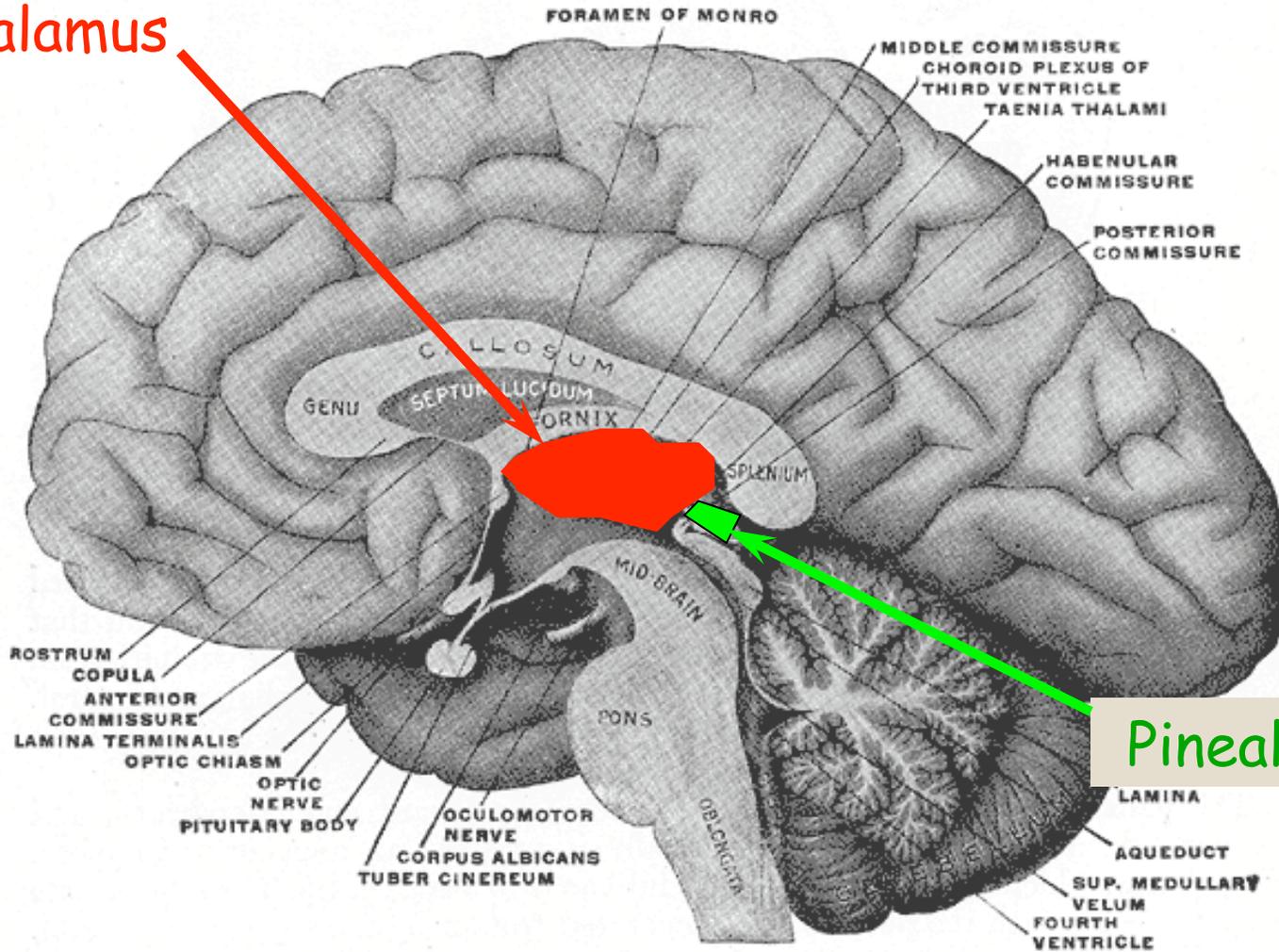


III. The thalamus

- ✧ Synchronizes cortical oscillations
- ✧ "Relay-Gateway" to cortex for major sensory systems (except smell)
- ✧ Evolved along with the cerebral cortex; a "seventh layer" of cortex (but with different neuron type)
- ✧ Each cortical area has an associated subnucleus of thalamus (sharper delineations in sensory areas)
- ✧ Cortico->thalamic projections roughly 9x thalamo->cortical projections

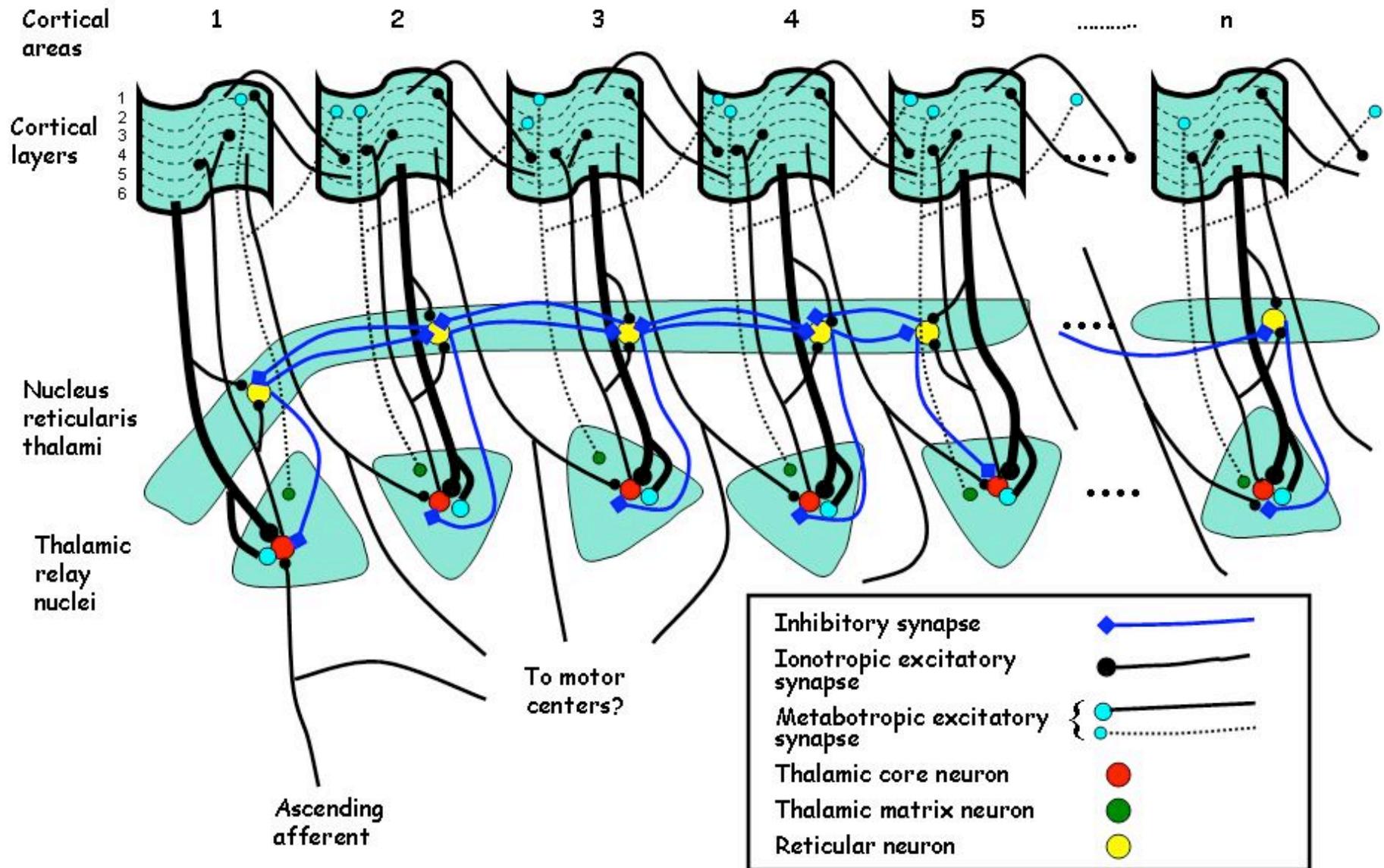
Where is the thalamus?

Thalamus



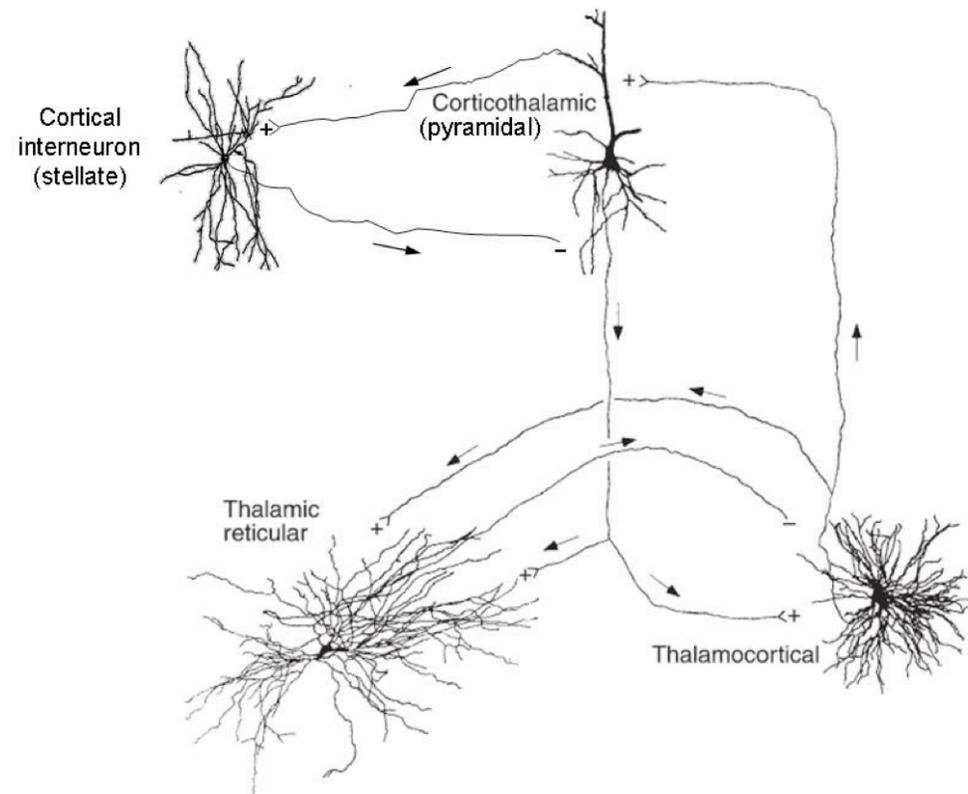
Pineal body

Gross Anatomy of some cortico-thalamic circuits



Details of cortico-thalamic and thalamo-cortical circuits

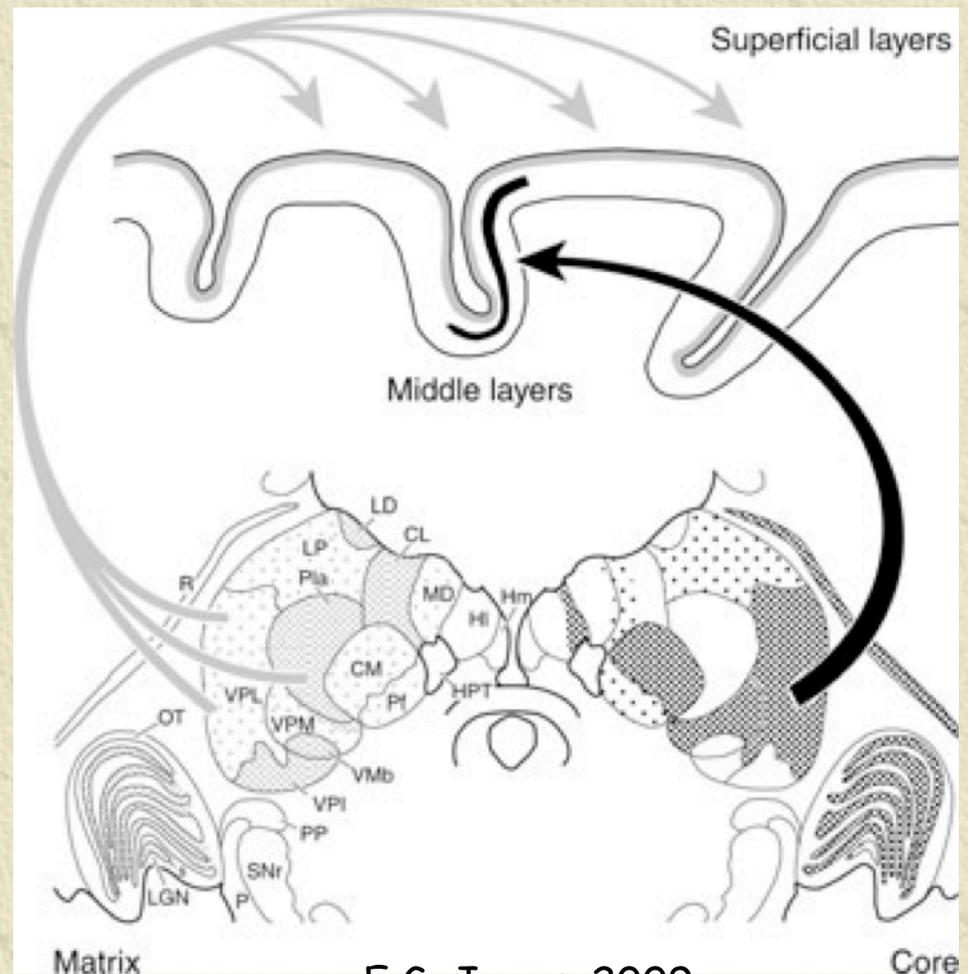
- Extensive dendritic tree in thalamocortical and thalamic reticular neurons
- Dendritic tree site of extensive neural integration



Modified from M. Steriade, 1999

E.G. Jones' core and matrix neurons

- ✦ Core cells specific projecting and dominate sensory nuclei
- ✦ Matrix cells diffusely projecting and dominate nuclei with more frontal connections
- ✦ Dynamic core associated with matrix (binding, integrative) thalamic relay neurons?



E.G. Jones, 2009

IV. Dynamic core and neural synchronization

- ✦ Proposal by Tononi & Edelman: The primary neural correlate of conscious awareness is the "dynamic core" (distributed cortical activity camp)
 - ◆ Large-scale (brain-wide, 200-msec time scale)
 - ◆ Coherent (statistically synchronous) activity
 - ◆ Millions of neurons involved
- ✦ DC simultaneously integrates activities of many brain areas (not all of them, a constantly changing subset) ...
- ✦ And also differentiates current conscious state from many other, possible conscious states.

IV. Synchronization: Binocular rivalry

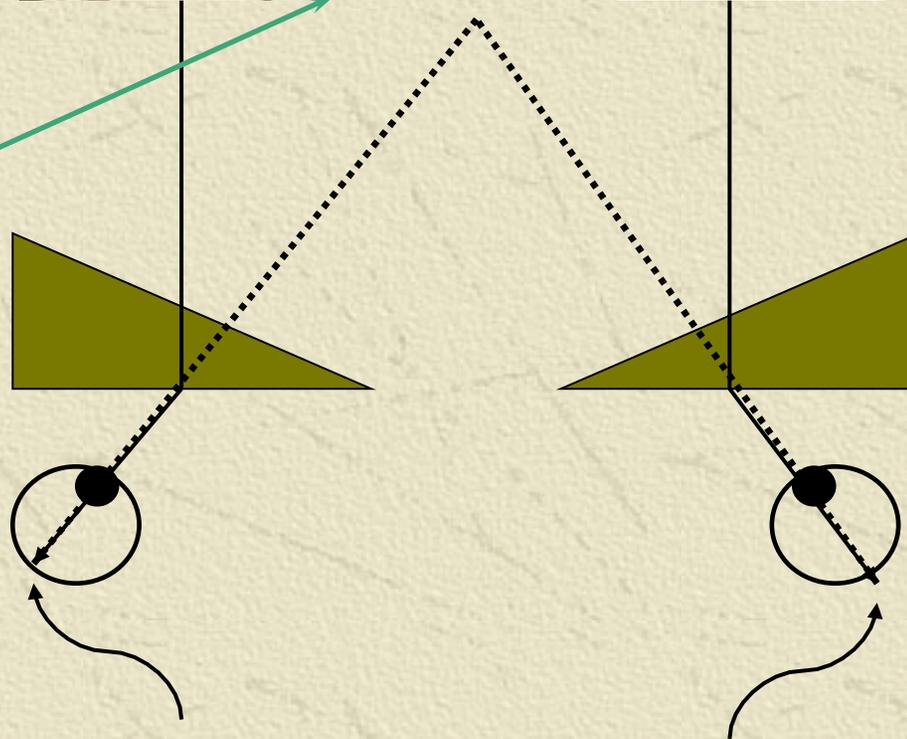
Stimuli



Apparent locus of fused object

Prisms

Eyes



Constant stimulation,
involuntarily
alternating
experience

Corresponding retinal areas

Rivaling images from
Cosmelli et al, (2004)
NeuroImage

Gray & Singer's cats

Neural synchrony occurs when neural activity, spiking or dendritic currents, in disparate locations rises and falls in a fixed relationship

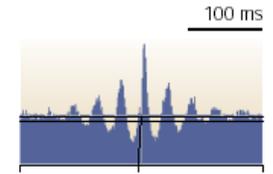
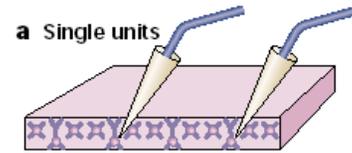
Ward et al's humans

Varela et al, 2001

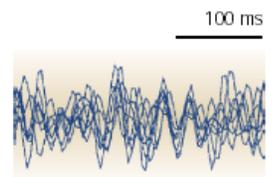
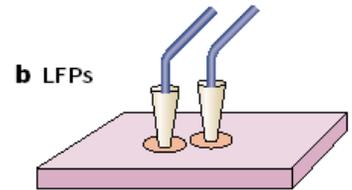
A Local scale

Spatial resolution

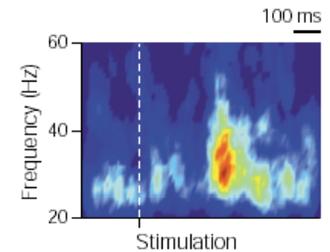
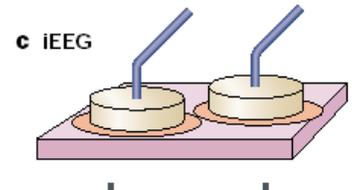
• ~1 μ m



• ~1 mm

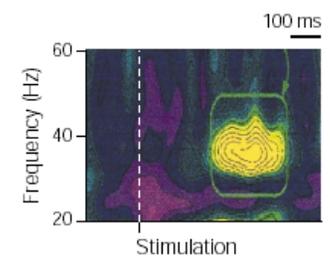
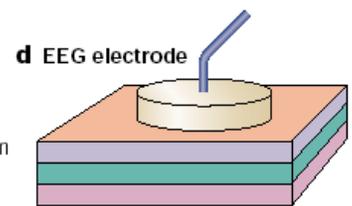


• ~1 cm



Surface diffusion

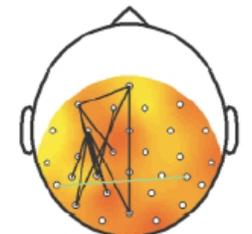
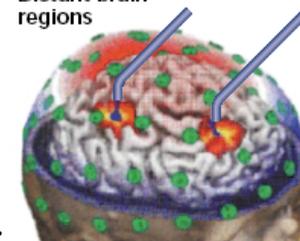
• ~1 cm



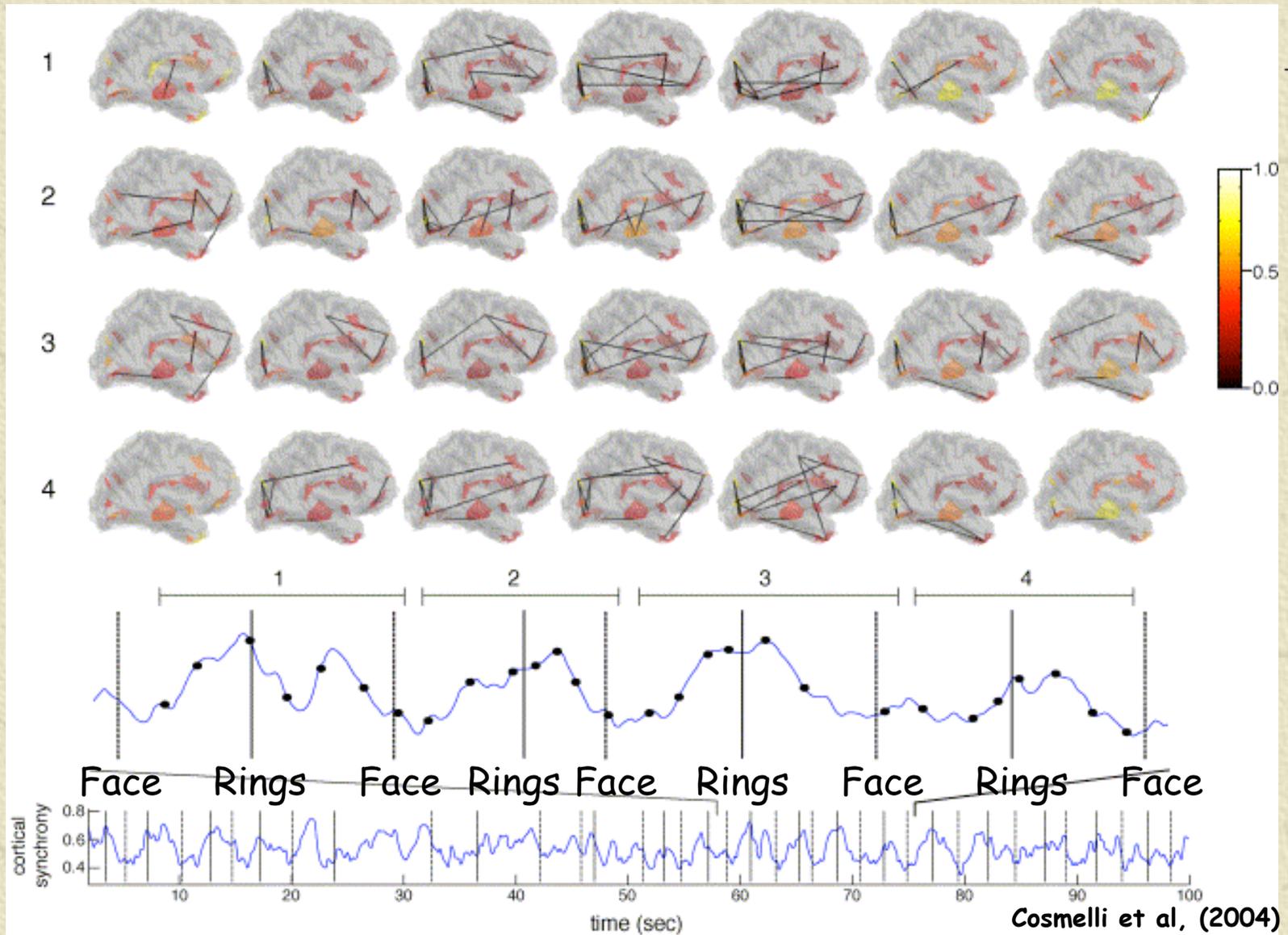
B Large scale

>2 cm

Distant brain regions



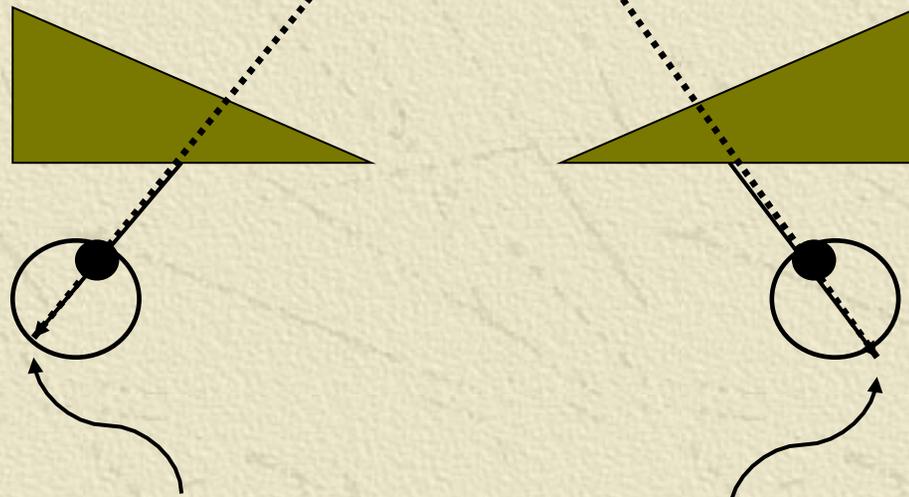
Widespread 5 Hz synchrony associated with perception of the 5 Hz stimulus



Binocular rivalry: a window to the neural correlates of consciousness



Constant stimulation,
involuntarily
alternating
experience

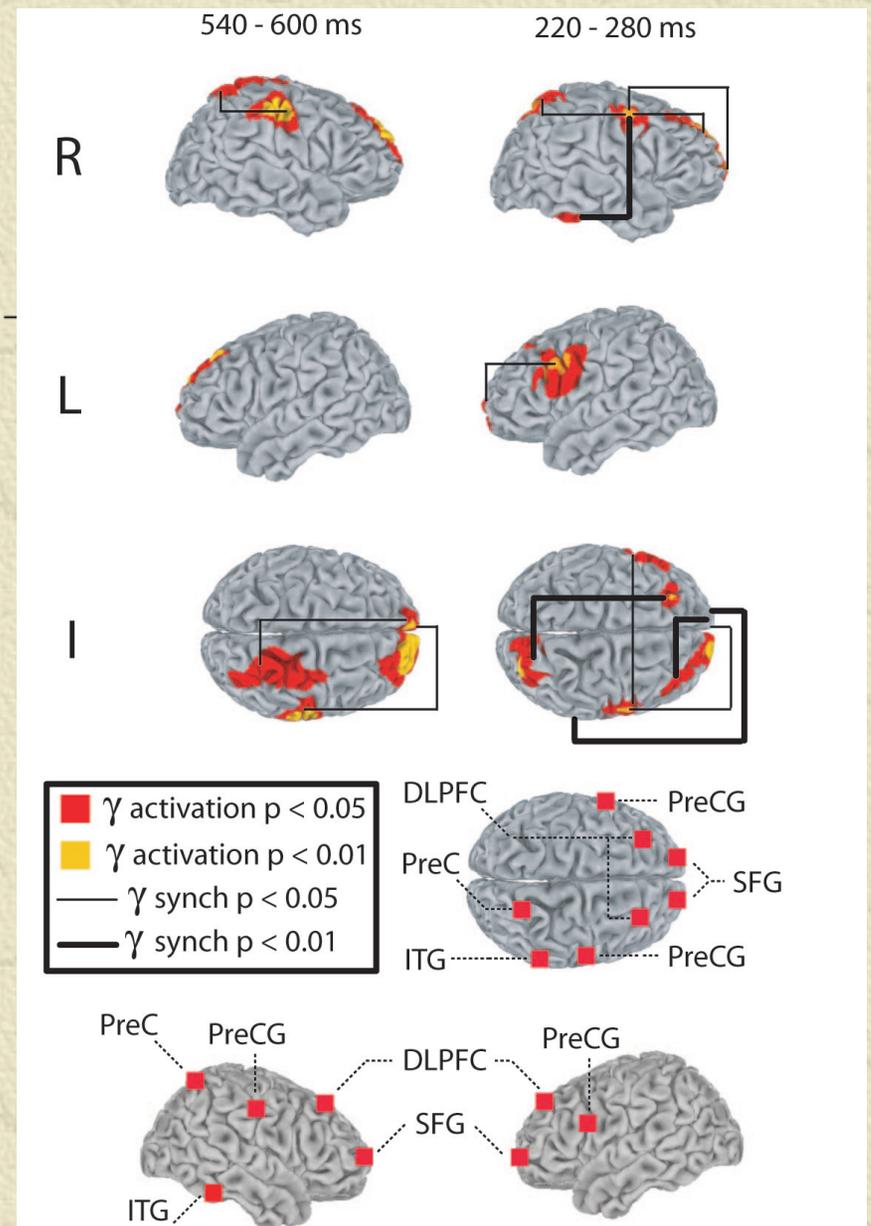


Corresponding retinal
areas

Rivaling images from
Cosmelli et al, (2004)
NeuroImage

Gamma-band consciousness network

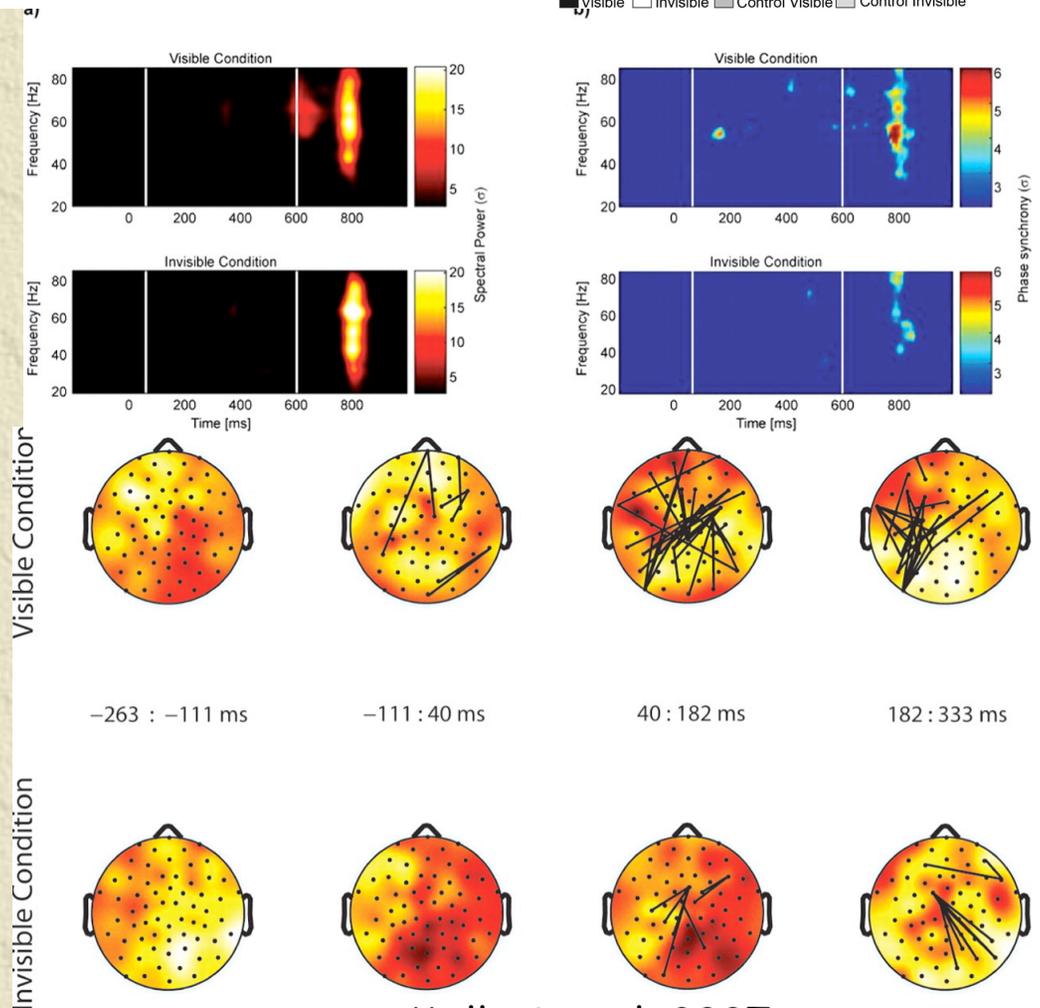
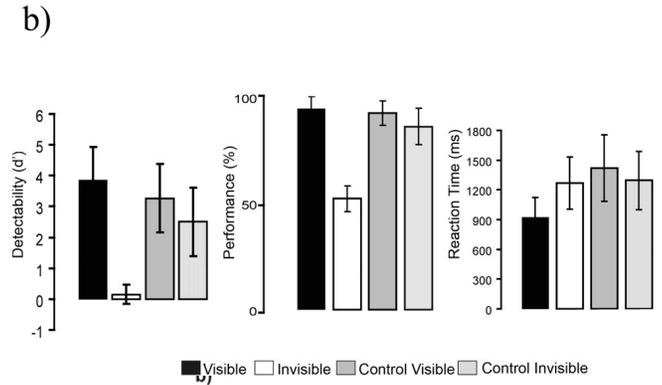
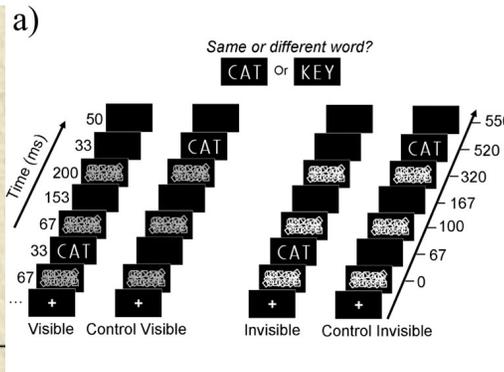
- ✦ biSFG, biDLPFC, RPreC and RPreCG active with some inter-regional synchrony at 540-600 ms constitute a consciousness maintenance network
- ✦ RITG (visual pattern) and LPreCG (RH response) also active at 220-280 ms \Rightarrow switch of percept
- ✦ Widespread synchrony in this network during perceptual switch



Doesburg, Green, McDonald & Ward, 2009

Masking

- ✦ Long-distance, gamma-band synchronization for seen but not unseen
- ✦ Persistent increase in frontal theta power during retention for seen but not unseen
- ✦ Enhanced P300 for seen relative to unseen



Melloni et al, 2007

Roles of the thalamus

-
- ✦ Relay station and gateway (attentional engagement) to cortex for sensory systems
 - ✦ Synchronizes neural activity in remote cortical areas
 - ✦ Active blackboard that echoes back to cortex results of latest computations (Mumford)
 - ✦ *Site of dynamic core of neural activity that gives rise to phenomenal experience(?): thalamic dynamic core*

Conclusions

- ✦ Primary consciousness is a synthetic construct of our brains
- ✦ The thalamus is a critical brain locus for consciousness, implicated in unconsciousness from brain injury and from anesthetics
- ✦ The relay neurons of the thalamus, particularly matrix neurons that extensively interact with frontal regions, are suited for integrative function
- ✦ Cortical synchronization is a NCC and seems to form a dynamic core of conscious contents
- ✦ My (radical?) proposal: the **thalamic dynamic core** is the critical neural correlate of phenomenal awareness
 - ◆ Cortex computes, thalamus experiences
 - ◆ Human cortex, with more neurons and more cortico-cortical fibers per thalamic fiber computes much more complex contents than do, e.g., rat, dog, or chimp cortices
 - ◆ Cortical DC arises from synchronization of cortical with thalamic activity

Implications for Definition of Brain Death

- ✦ Subcortical circuits necessary for consciousness
- ✦ Thalamus does more than relay and integrate cortical activity - it may be where experience is generated
- ✦ Theoretical types of brain death (emended)
 - ◆ Whole brain death (cortex, diencephalon, brainstem)
 - ◆ Cortical death (subcortical regions intact)
 - ◆ Diencephalic death (cortex intact or not)
- ✦ Consequences for consciousness
 - ◆ Whole: no consciousness possible
 - ◆ Cortical: no complex perceptions or cognitions, only feelings, vague unintegrated sensations
 - ◆ Diencephalic: no consciousness possible
- ✦ Partial cortical/diencephalic function (preserved isolated loops) supports fragmented consciousness, incoherent behavior
- ✦ Is a brain that is only capable of unconscious activity "alive" in the sense of a human person?