Introduction to the neuronal basis of consciousness

2015 Aug 3

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Monash University, Australia

Psychology

Clinical neuroscience

Neuroscience

Consciousness/
Awareness

Philosophy

Artificial intelligence

Complex systems

Psychology

Clinical neuroscience

Association for Scientific Studies of Consciousness (ASSC)

Neuroscience

Consciousness

Philosophy

Artificial intelligence

Complex systems

Psychology

Clinical neuroscience

Neuroscience

Awareness

Philosophy

Initiative for a Synthesis
in Studies of Awareness
(ISSA)

Artificial intelligence

Complex systems

Psychology

Clinical neuroscience

Neuroscience

Consciousness Science

Philosophy

Artificial [Intelligence] Consciousness?

[Complex systems] Pan-psychic view of consciousness

Aims

- To give a background of consciousness research (Dehaene 2011, Boly 2013, Tononi 2015)
- To provide food for thoughts towards final projects
  - No-report paradigms
  - Empirical testing of IIT

Topics

1. neurons and their connectivity

2. a brief remark on the history of consciousness science

3. levels of consciousness

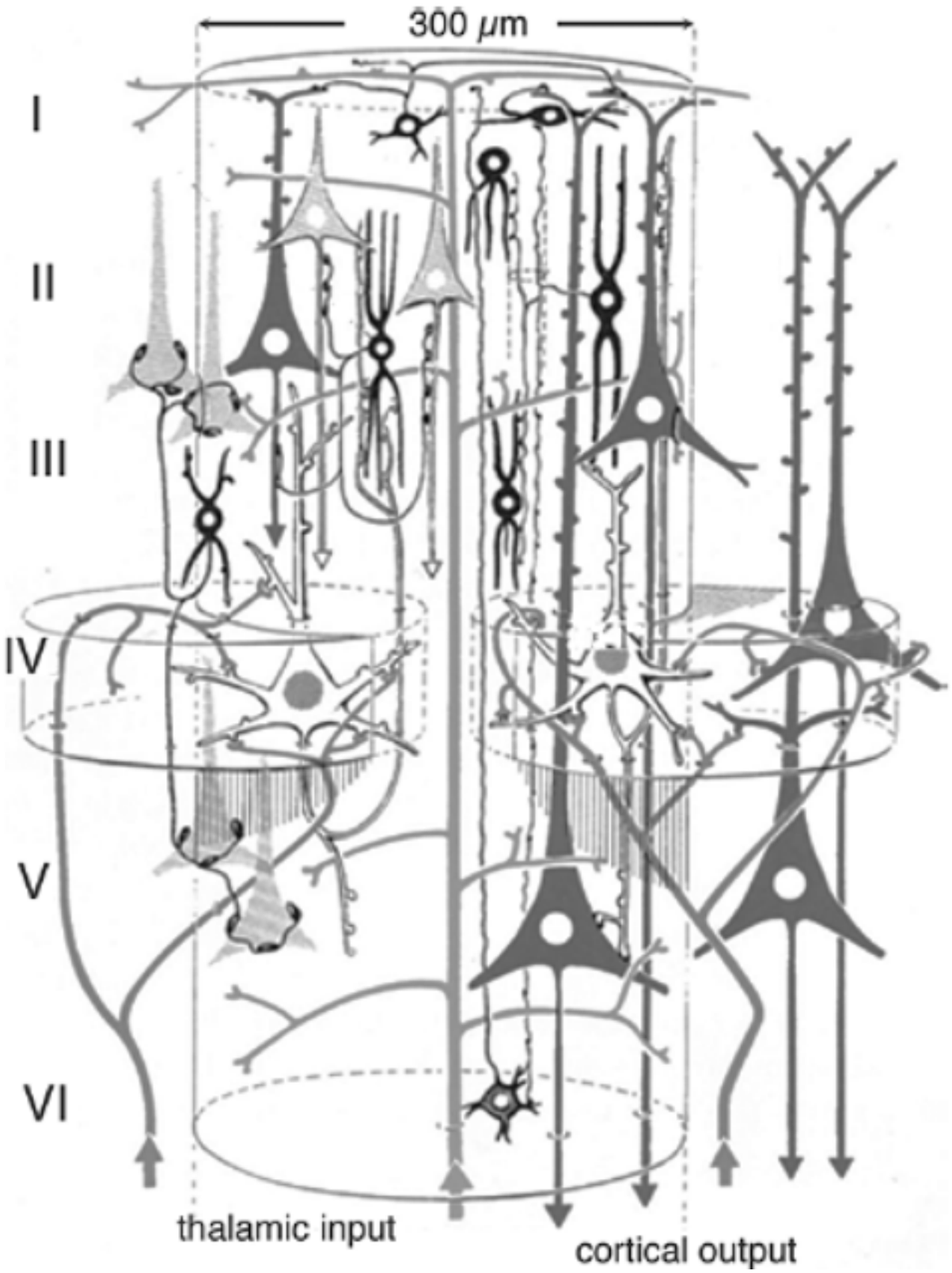
4. contents of consciousness = qualia and the Hard problem

break

5. no-report paradigms

6. integrated information theory

1. Neurons

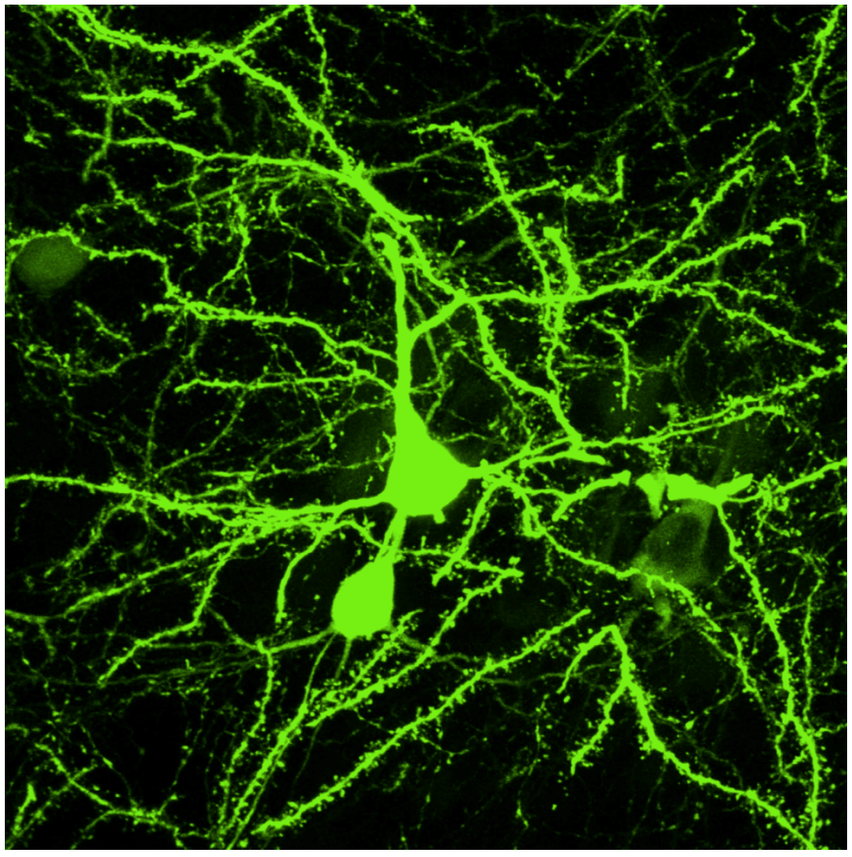


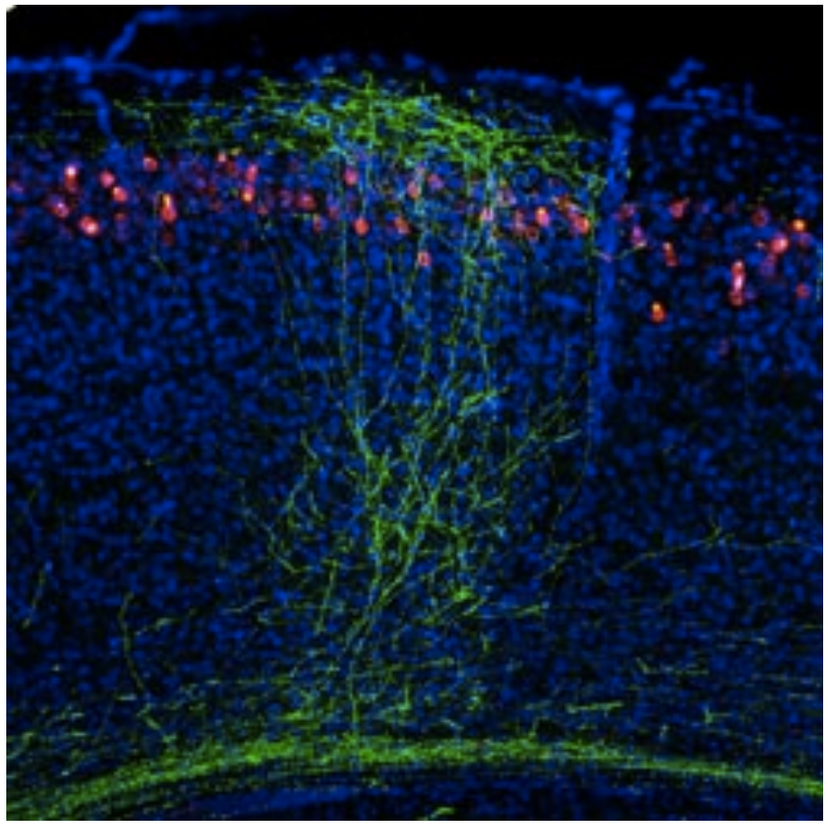
Cell body
  Axon
  Dendrites

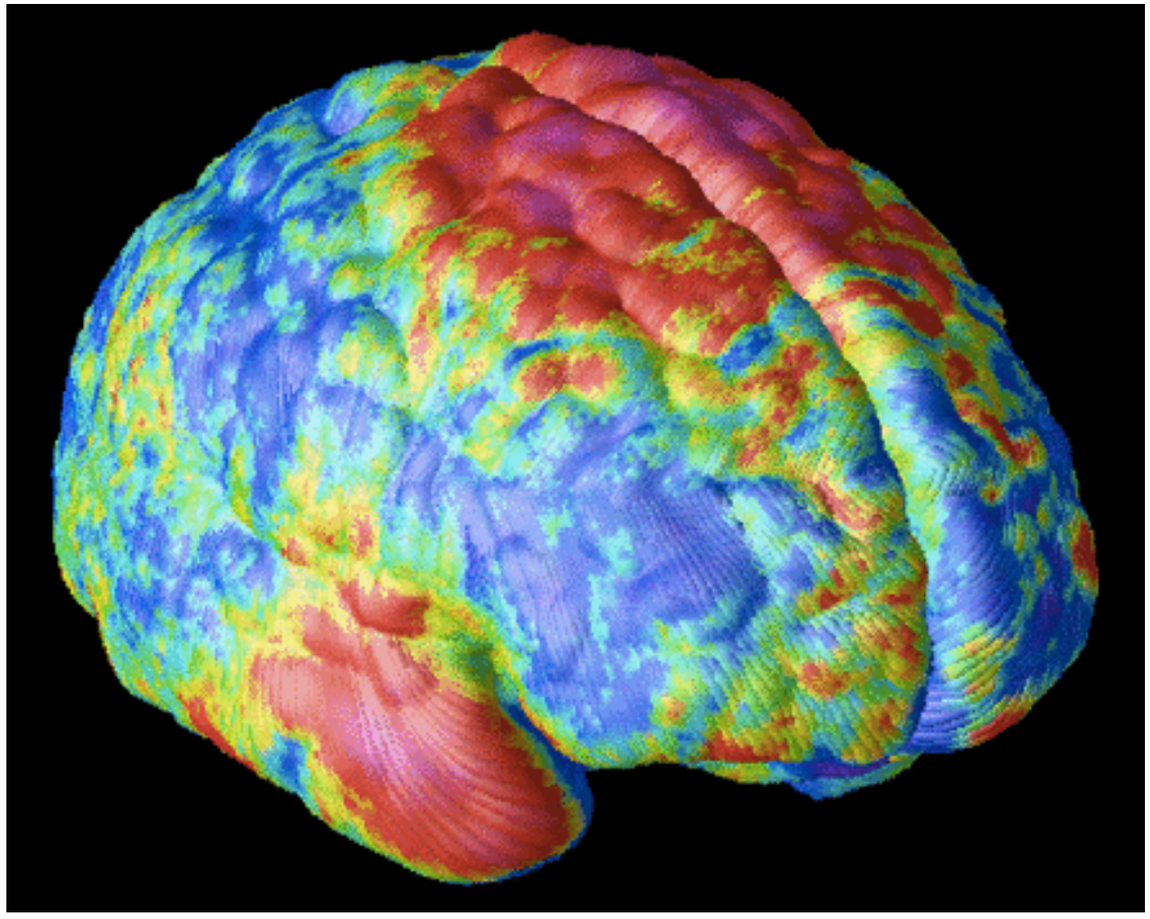
Synapses

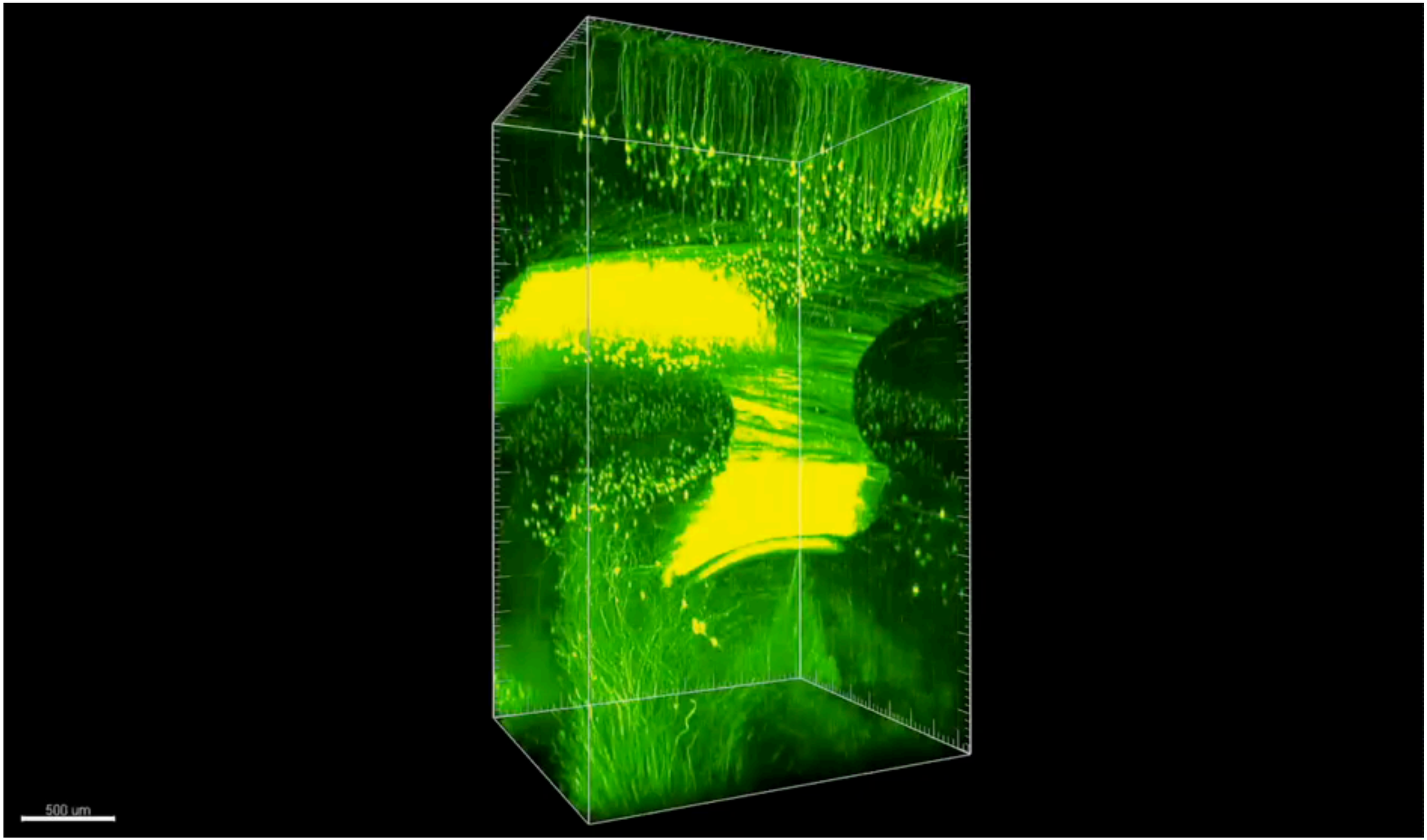
Excitatory vs Inhibitory

Spikes









1. Video 2: 3D visualization of the YFP-expressing neuronal circuit elements from pial surface to the thalamus in the intact Thy-1:eYFP mouse brain (16 weeks old) shown in Fig. 2. (11,386 KB, Download)
   Fly-through animation of the 3D volume data (2,037 Å~ 1,694 Å~ 3,405 µm; step-size=1.976 µm) illustrates visualization of all layers of cortex, the hippocampus, and the thalamus without degradation of resolution at depth. 1p excitation (514nm) and a 10Å~ objective (NA 0.3, WD 3.6 mm) were used.

Important numbers

- In total 10^ neurons.
- One neuron receives inputs from ~10^ other neurons
- Most connections are with neighboring neurons. A minor proportion of axons go outside of the local region
- % of synapses is excitatory (Binzegger et al 2009 Neural Networks)
- Cerebellum — times more neurons than in cerebral cortex (Herculano-Houzel et al 2012 PNAS)

Important numbers

- In total 10^11 neurons.
- One neuron receives inputs from ~10^3 other neurons
- Most connections are with neighboring neurons. A minor proportion of axons go outside of the local region
- 80% of synapses is excitatory (Binzegger et al 2009 Neural Networks)
- Cerebellum — 4 times more neurons than in cerebral cortex (Herculano-Houzel et al 2012 PNAS)

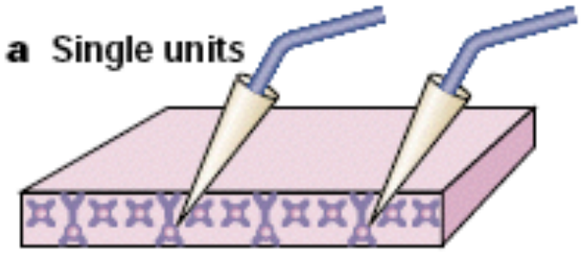
Methods

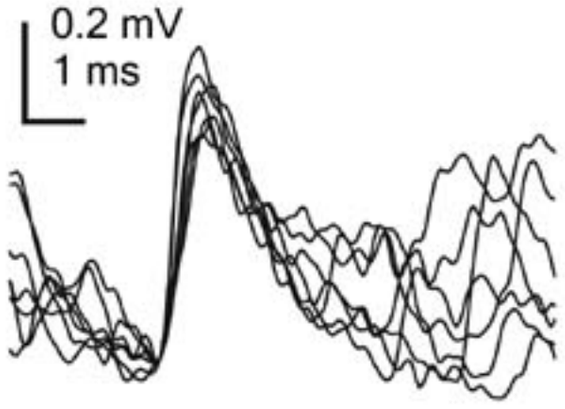
A Local scale

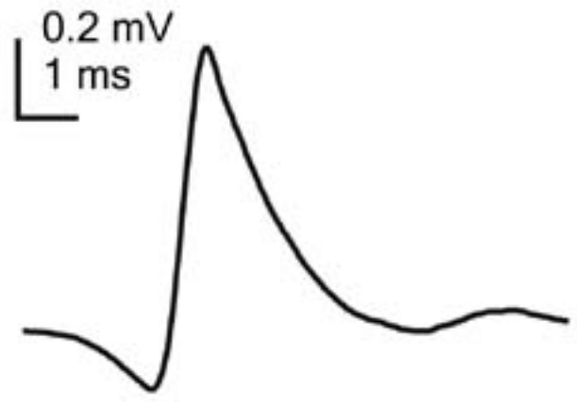
Spatial resoultion

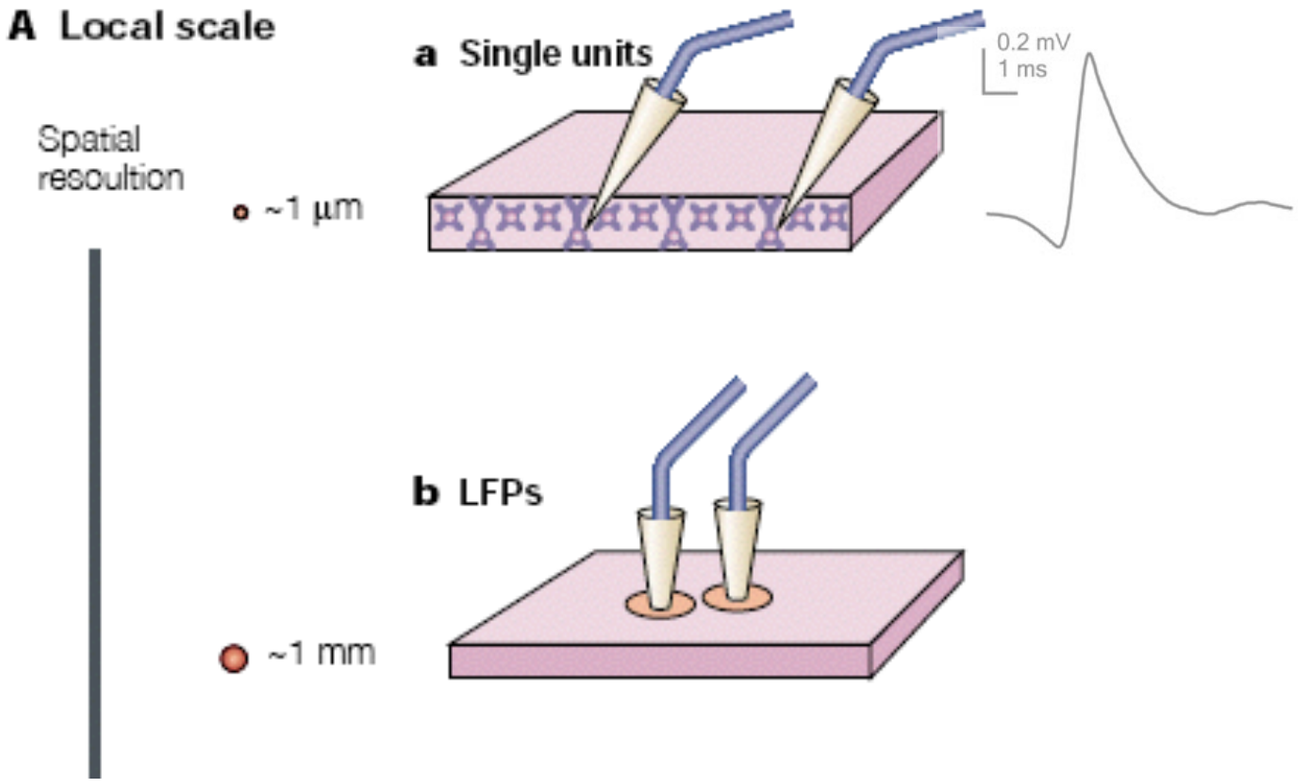
~1 µm

a Single units







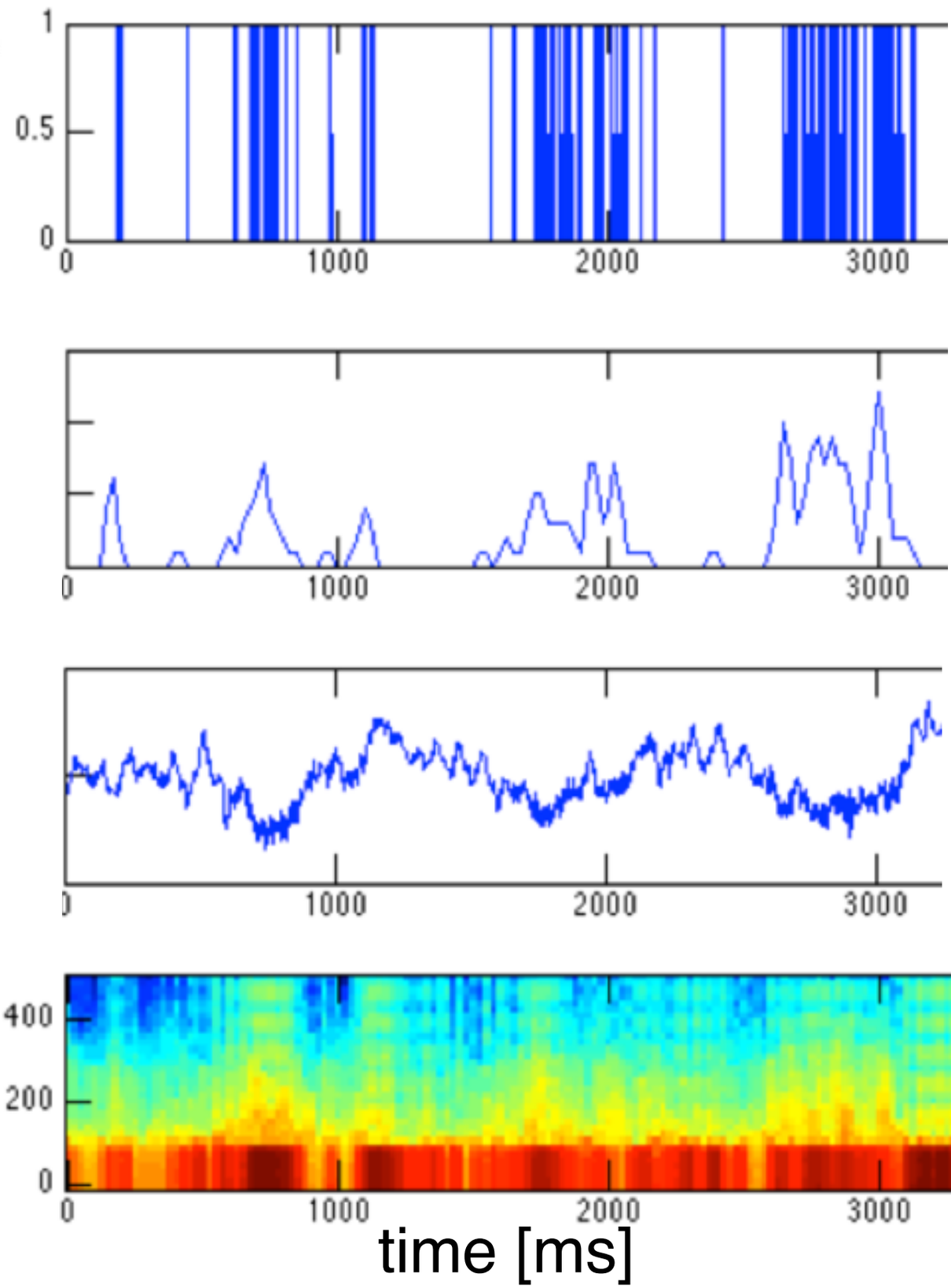


Multi units

Smoothed MUA

Local field potentials

Spectrogram of LFP

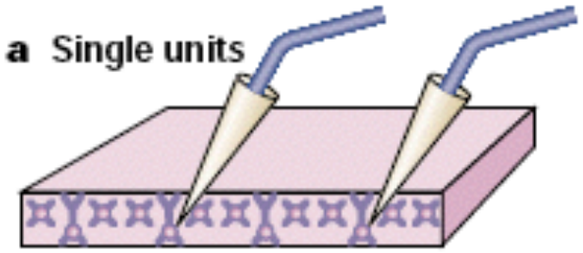


A Local scale

Spatial resolution

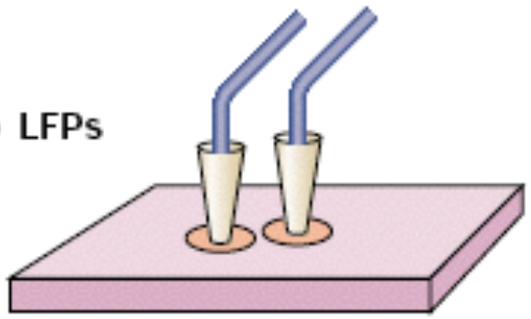
~1 µm

a Single units



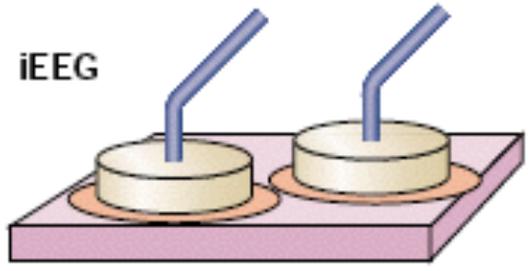
~1 mm

b LFPs



~1 cm

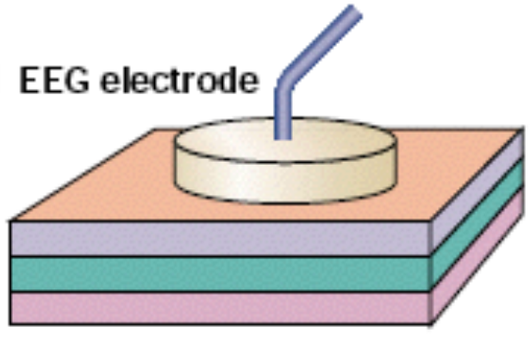
c iEEG

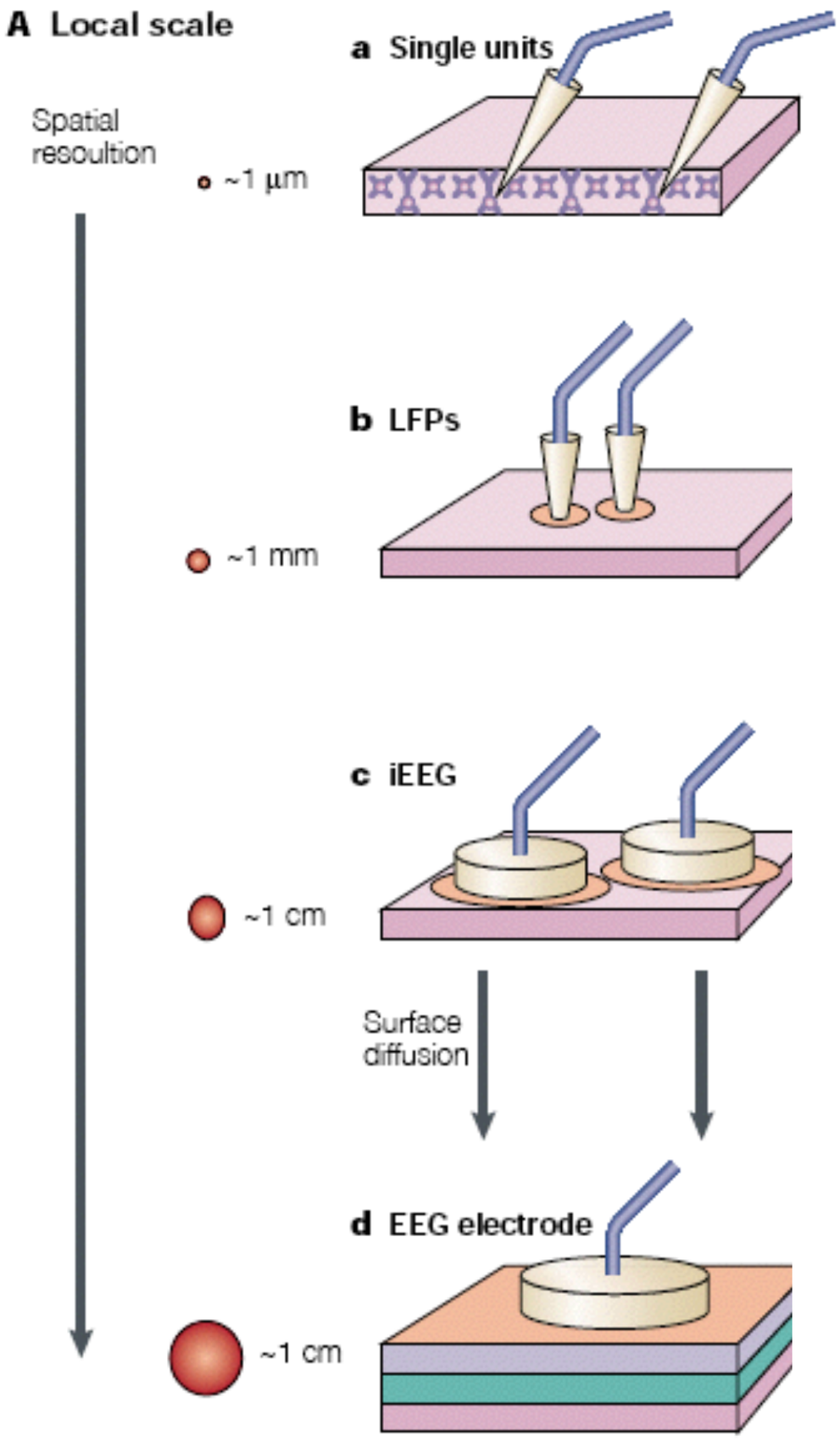


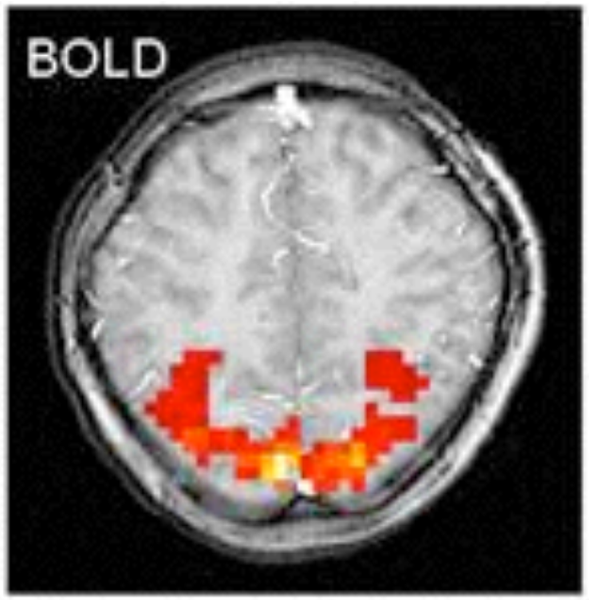
Surface diffusion

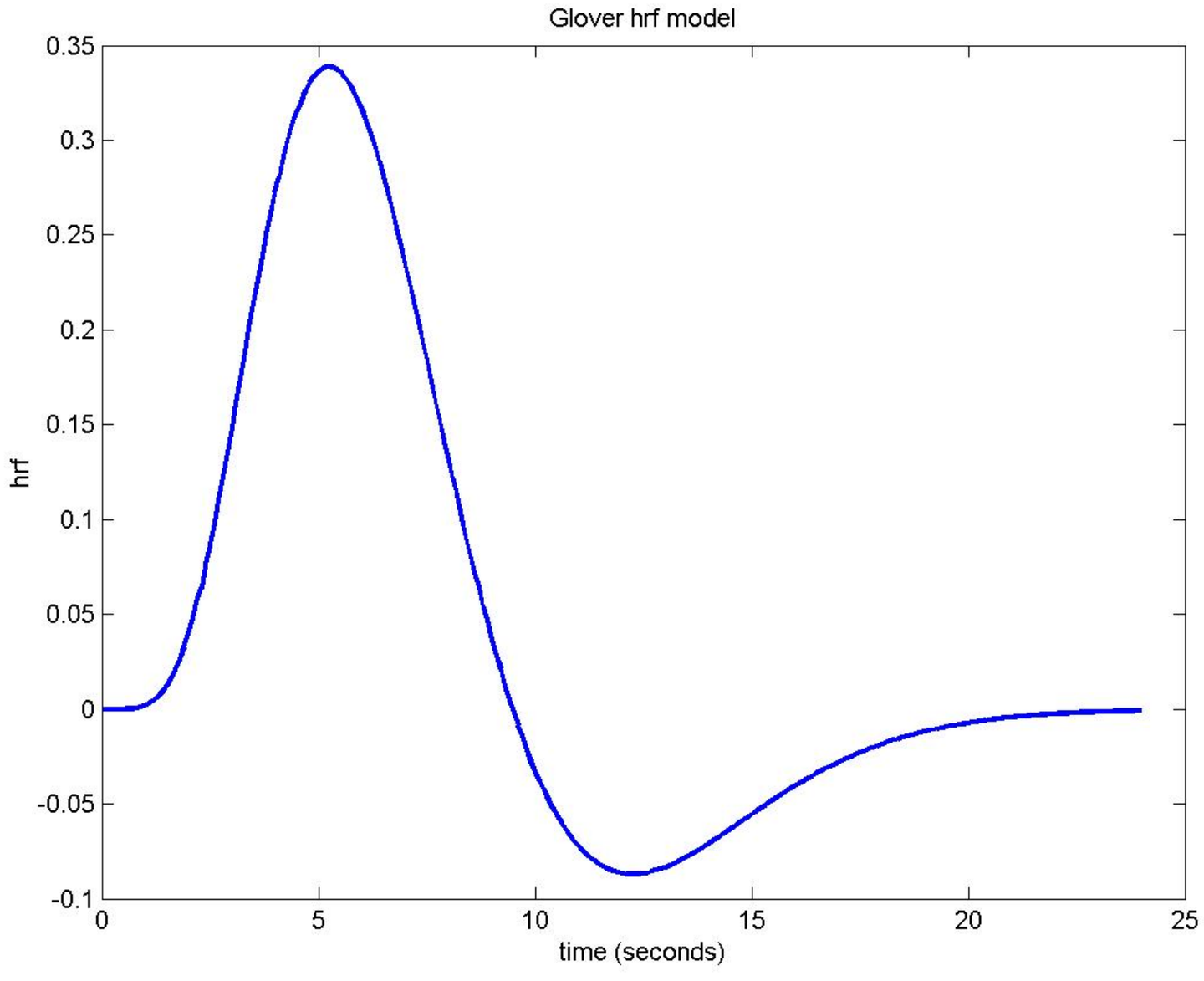
~1 cm

d EEG electrode




A Local scale
Spatial resolution
~1 µm
a Single units
~1 mm
b LFPs
~1 cm
c iEEG
Surface diffusion
~1 cm
d EEG electrode


BOLD


Glover hrf model
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
-0.05
-0.1
hrf
0
5
10
15
20
25
time (seconds)

2. A brief history of the consciousness research

~1900

Phenomenology

Gestalt psychology

~1920

Behaviorism

~1960

Cognitive revolution

~1990

Consciousness research

Neural correlates of consciousness

- *A selected list of the breakthroughs in the last 25 years of consciousness research (Boly et al 2013)*

- Understanding of the neural mechanisms that regulates **levels** of consciousness

- Limits and scopes of **non-conscious** processing; its neuronal correlates; and its behavioral consequences

- **Relationship** between consciousness *per se* and cognitive processes that supports it

In what sense do we use the word “consciousness” and “awareness”?

Commonsense definitions of "consciousness"

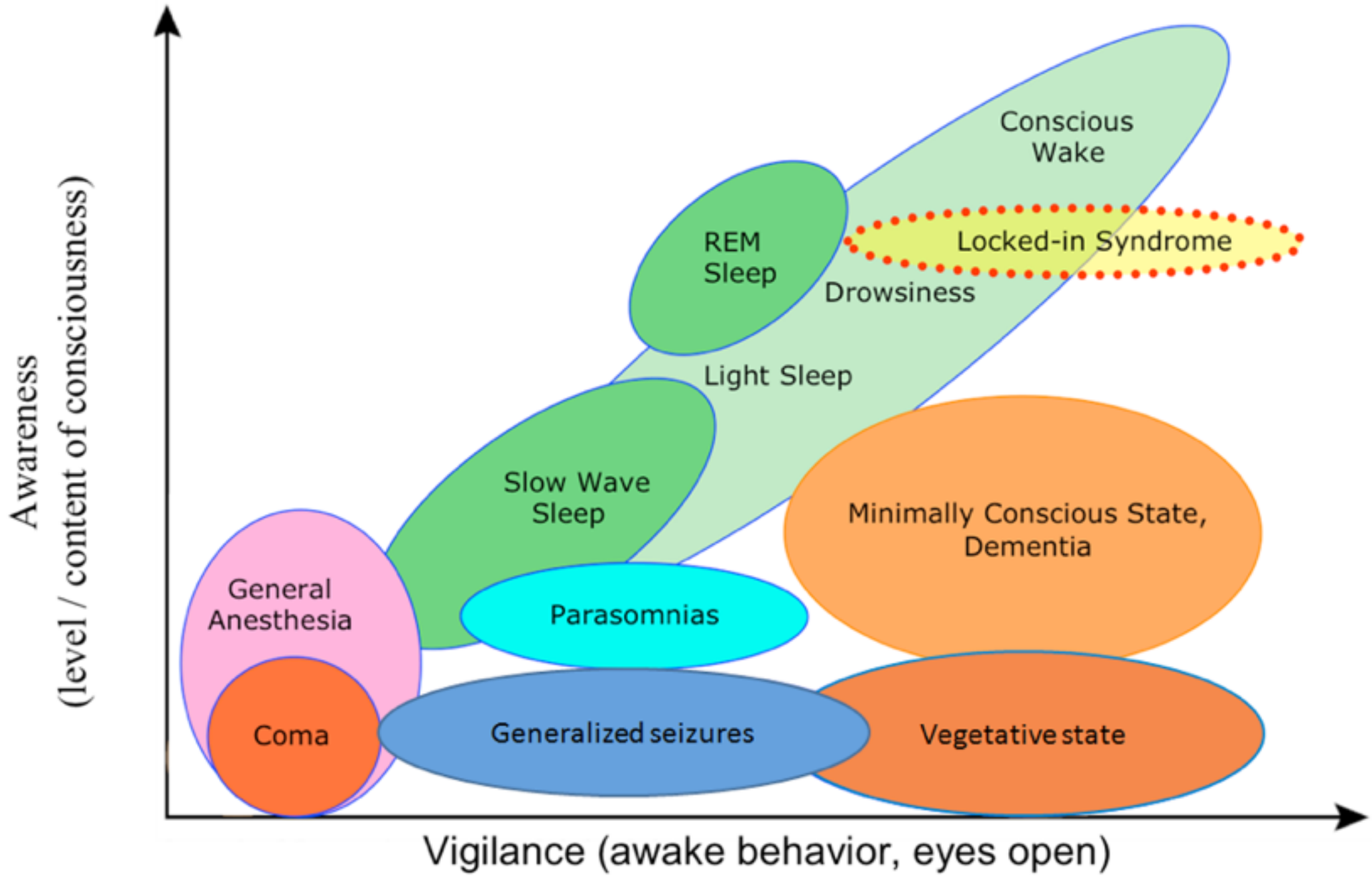
- **Level** of consciousness (as opposed to coma, anesthesia, dreamless sleep)
- **Contents** of consciousness (e.g., redness of red, pain, thoughts)
- (Self consciousness)

Contrastive approach

- Compare the neural activity that accompanies “conscious” and “unconscious” X
- X can be states, perception, motor planning, intention, emotion, ….

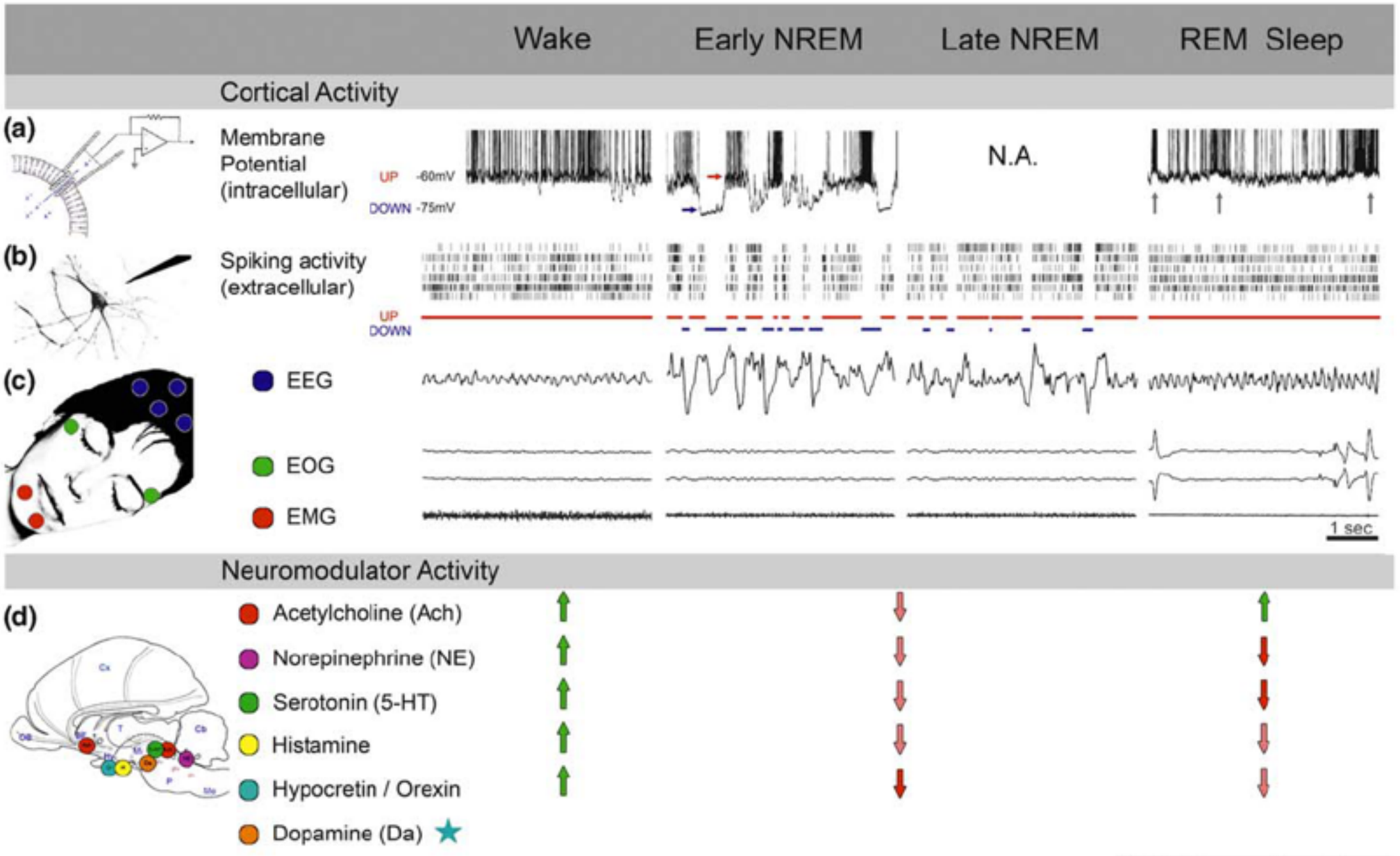
3. level of consciousness

Level and Content of consciousness vs behavioral signs of consciousness



Boly et al 2013 Frontiers in Consciousness Research

During loss of consciousness, brain can be very active!



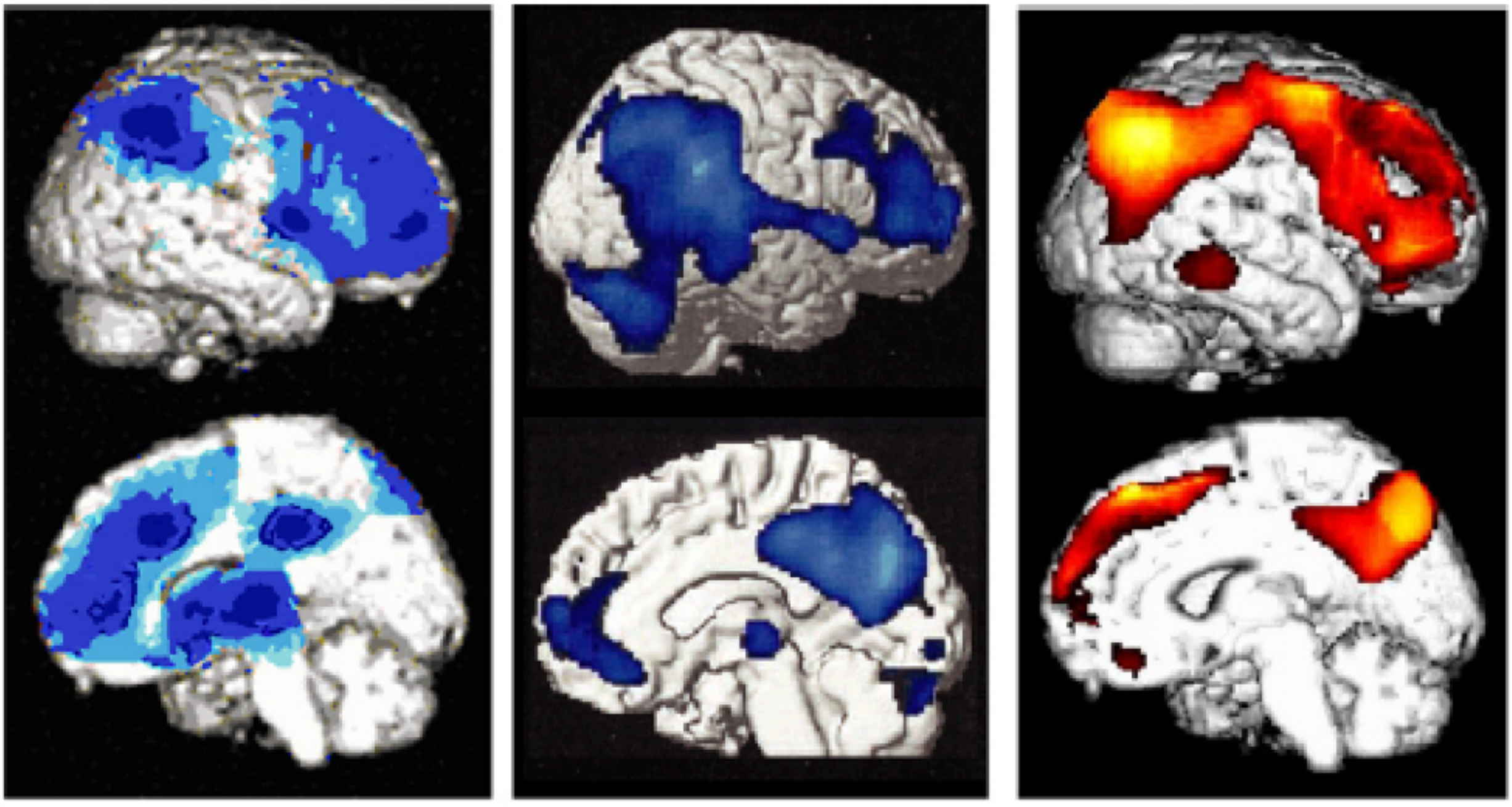
Nir & Tononi 2010 TICS

Reduced metabolism during loss of consciousness

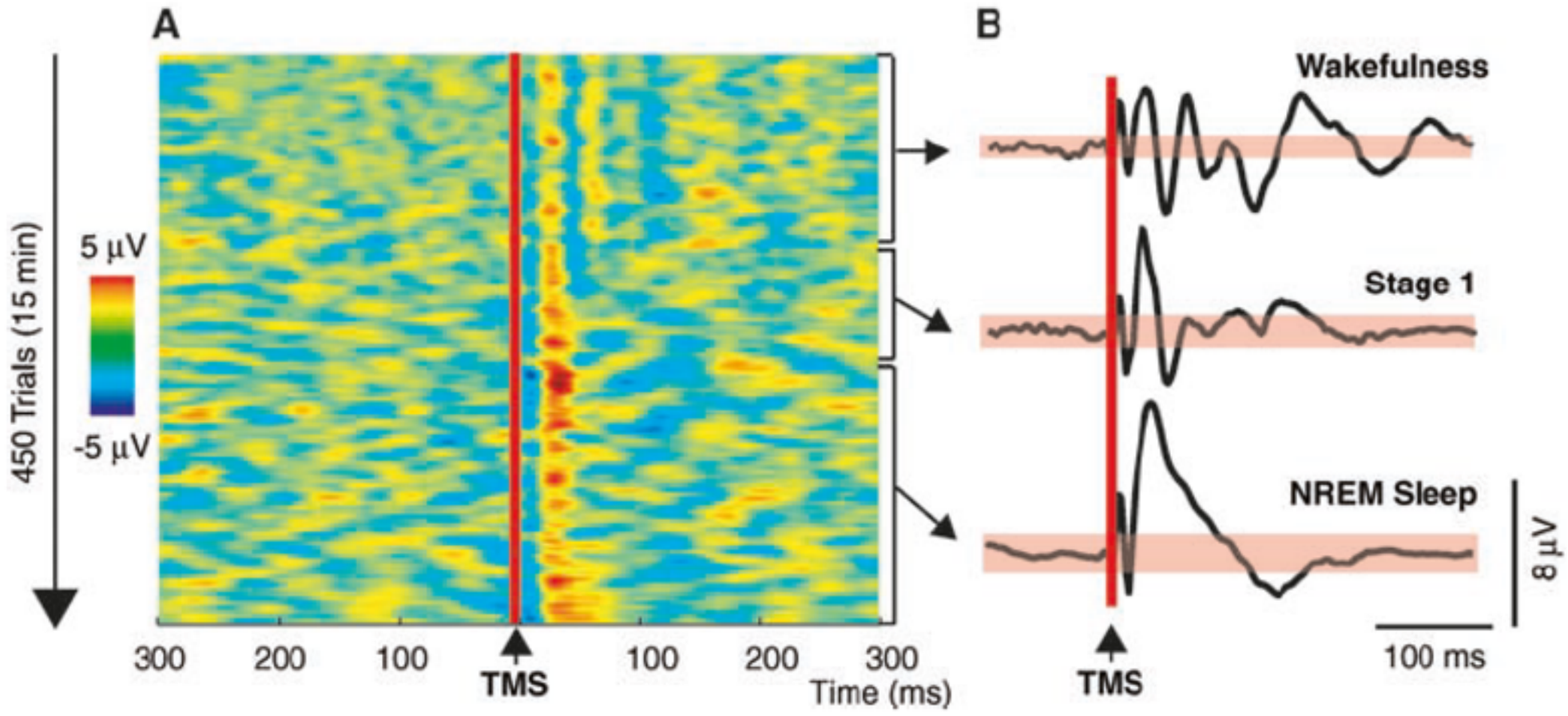
Slow-wave sleep

Anesthesia

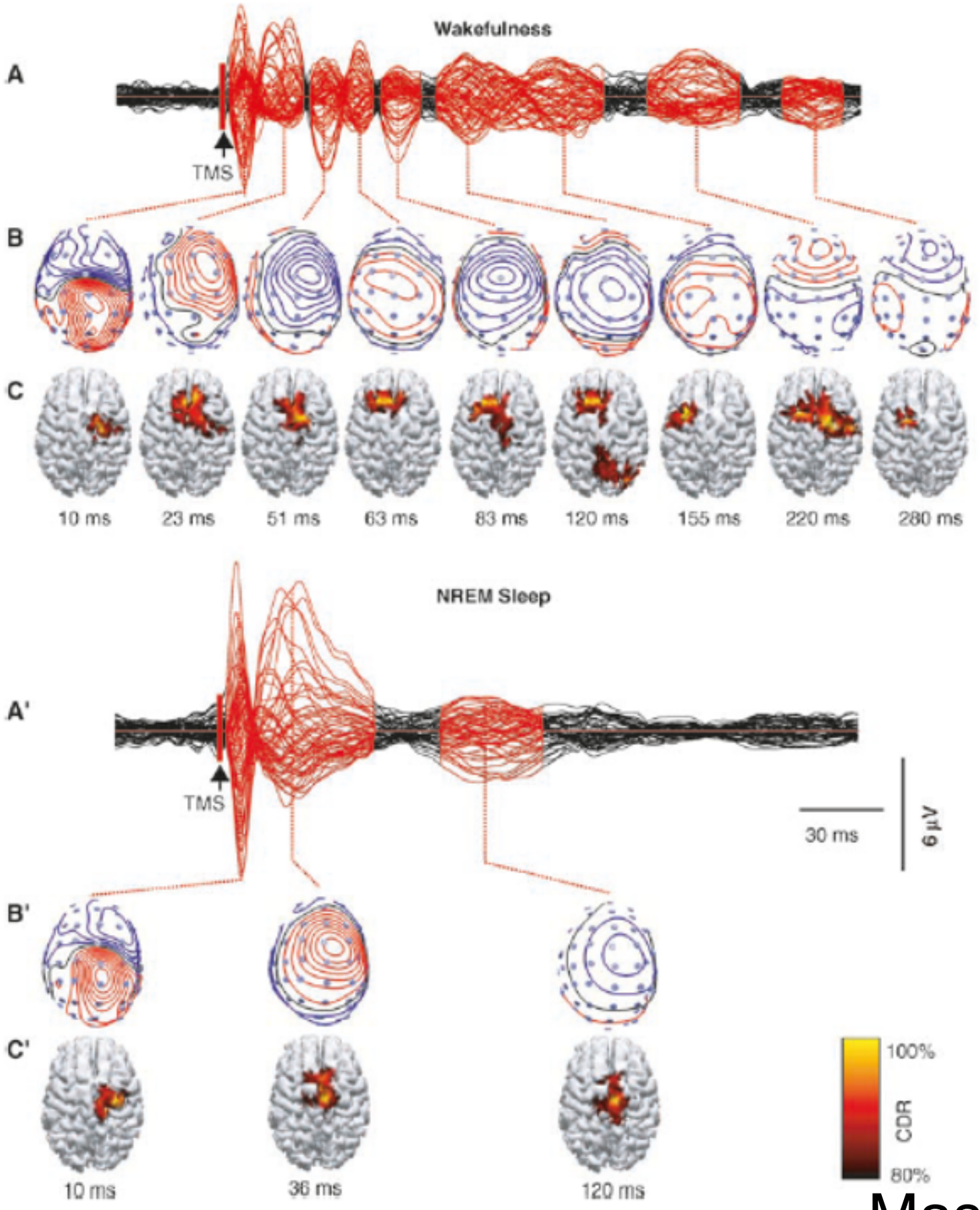
Vegetative state



Breakdown of global connectivity as a key for loss of consciousness

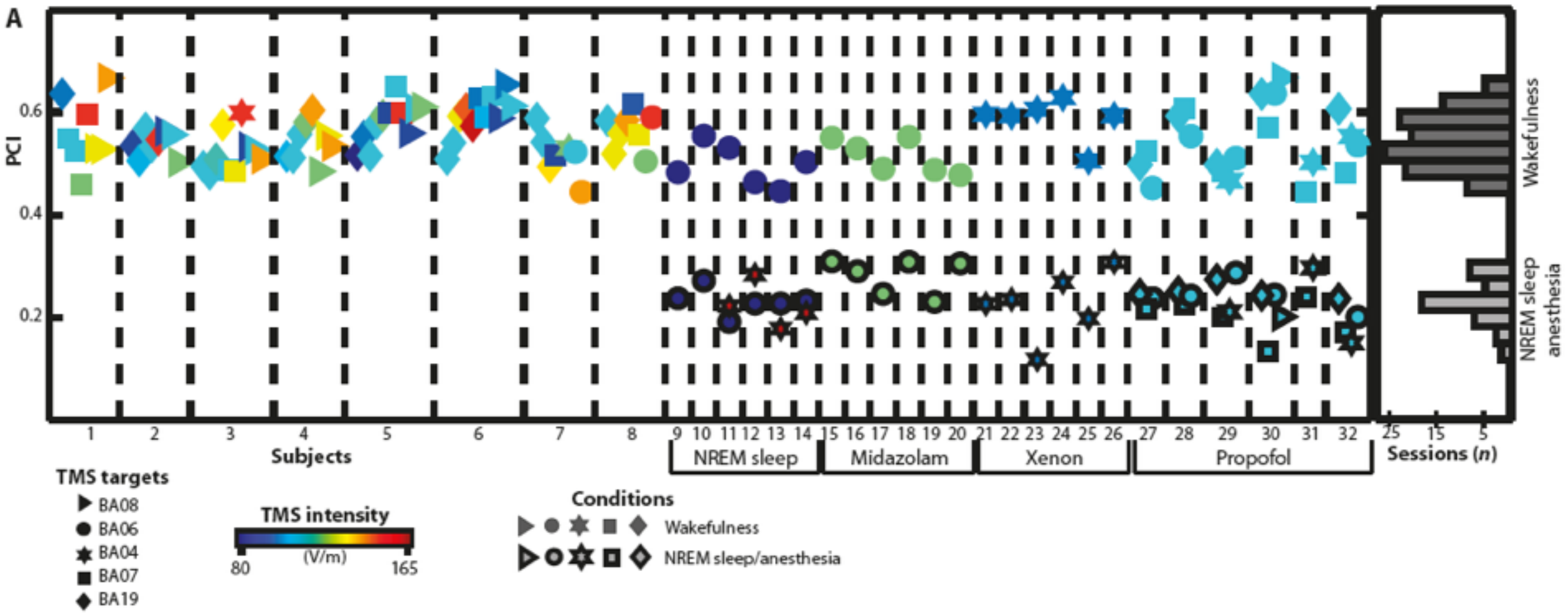


Massimini et al 2005 Science



Massimini et al 2005 Science

Breakdown of global connectivity as a key for loss of consciousness



Casali et al 2013 Science Trans Medicine

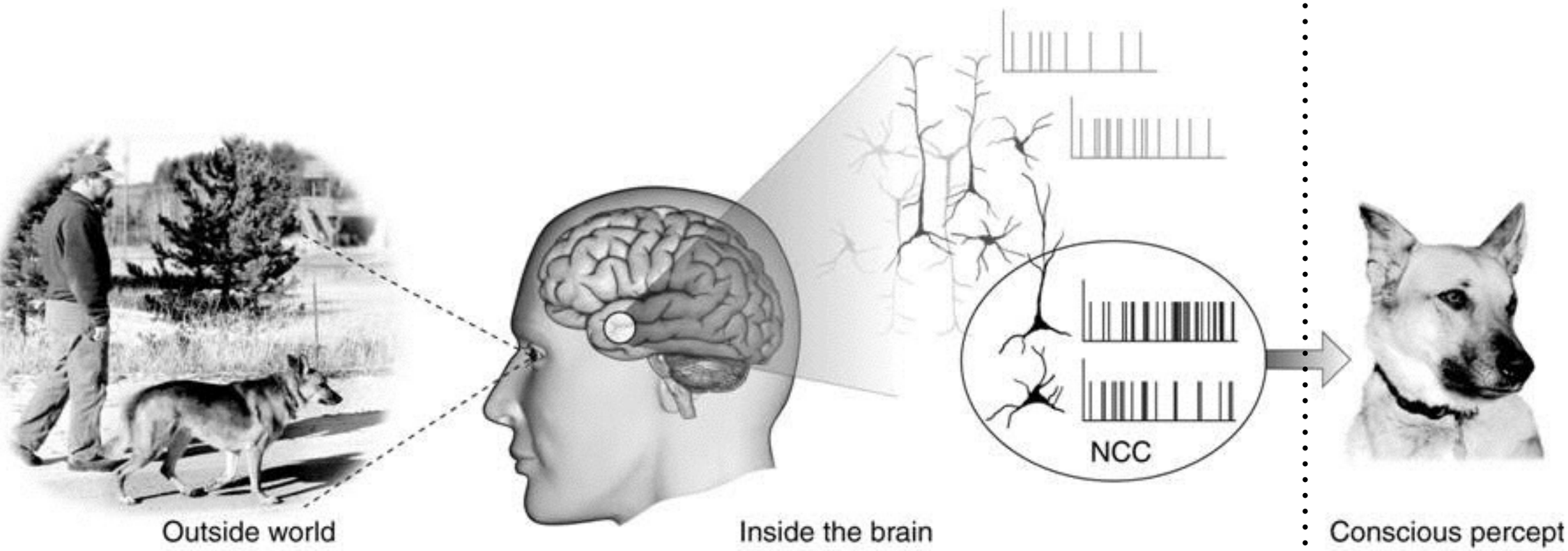
4. contents of consciousness

= qualia

and the Hard problem

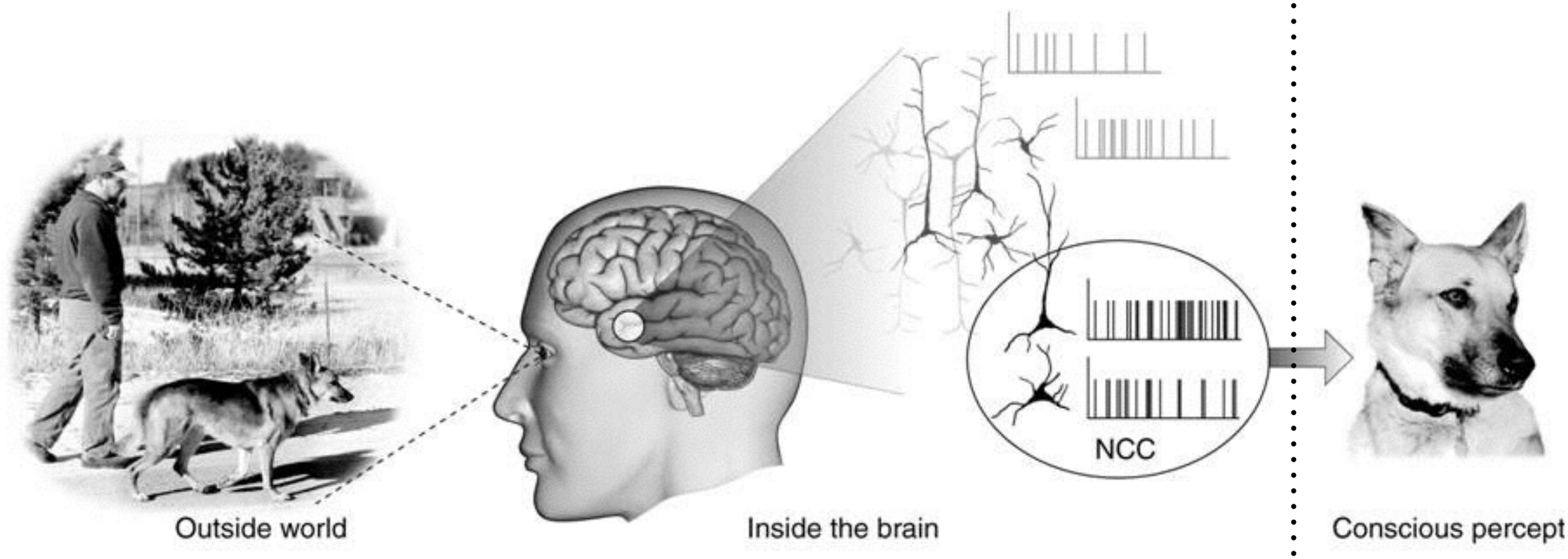
physical
electromagnetic
chemical
interactions

subjective
consciousness,
experience,
phenomenology



physical
electromagnetic
chemical
interactions

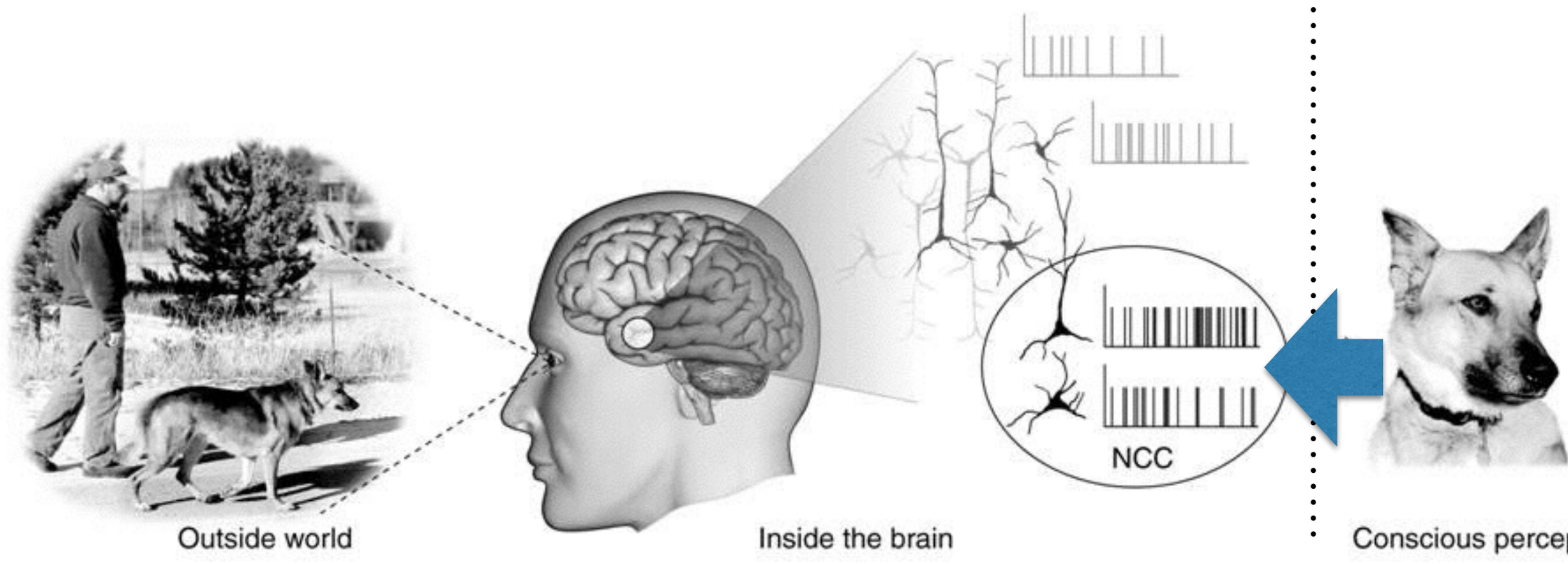
subjective
consciousness,
experience,
phenomenology



Hard Problem of consciousness

physical
electromagnetic
chemical
interactions

subjective
consciousness,
experience,
phenomenology

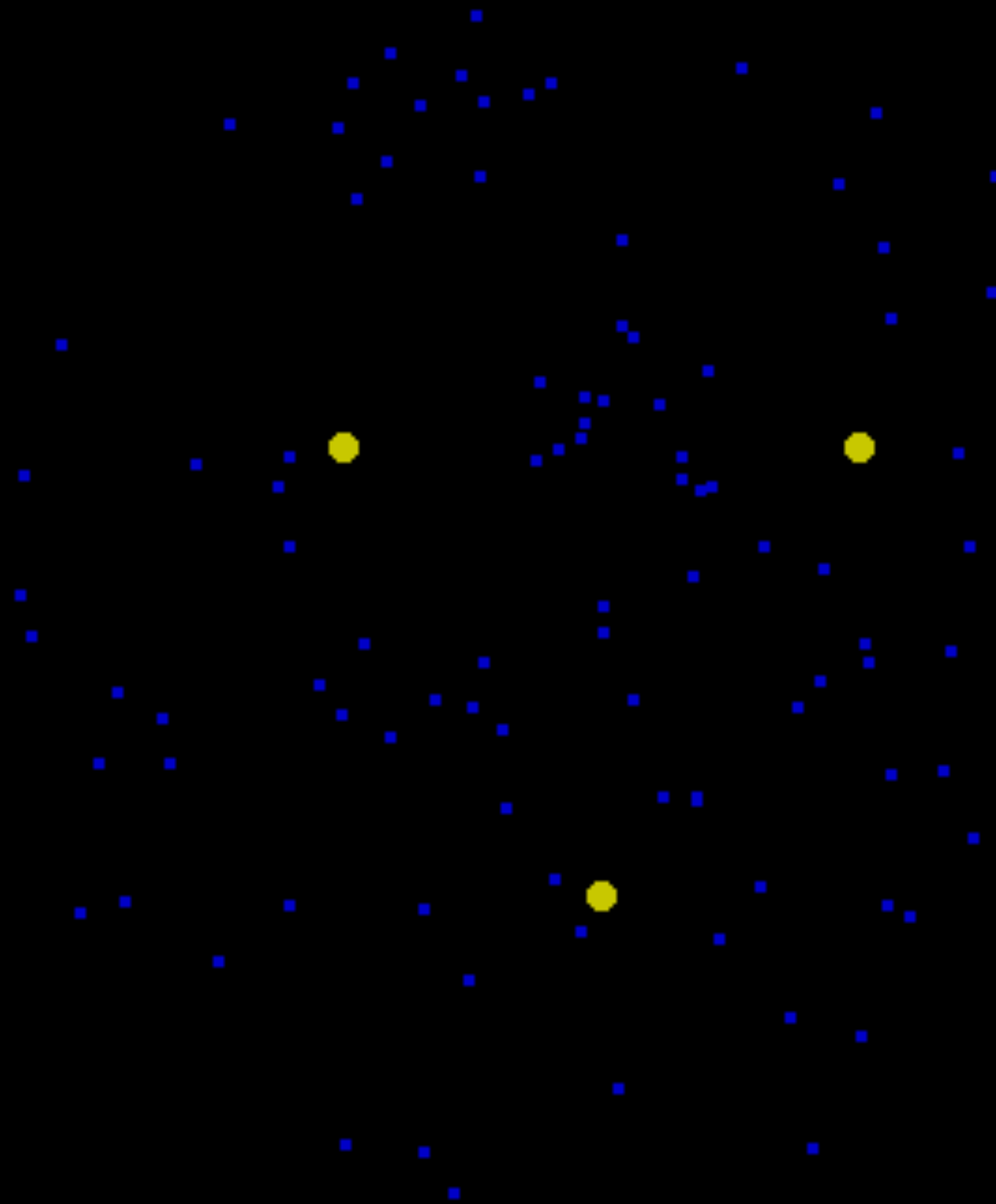


The problem of consciousness:
Is it really Hard?

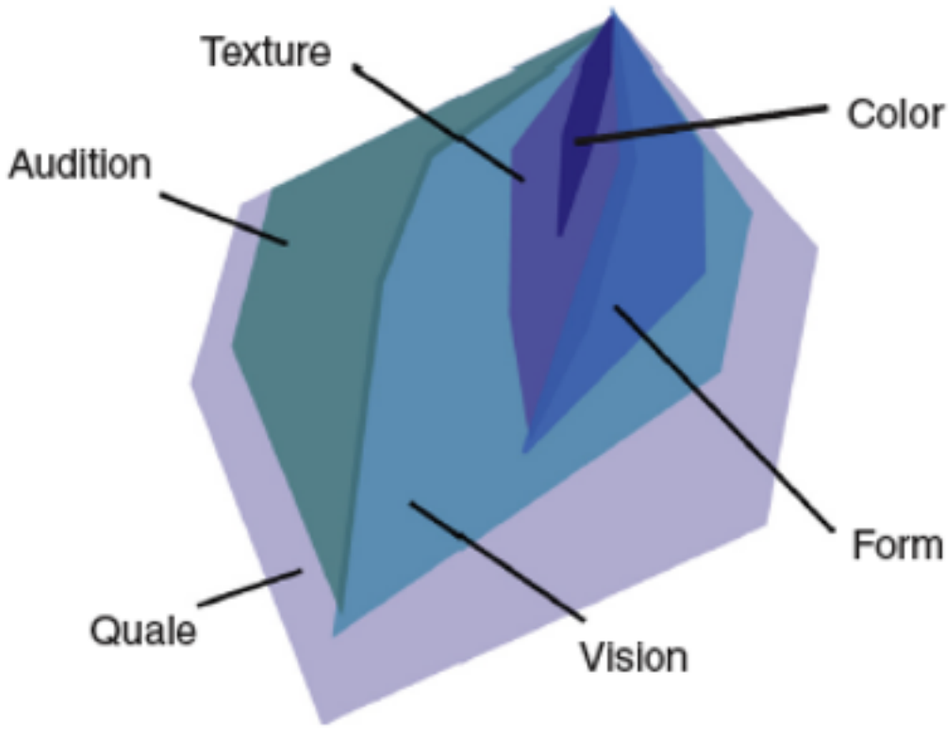
Integrated information theory of consciousness (Tononi 2004 BMC)

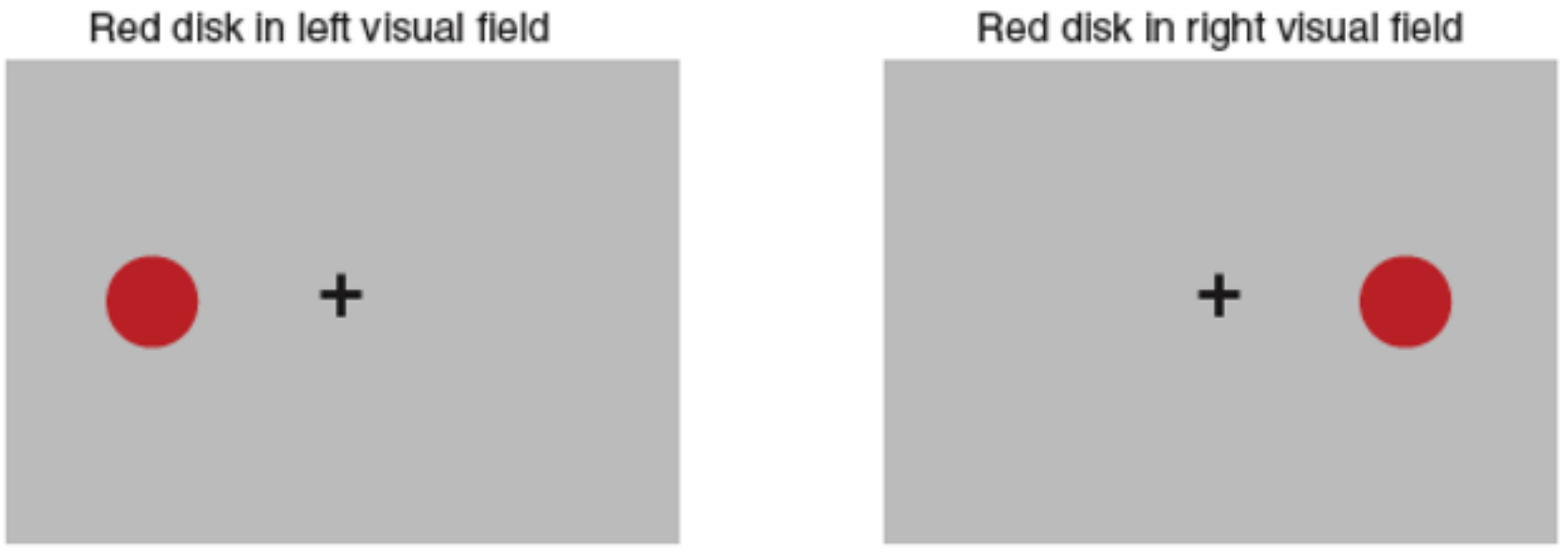
What do I mean by a quale of a yellow dot?

Motion-induced blindness
(Bonneh, Cooperman, Sagi 2001 Nature)



Broad- vs. Narrow- sense qualia





Broad sense: These two experiences are different qualia.

Narrow sense: The redness of the disks refers to the same quale.

Kanai & Tsuchiya 2012 Current Biology

The powerful NCC paradigm

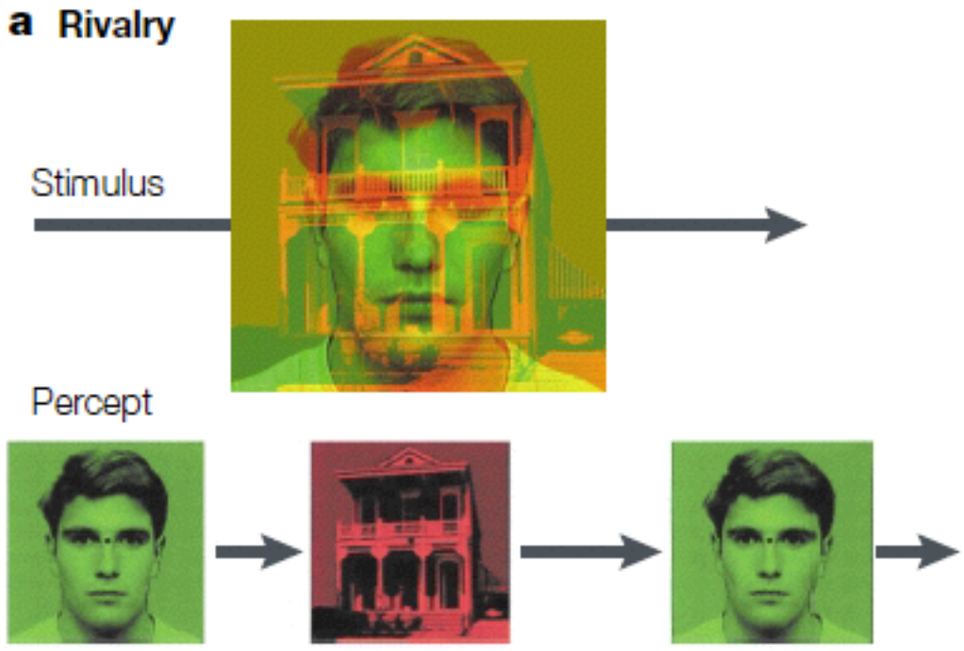
- Keep sensory stimuli **constant;** use perceptual thresholds or ambiguous stimuli

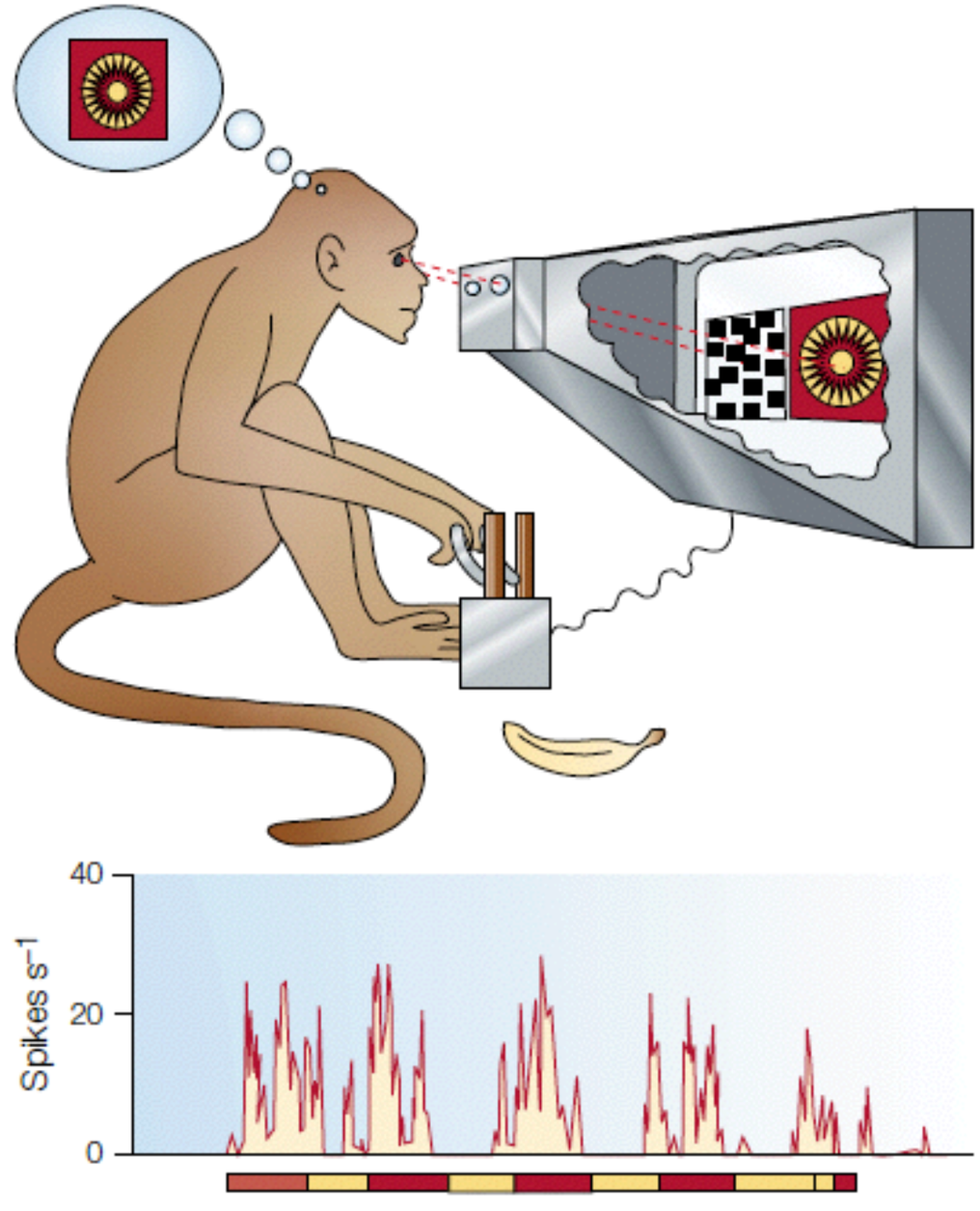
- Manipulate or obtain **variable reports**

- Find the neural activity that correlates with **consciousness**

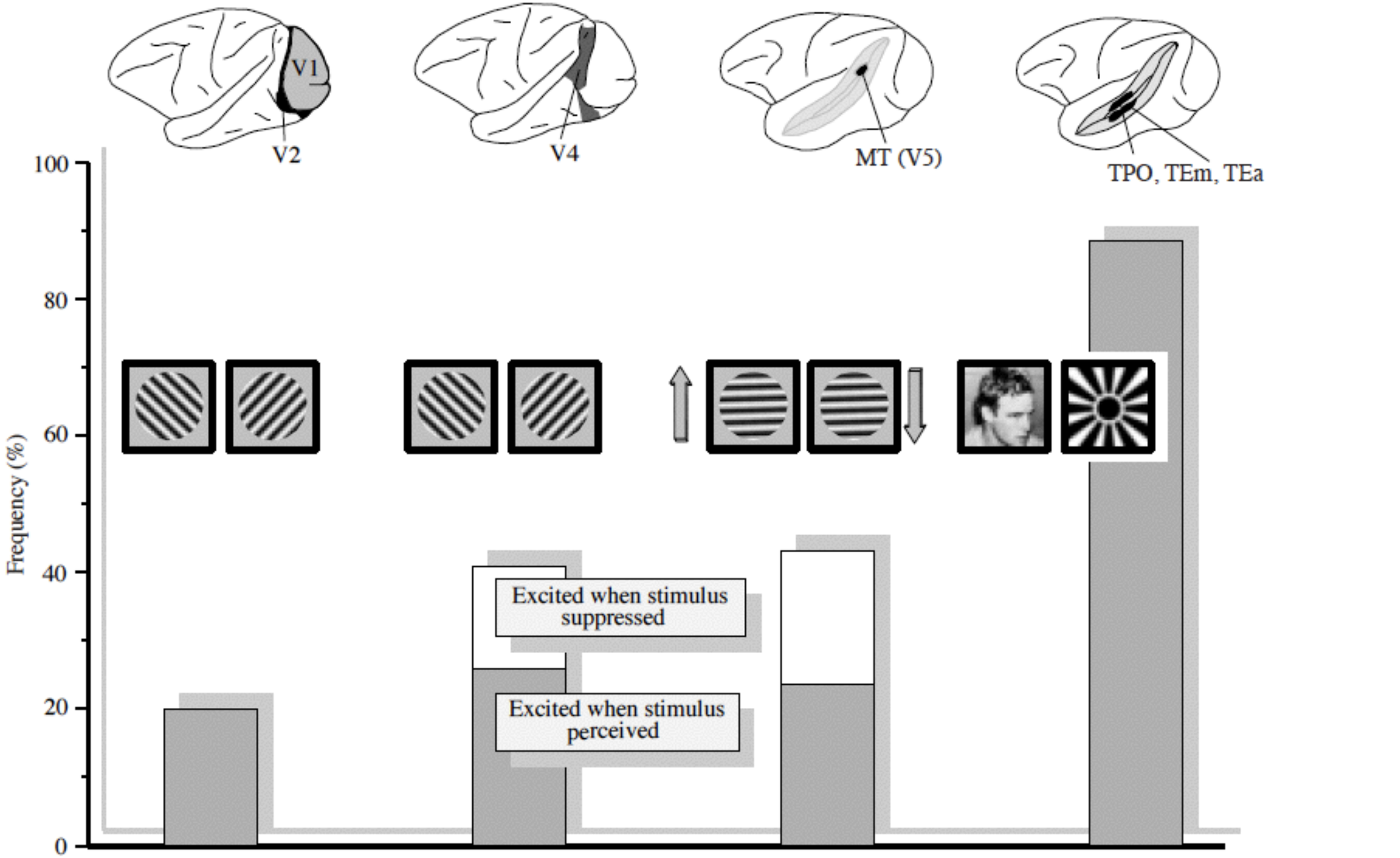
  - ***Contingent on reports!***

Trying to find the NCC with binocular rivalry

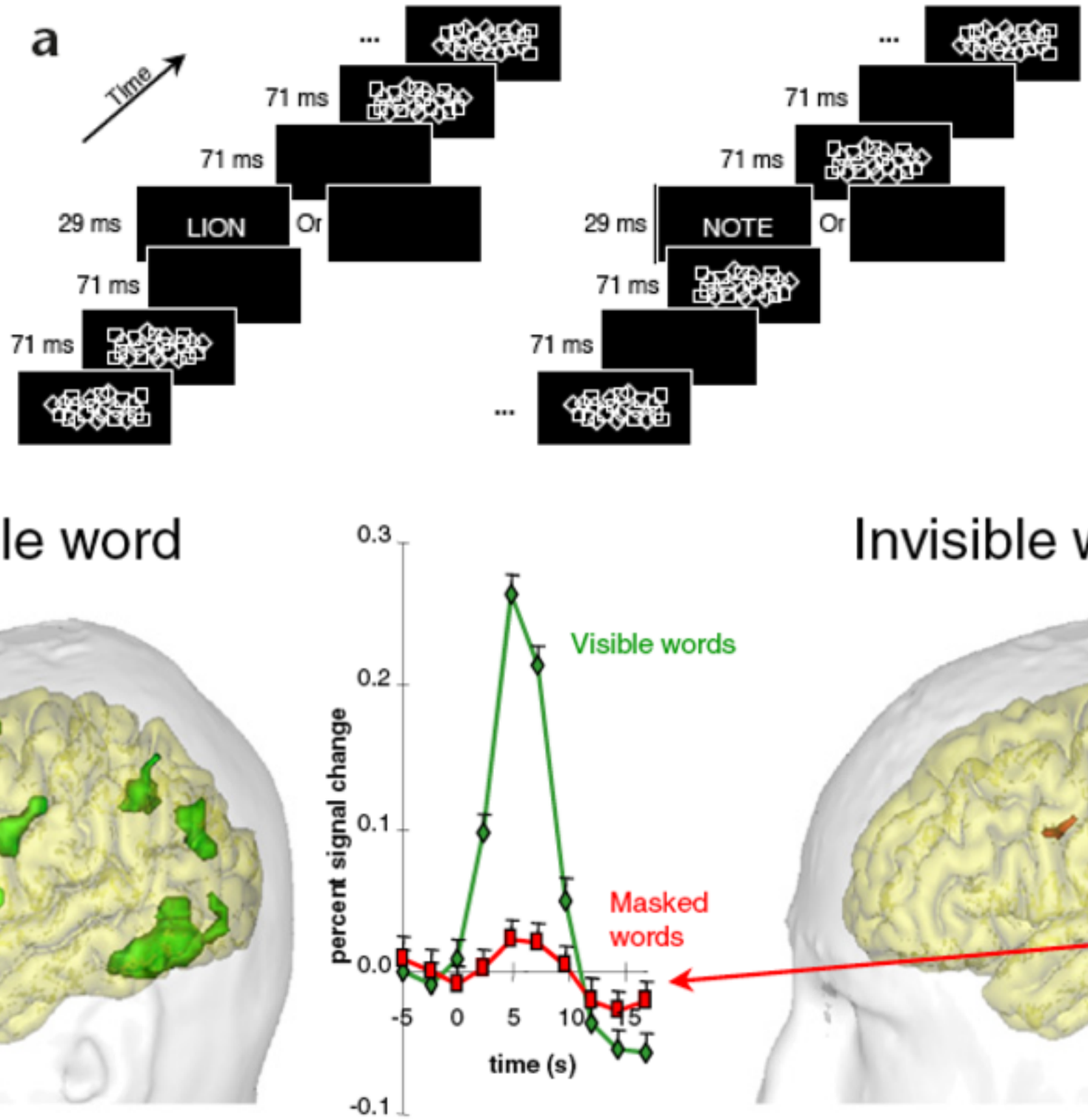




Blake & Logothetis 02 Nat Rev Neuro

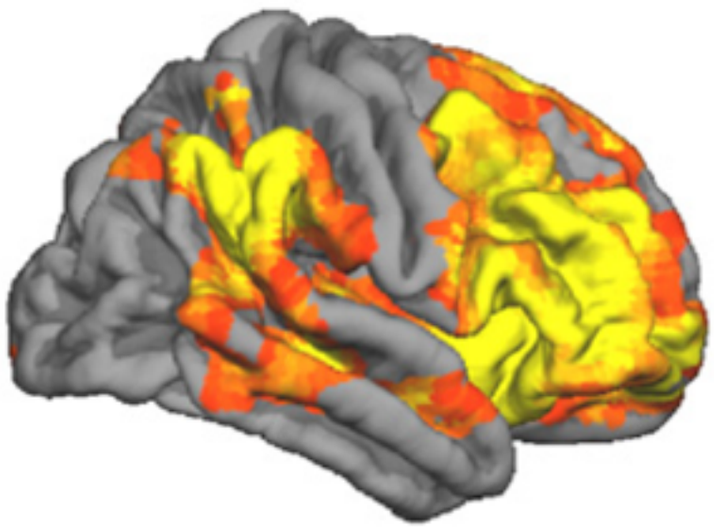


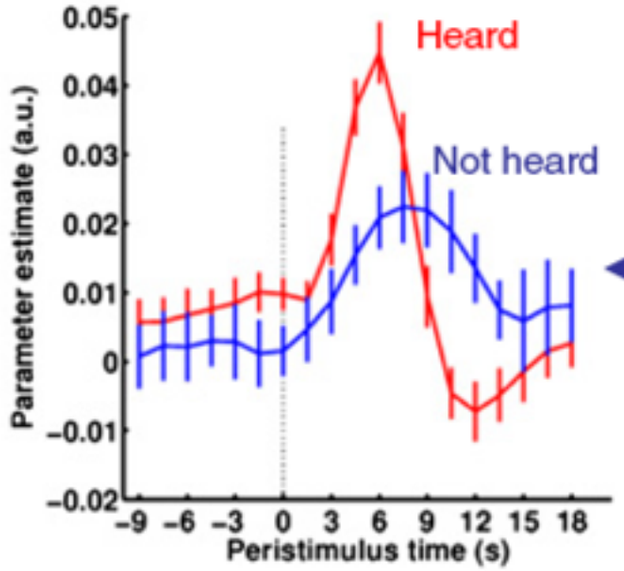
Logothetis 98 Phil Trans



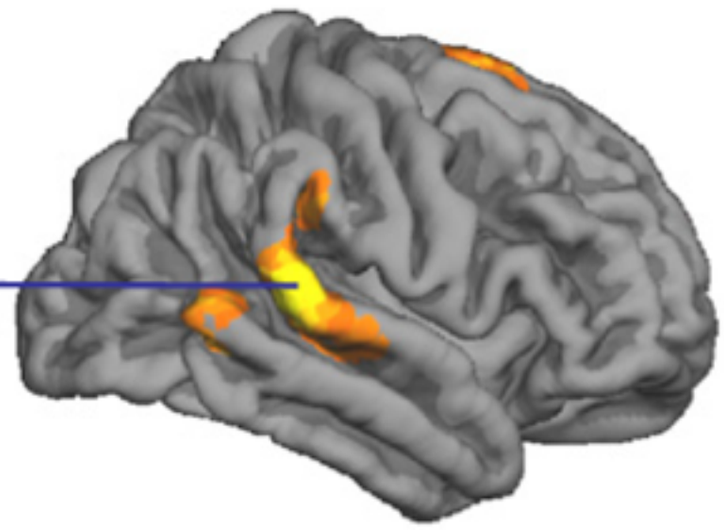
Dehaene 2001 Nat Neuro

Detected sound

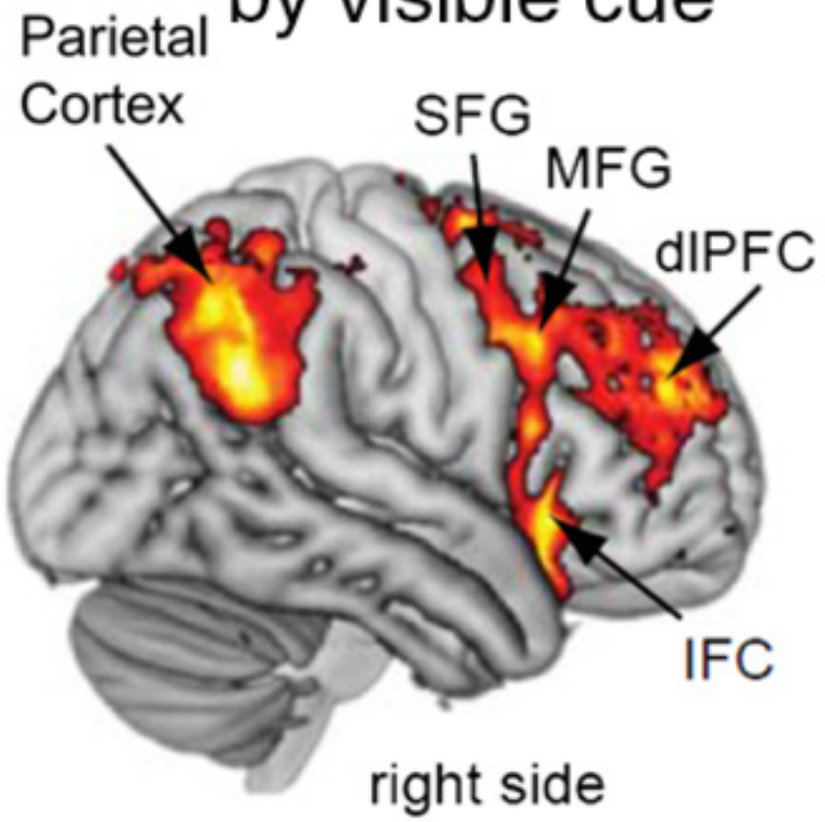


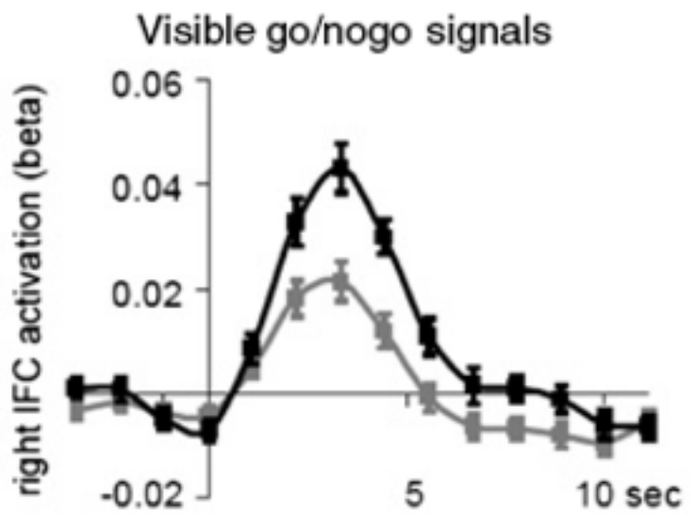


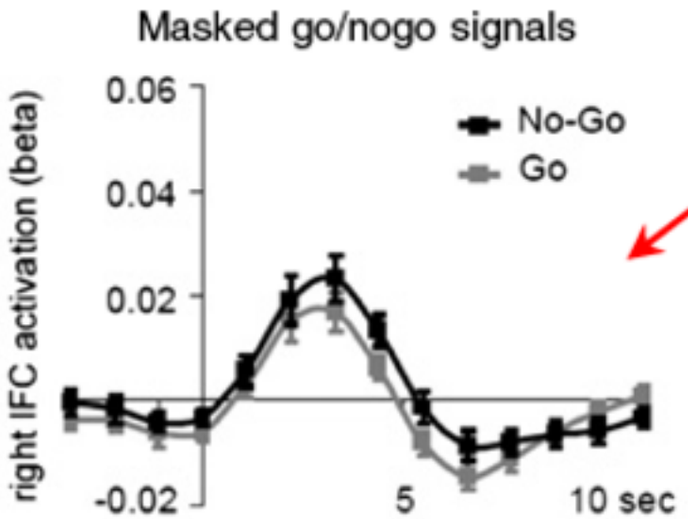
Non-detected sound



Inhibitory control by visible cue

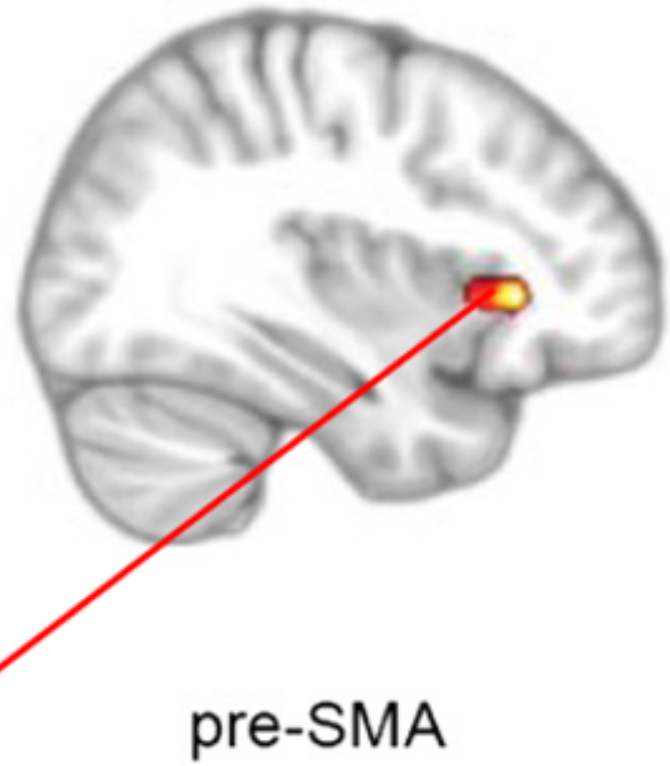


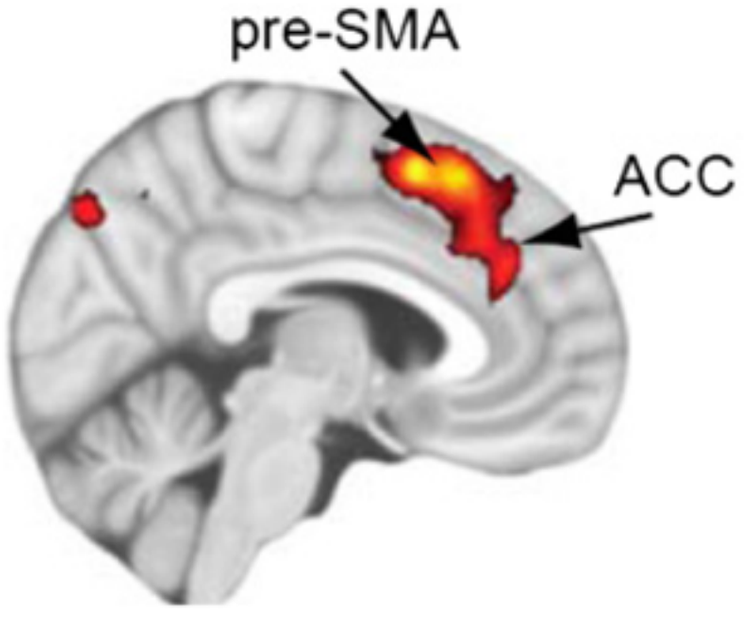


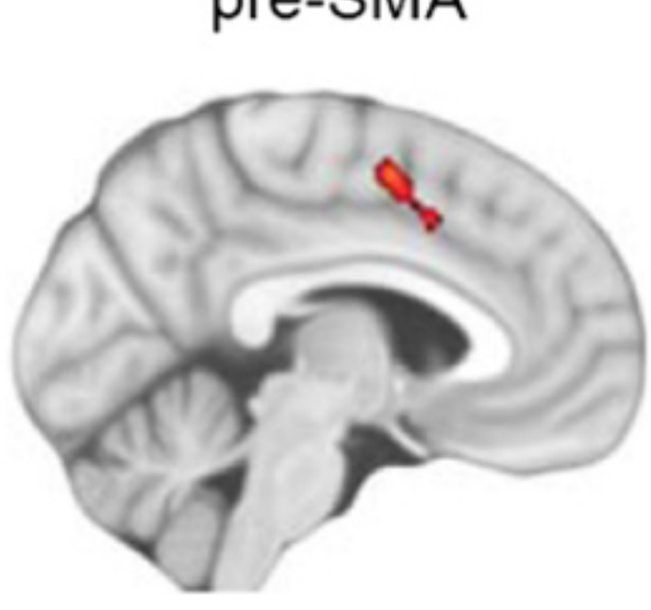


Inhibitory control by invisible cue

right IFC/anterior insula







Top-down attention

Bottom-up stimulus strength ↓	Absent	Present
Weak or interrupted	**Subliminal** (unattended) • Very little activation • Activation is already weak in early extrastriate areas • Little or no priming • No reportability	**Subliminal** (attended) • Strong feedforward activation • Activation decreases with depth • Depth of processing depends on attention and task set • Activation can reach semantic level • Short-lived priming • No durable fronto-parietal activity • No reportability
Sufficiently strong	**Preconscious** • Intense activation, yet confined to sensori-motor processors • Occipito-temporal loops and local synchrony • Priming at multiple levels • No reportability while attention is occupied elsewhere	**Conscious** • Orientation of top-down attention • Amplification of sensori-motor activity • Intense activation spreading to parieto-frontal network • Long-distance loops and global synchrony • Durable activation, maintained at will • Conscious reportability

Dehaene 2006 TICS

- But, does it explain conscious experience? (qualia in a broad sense)

- Are we studying contents of consciousness per se? Or are we confounding NCC with attention, working memory, and report/access?

Change Blindness

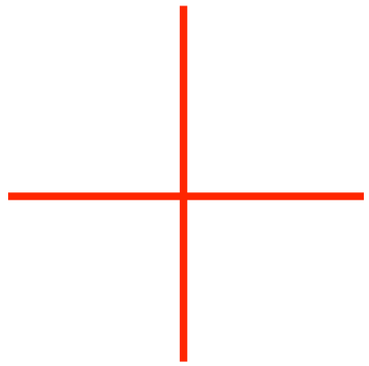
Rensink et al 1997 Psych Sci,
Simons & Rensink 2005 TICS

Change blindness makes us realize how little we can be aware of our surroundings.

Like a lamp in a refrigerator?

Are these illusions really useful in capturing the essential features of conscious experience?

Another type of change detection

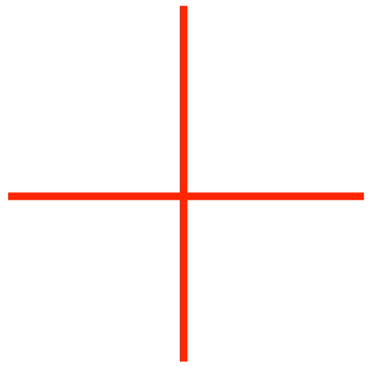


Freeman & Simoncelli 2011 Nat Neuro, Rosenholtz 2012 Fronteirs

Another type of change detection

Freeman & Simoncelli 2011 Nat Neuro, Rosenholtz 2012 Fronteirs

Another type of change detection

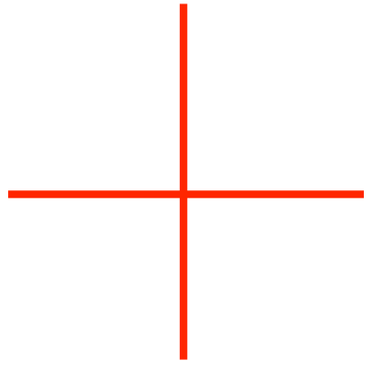


Freeman & Simoncelli 2011 Nat Neuro, Rosenholtz 2012 Fronteirs

Another type of change detection

Freeman & Simoncelli 2011 Nat Neuro, Rosenholtz 2012 Fronteirs

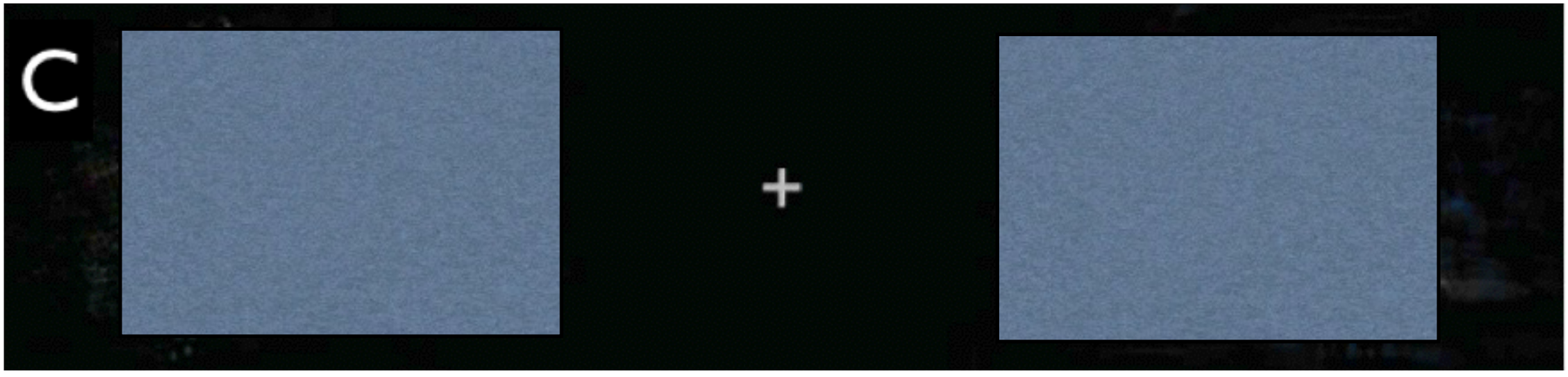
Was there any difference between the two?



Freeman & Simoncelli 2011 Nat Neuro, Rosenholtz 2012 Fronteirs

What do we see at periphery?

Which one contains an animal?



Freeman & Simoncelli 2011 Nat Neuro, Rosenholtz 2012 Fronteirs

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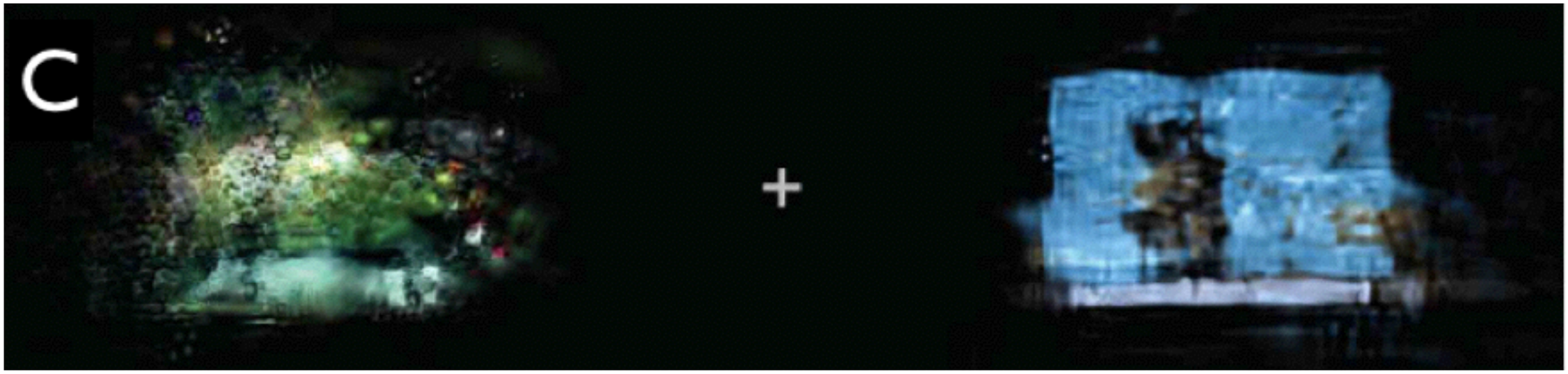

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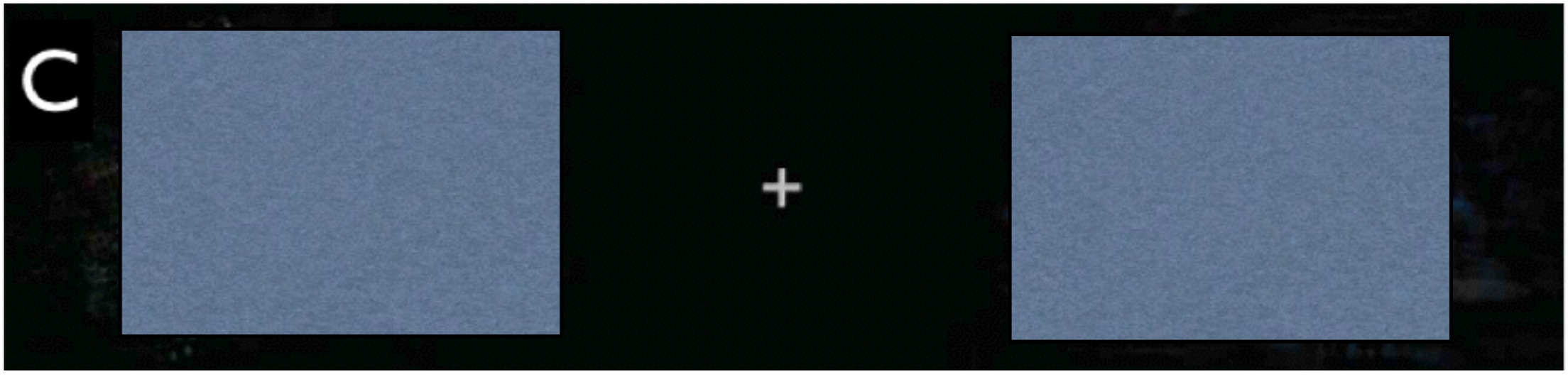

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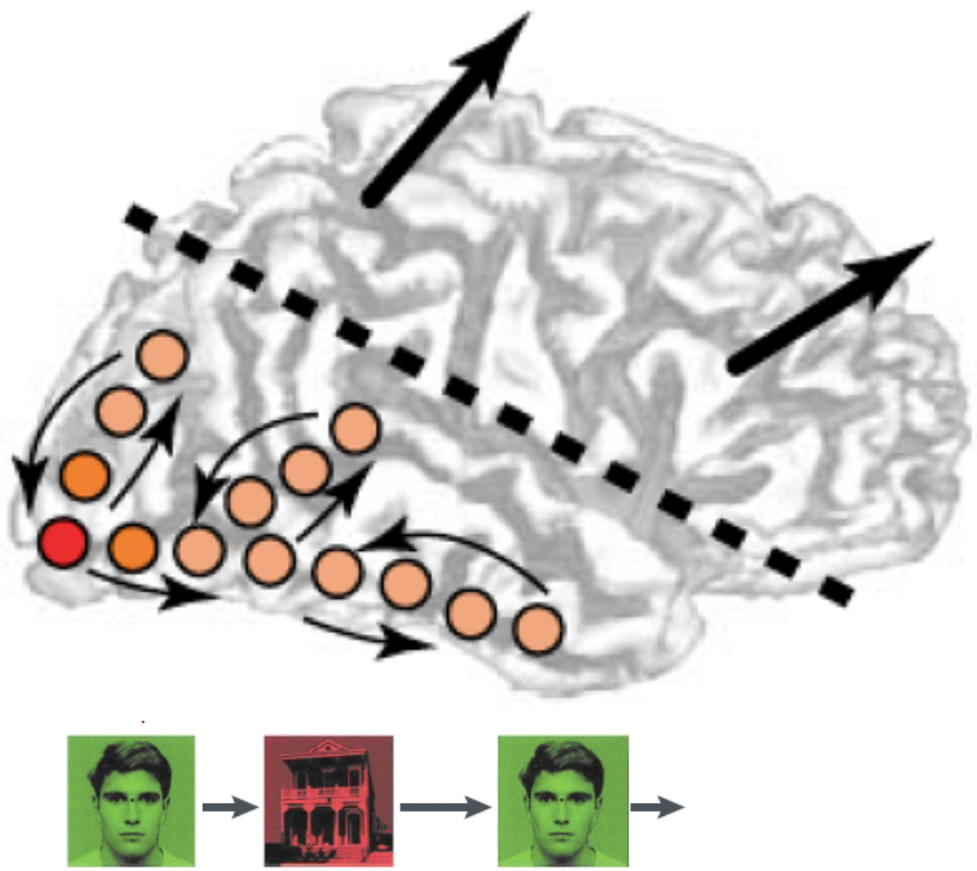
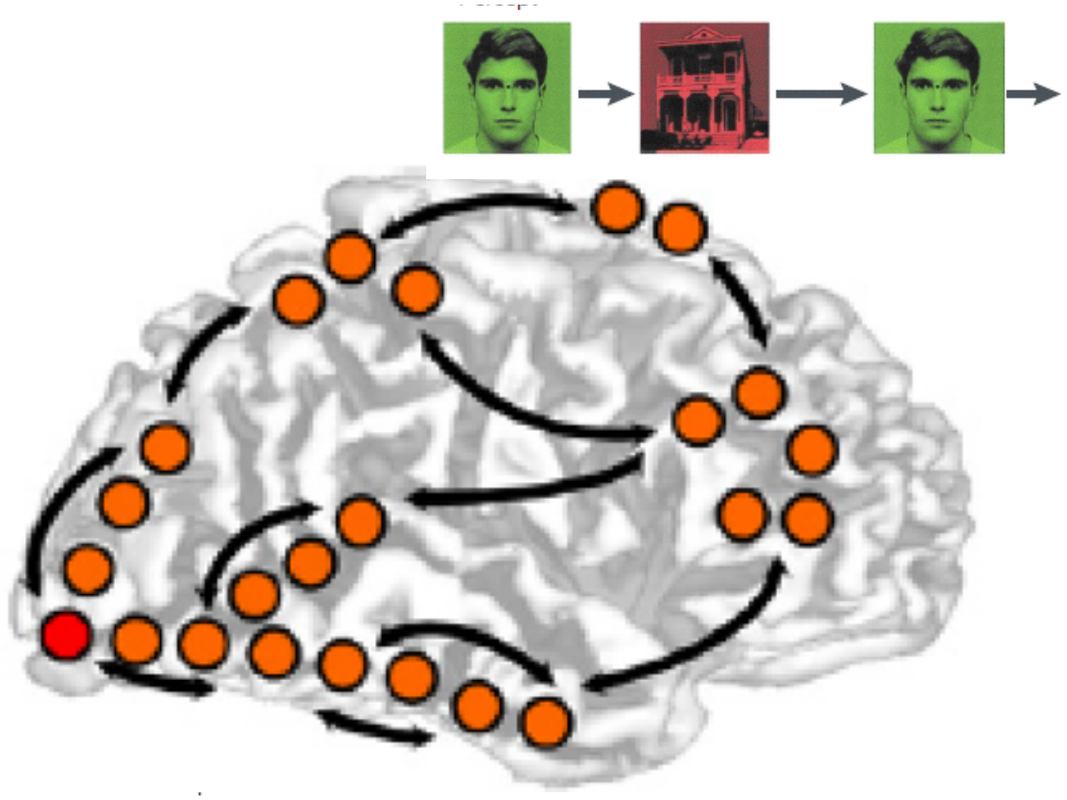


Pre-conscious

vs

Conscious, unattended, unreported



Conscious

Recent debates

- Do we perceive more than we can report? (e.g., broad-sense qualia, texture, animal outside of attention)

- Is there conscious perception without top-down attentional amplification?

- Is report always necessary and critical to study consciousness? (e.g., change detection, frontal-parietal amplification)

- Is introspection/metacognition critical for experience? Is consciousness only experienced by humans?

Why does it matter?

- Behaviorist **vs** Phenomenologist
- 3rd person **vs** 1st person
- Artificial Intelligence **vs** Artificial Consciousness
- Extrinsic Information **vs** Intrinsic Information
- Report paradigm **vs** No-report paradigm
  - To be continued ….

- BREAK!

5. No-report paradigm

Which of 1-4 best describes your opinion about the usages of “reports” in consciousness research?

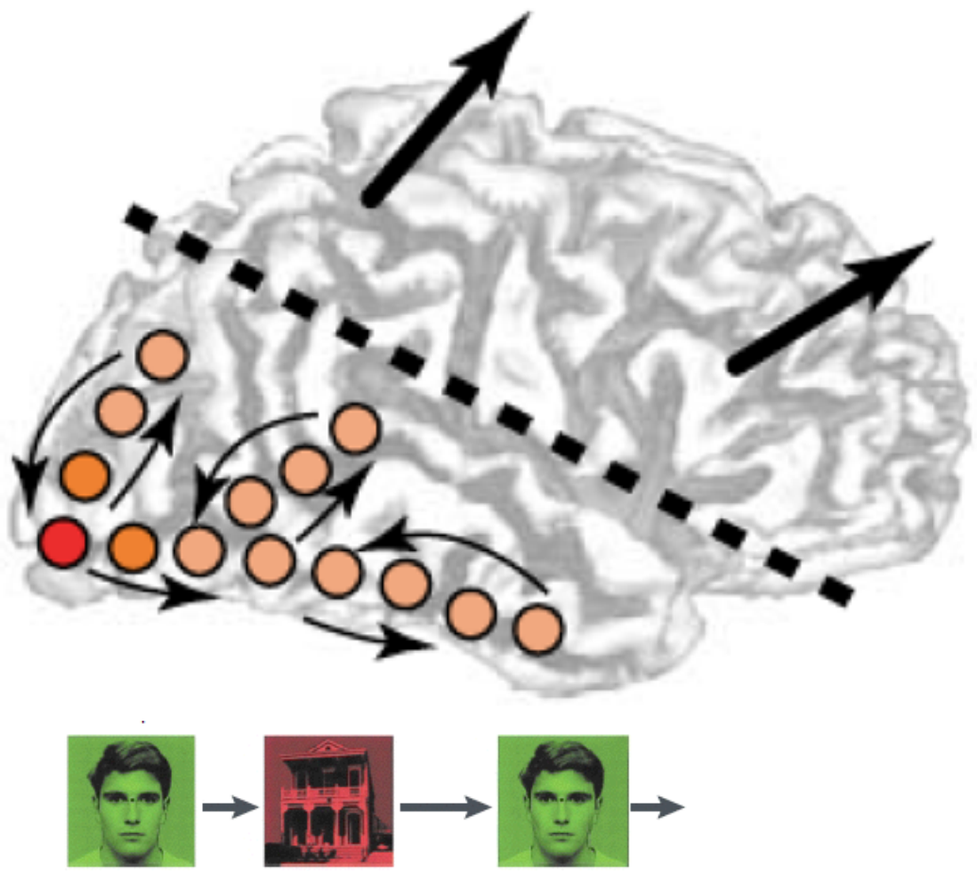
To understand the neural basis of
conscious experience:

1) behavioral **reports** from subjects
are really **essential** and always **necessary**.

2) **reports** are not always necessary,
and they may be **harmful**.

3) not interested in conscious experience.

4) other



Pre-conscious

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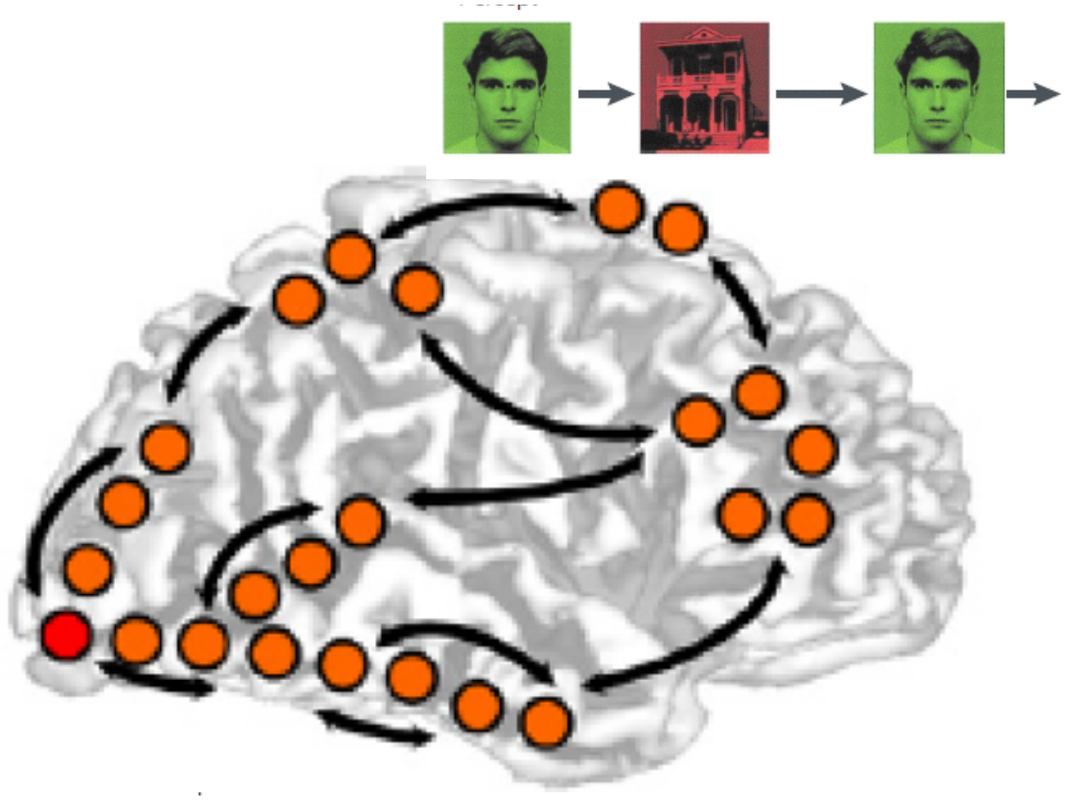
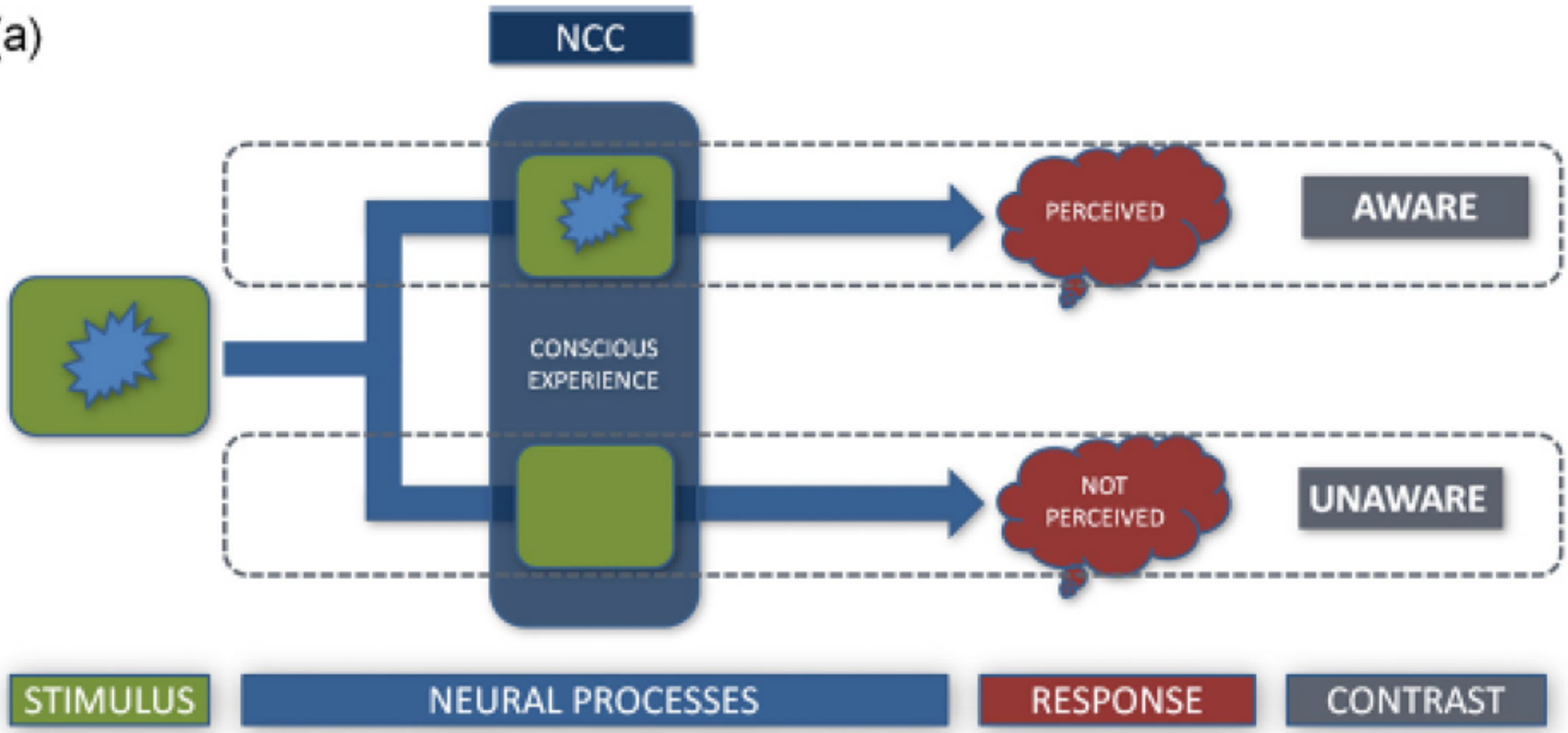


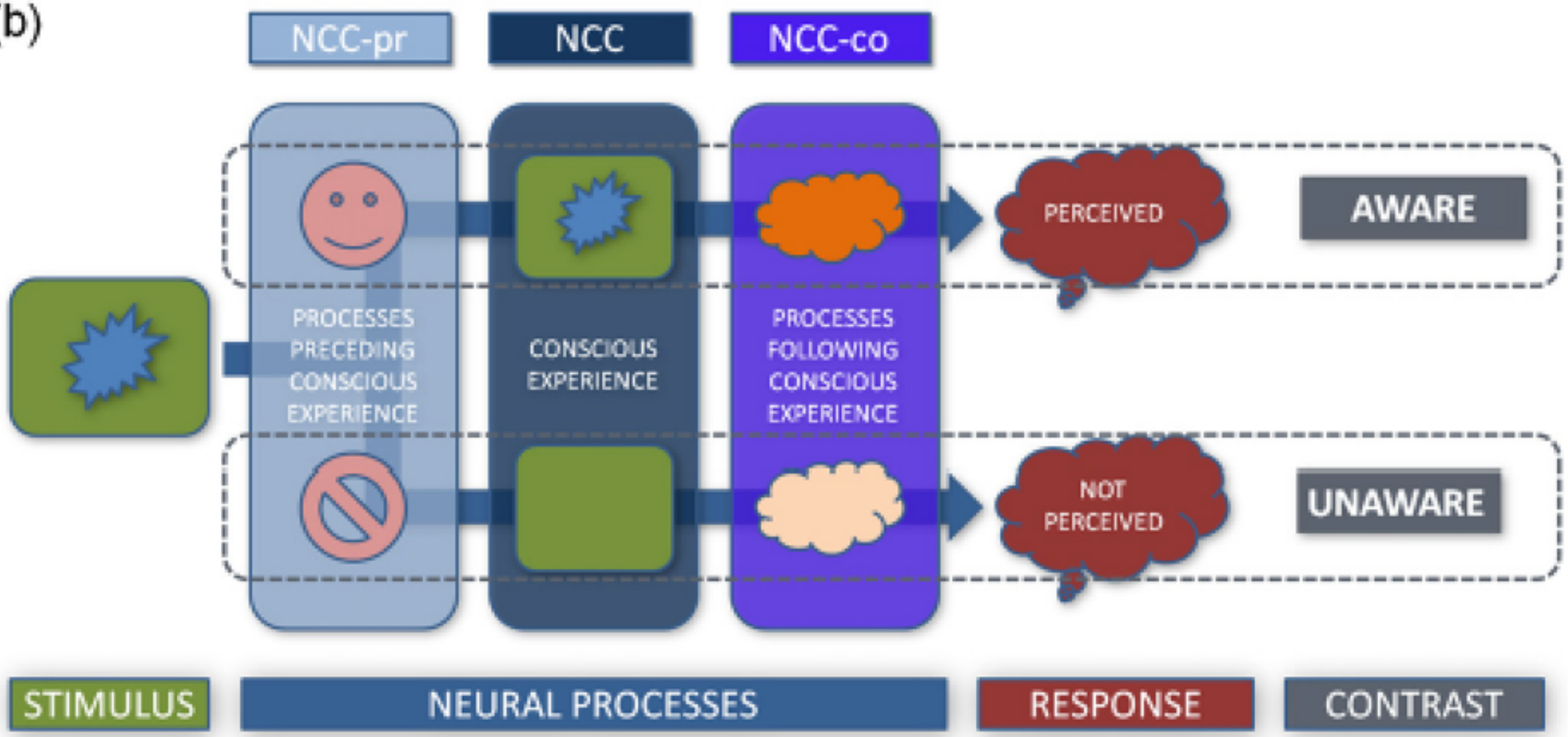
Conscious

(a)



Aru et al 2011

(b)

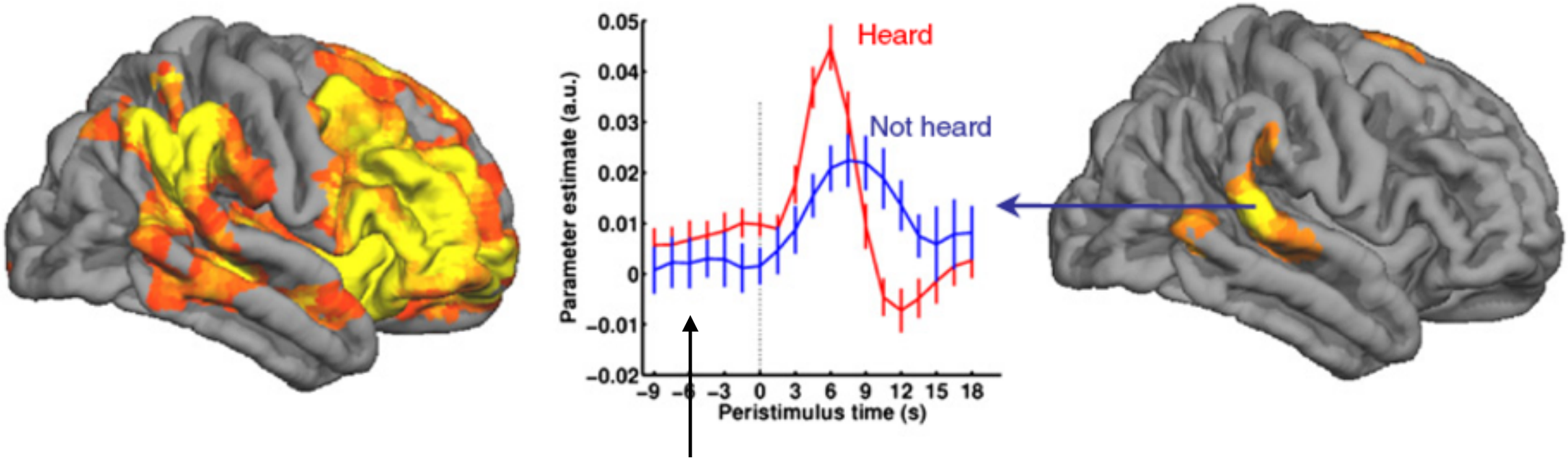


Aru et al 2011

- What are the processes that
  - preceding conscious experience?
  - following conscious experience?

Detected sound

Non-detected sound



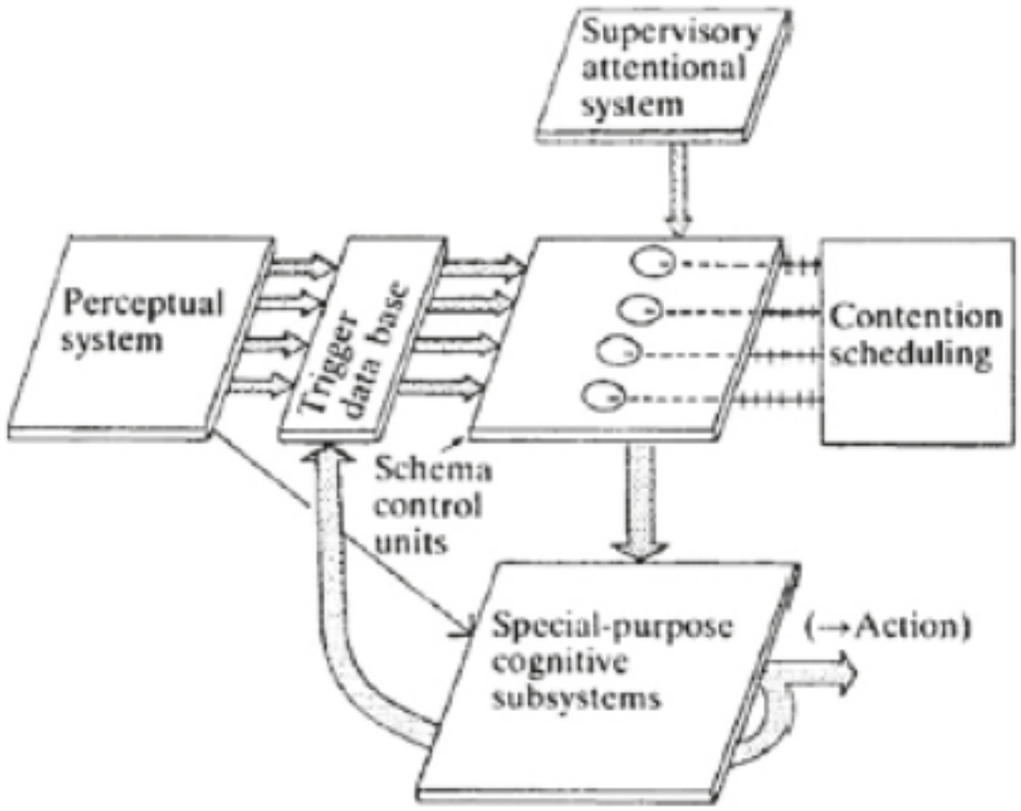
NCC-pr?

What about NCC-co?

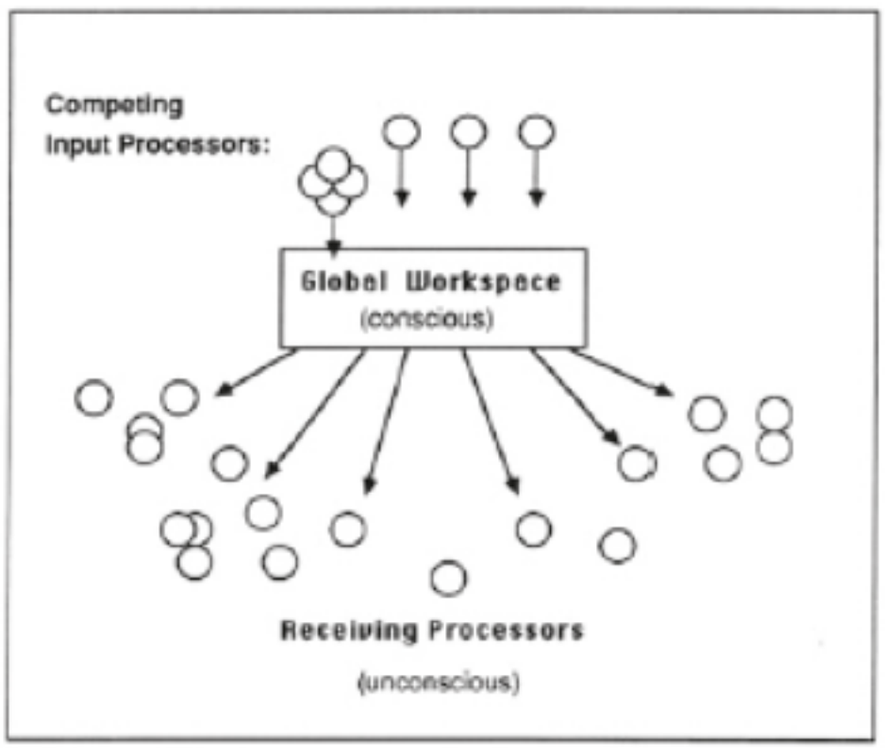
Functions of conscious phenomenology?

- Flexible access and selective use of incoming information retained for a long period in working memory, for a better and longer term planning?

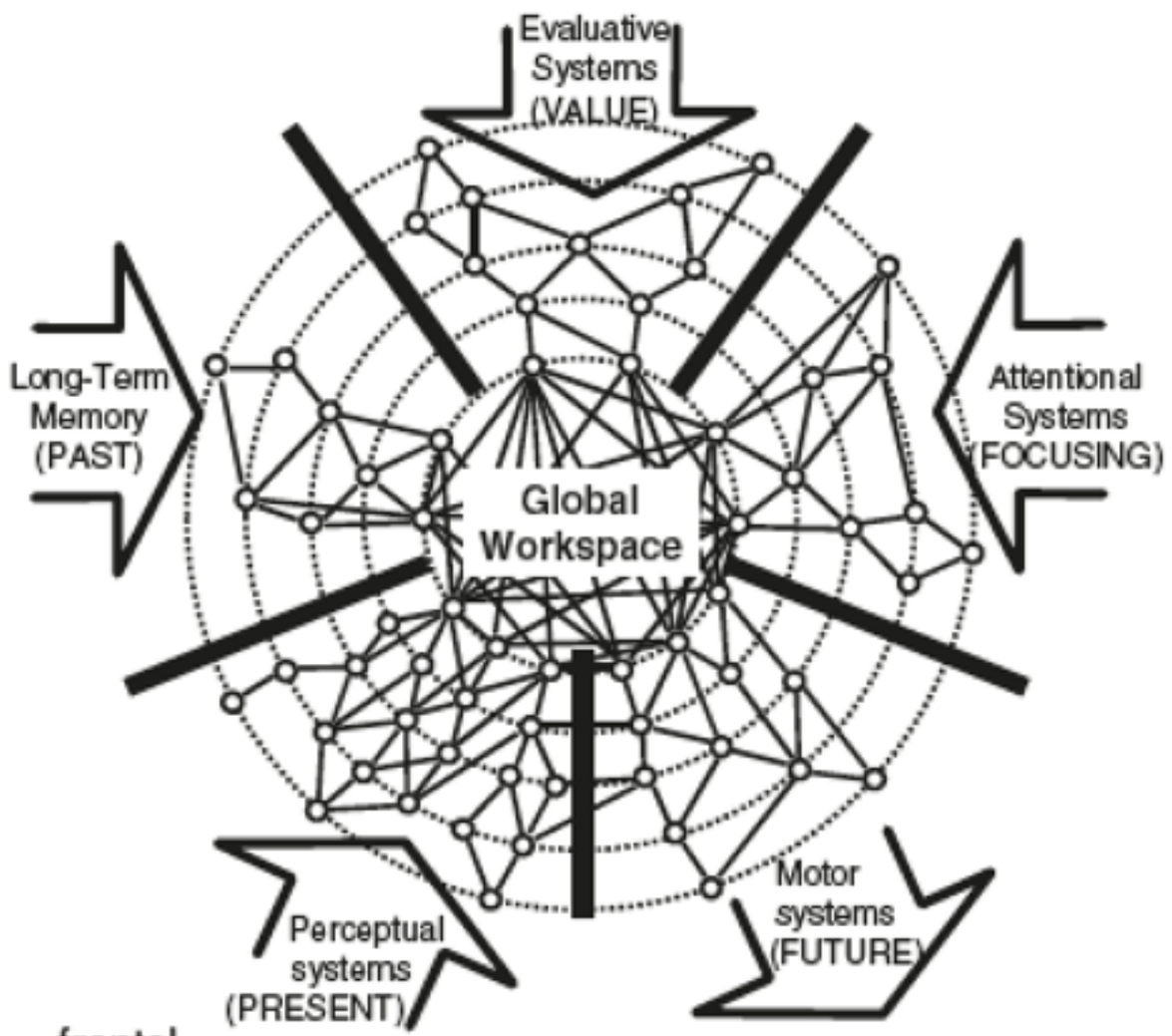
- implying **attention, working memory** and **access/report** as critical functions of consciousness?

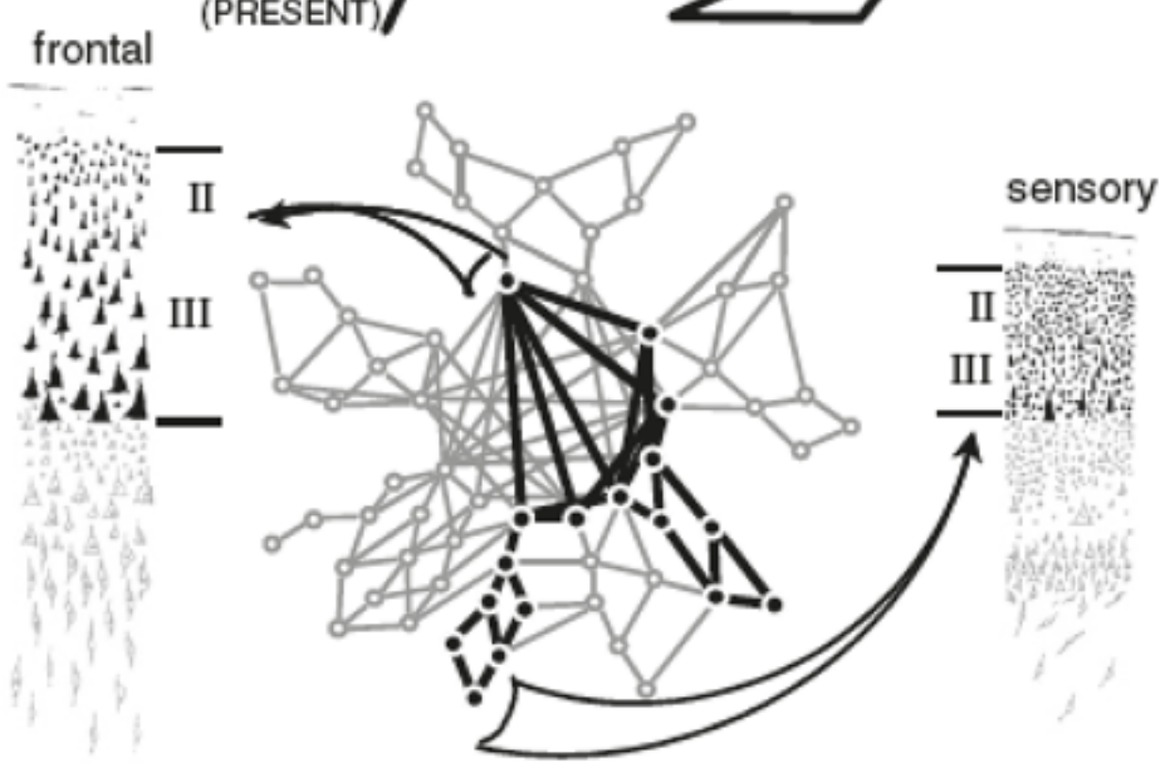


Norman-Shallice 1980



Baars 1989



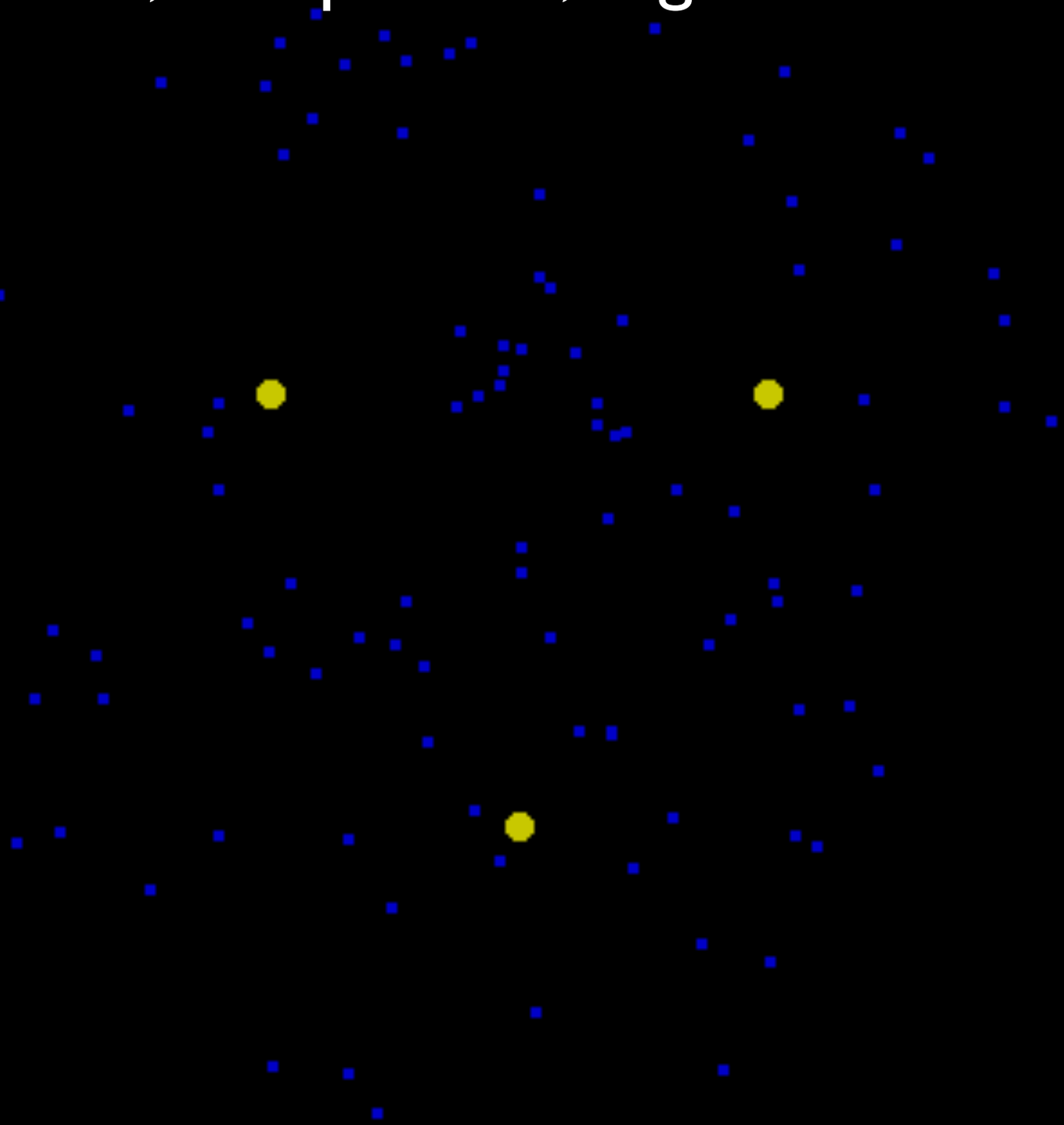


Dehaene, Kerszberg & Changeux 1998

Relationship between top-down attention and consciousness?

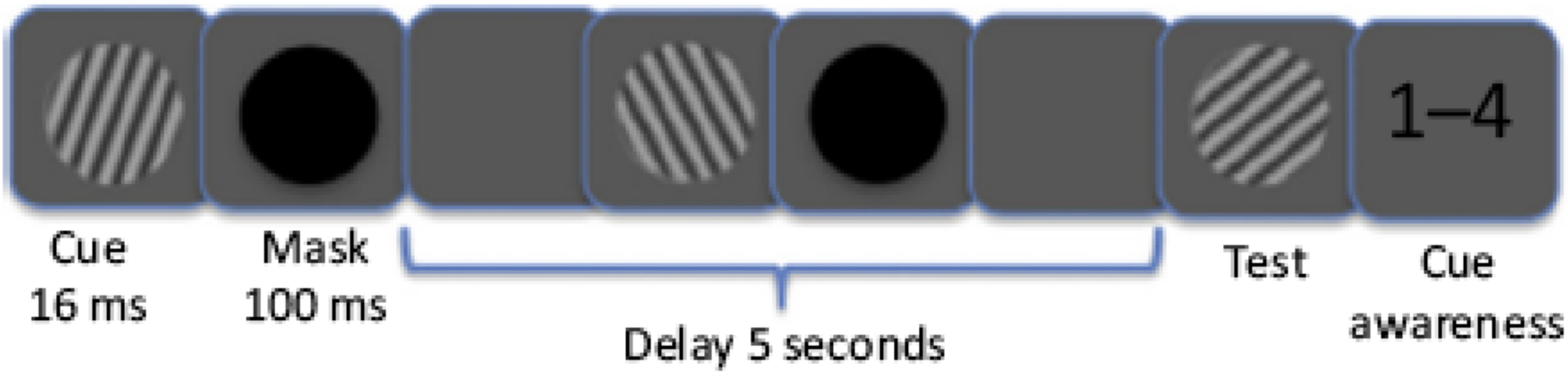
- Attention without consciousness?
- Consciousness without attention?
- Dissociable/opposing behavioral/neural effects of attention and consciousness?

Motion-induced blindness
(Bonneh, Cooperman, Sagi 2001 Nature)



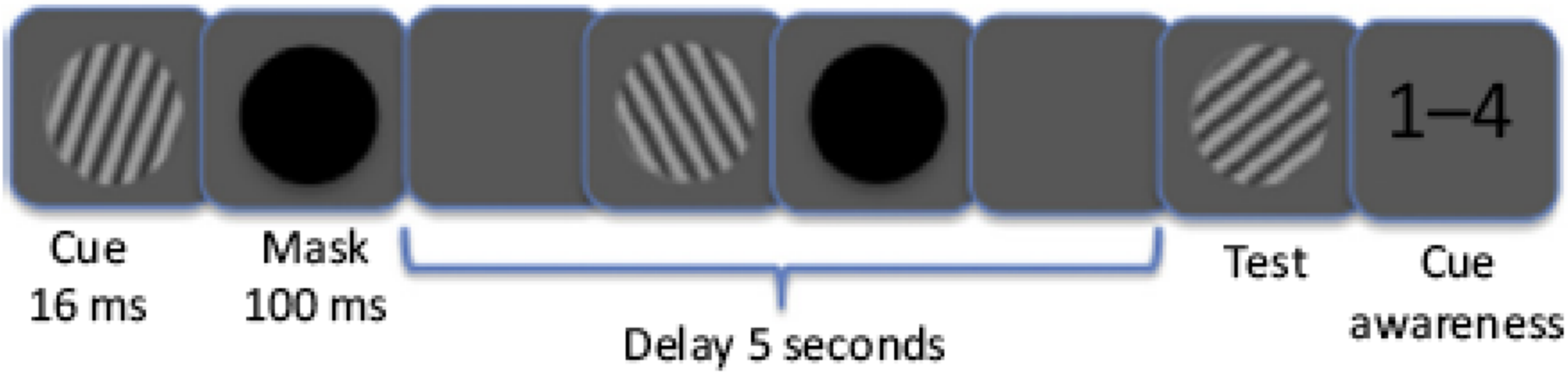
Opposing effects of C and A on afterimages
Attentional effects on invisible targets

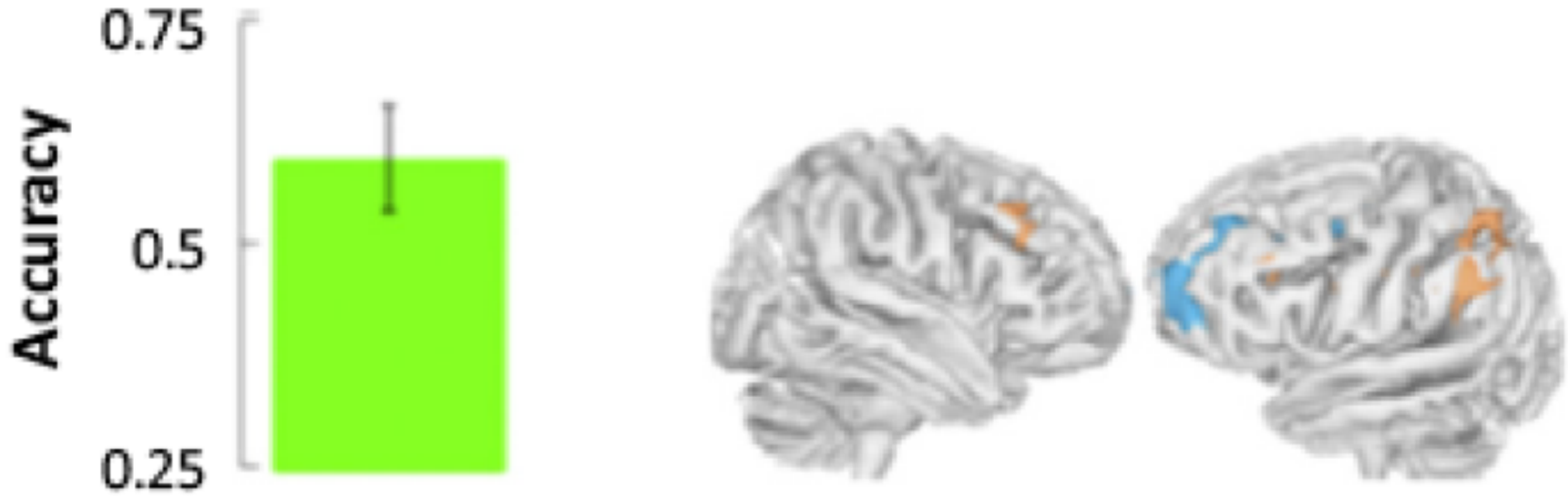
Unconscious working memory



Soto & Silvanto 2014 TICS

Unconscious working memory





Performance and BOLD on 1-rating unaware trials

Unconscious addition, subtraction, reading …

Soto & Silvanto 2014 TICS

Functions of conscious phenomenology?

- Can biology understand something that (may) have no (apparent) direct functions?

- Attention? (Lamme 2006, Koch & Tsuchiya 2007)

- Working memory? (Soto & Silvanto 2014)

- Detection of abnormality? (Mudrik 2011 Psych Sci)

- Access/Report?

    - Accessible and reportable contents of consciousness seem very useful…

What about report/ access?

1. A brief history of the consciousness research

~1900 Phenomenology

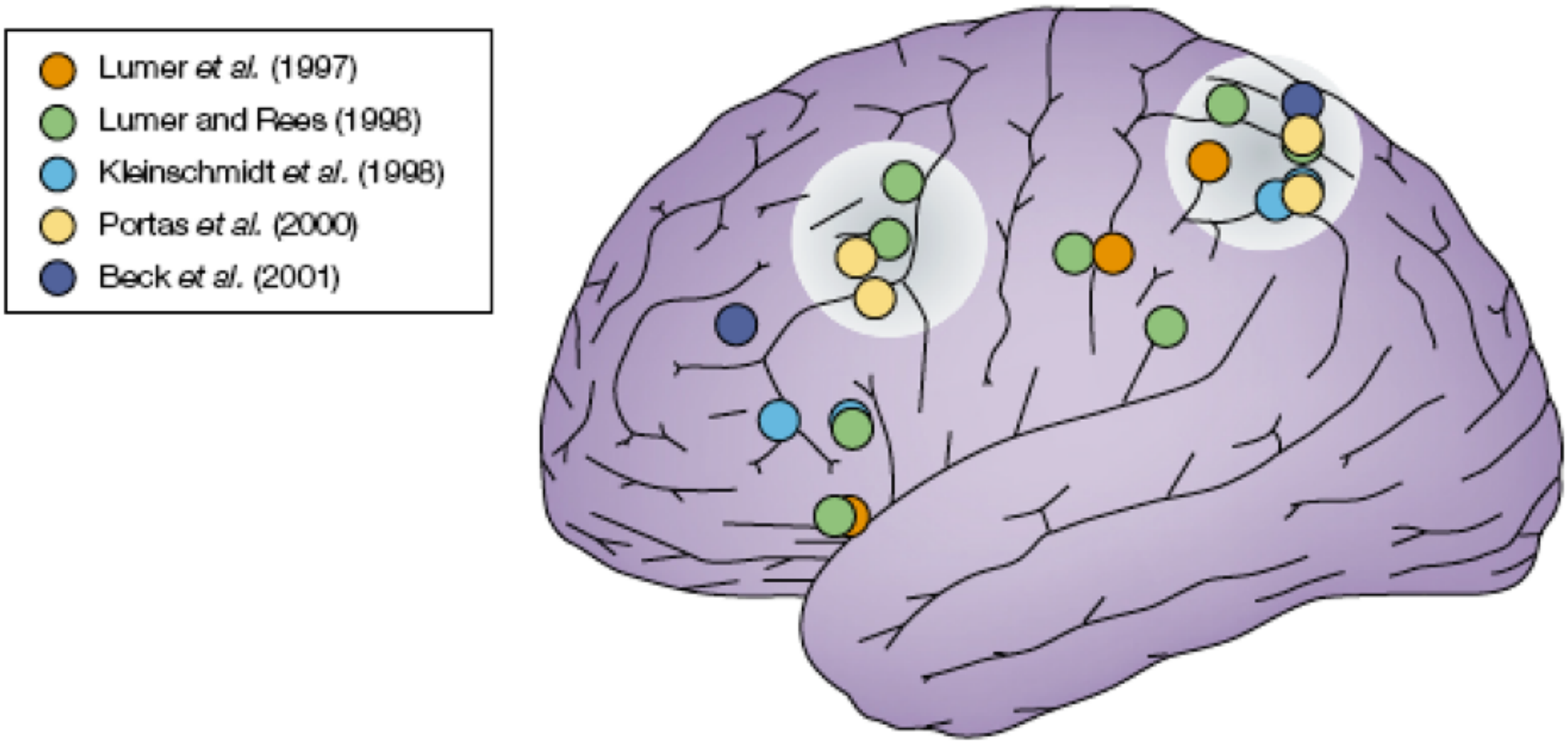
Gestalt psychology

~1920 Behaviorism

~1960 Cognitive revolution

~1990 Consciousness research

Neural correlates of consciousness



Frontal and parietal activity/integrity is critical for consciousness

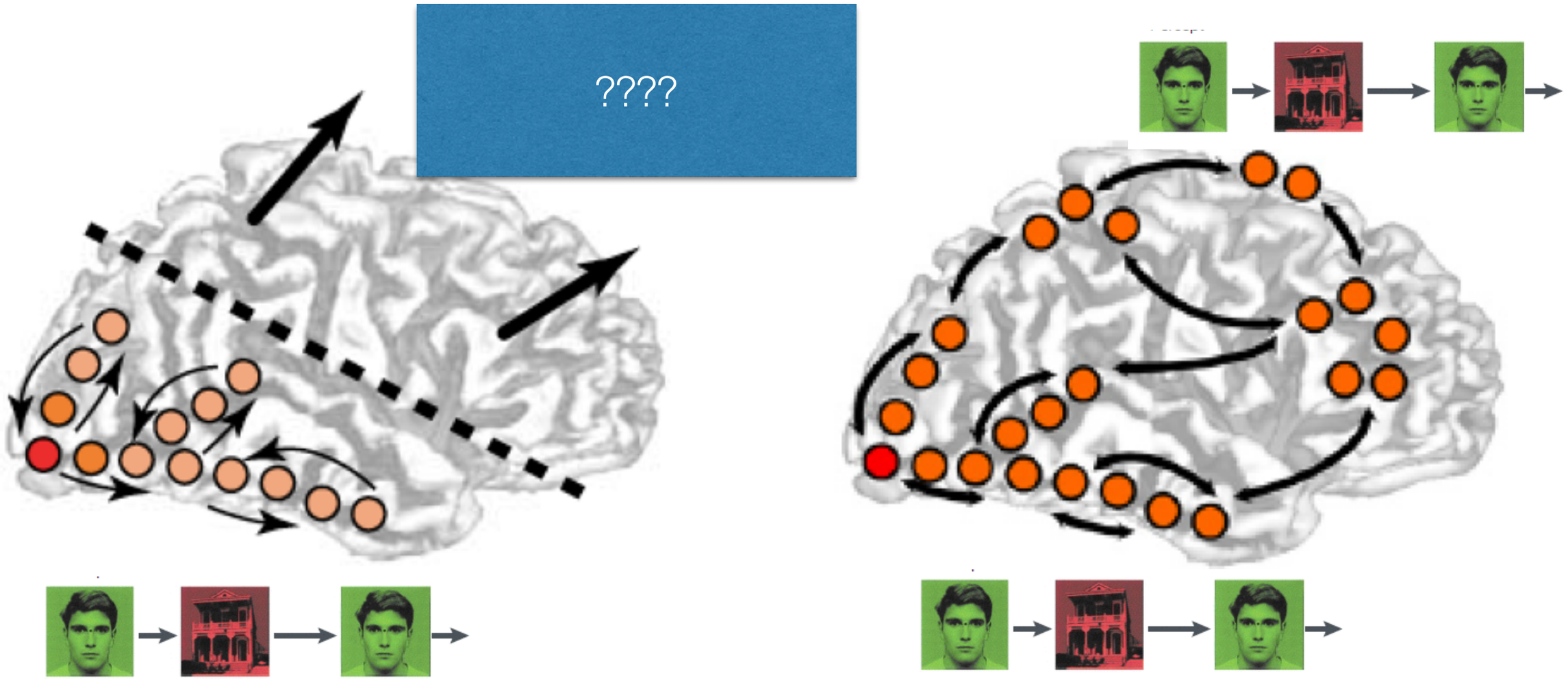
Rees, Kreiman, Koch 2002 Nat Rev Neuro

Zaretskaya & Narinyan 2014 Frontiers

Bor & Seth 2012 Frontiers

“Consciousness cannot be separated from functions”
Cohen & Dennett 2011 TICS

Frontal & parietal involvement in visual perception (?)



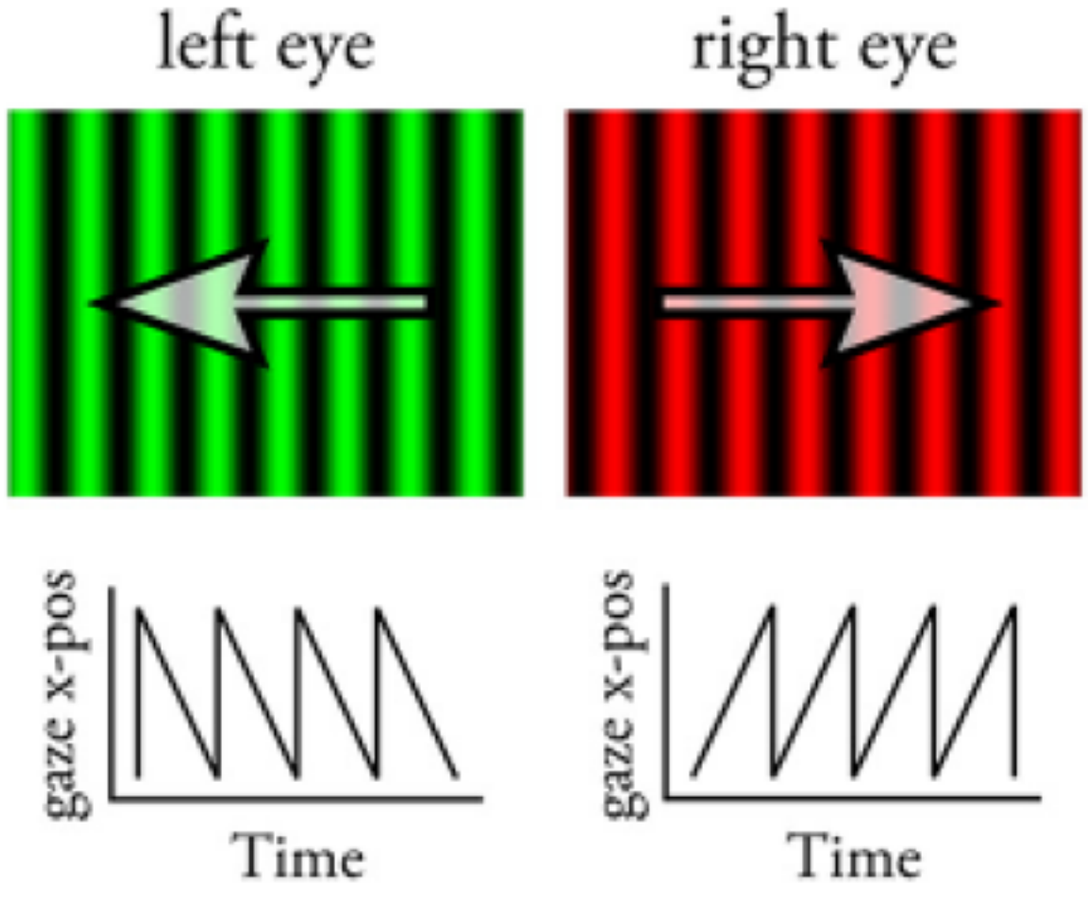
Known properties of binocular rivalry

- Cannot be stopped by attention, training, efforts, etc

  > highly automatic and vivid

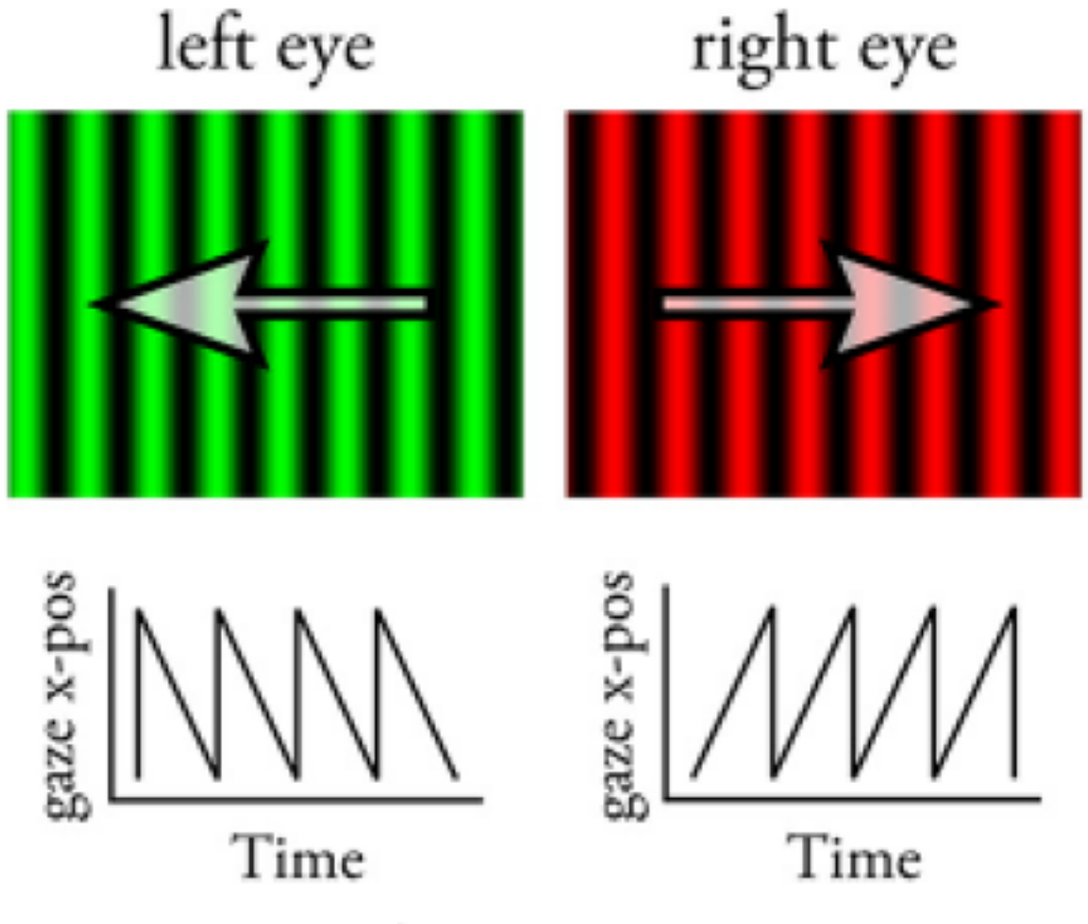
  > require no report

- Under optimal conditions, eye movements highly correlates with the contents of consciousness



Eye movements can be used to infer the contents of rivalry

Frassle et al 2014 J Neurosci



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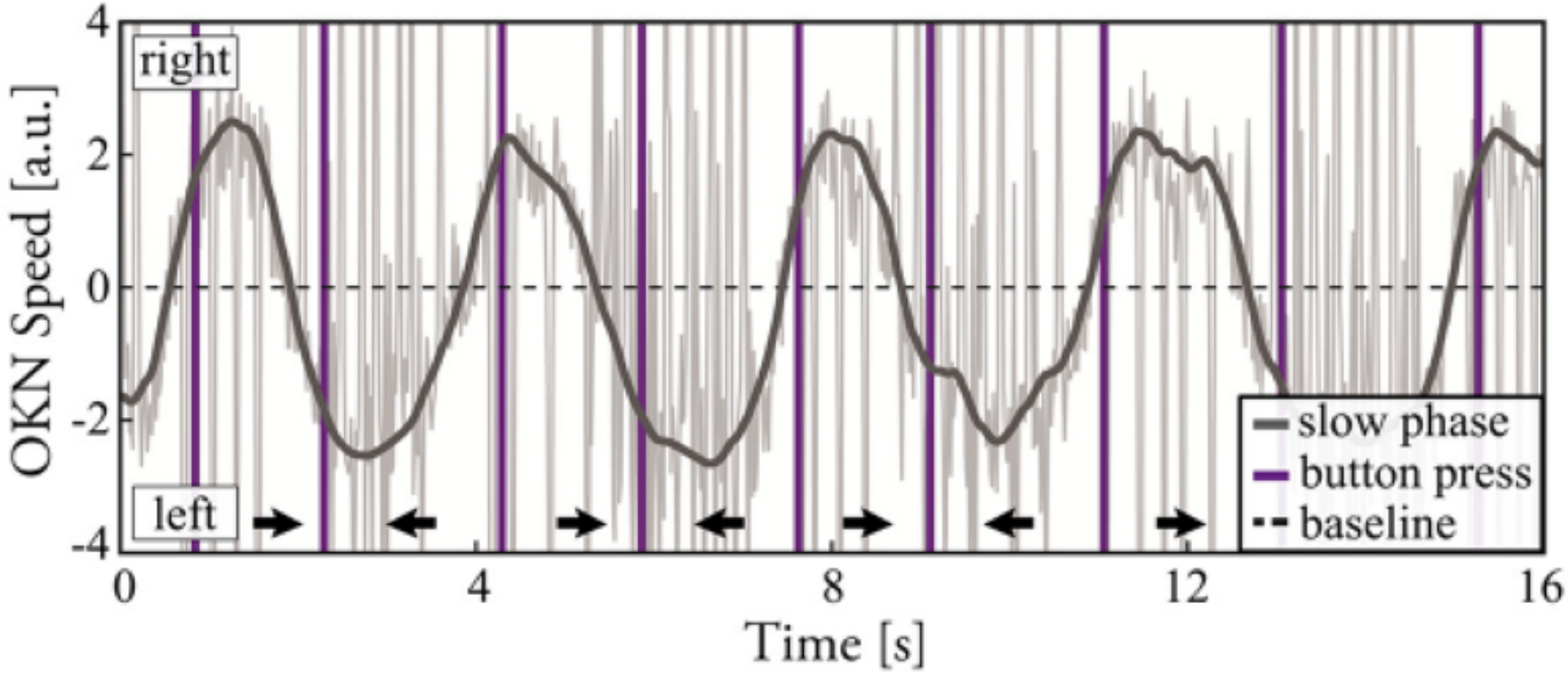
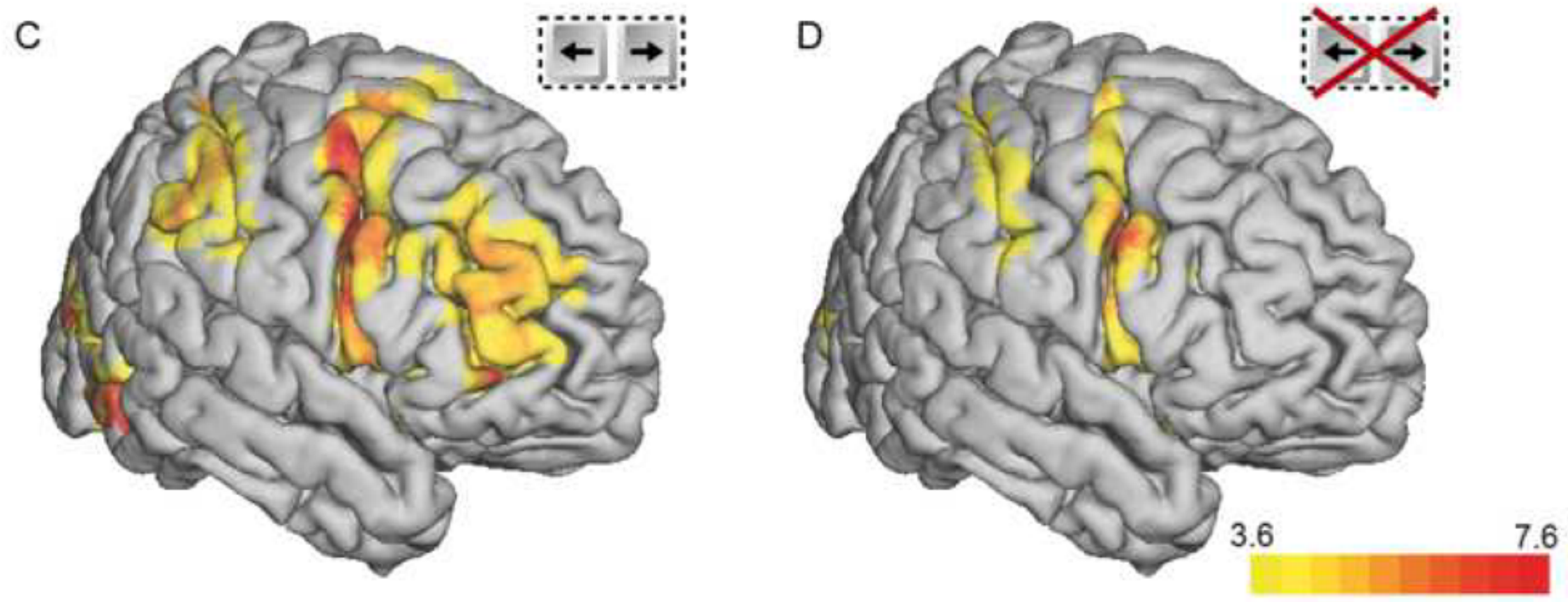


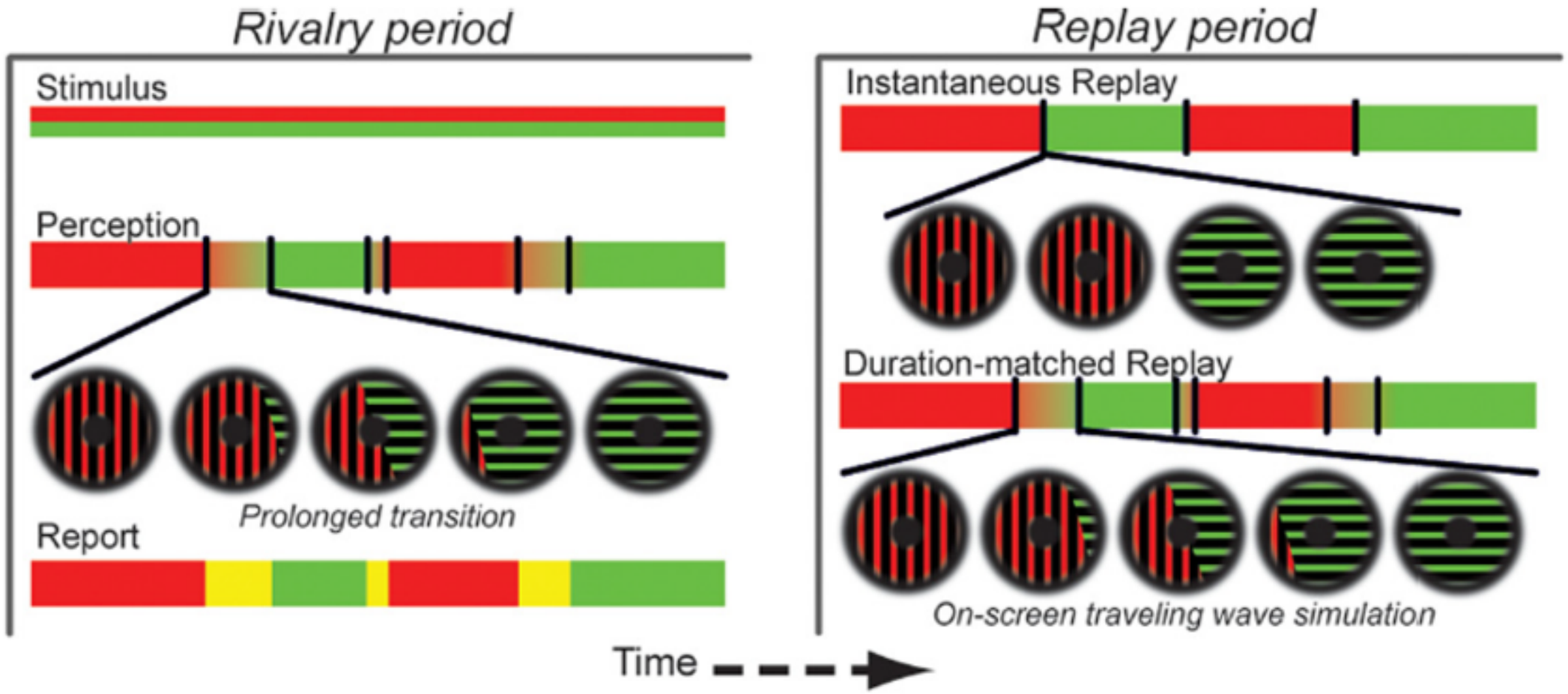
Frassle et al 2014 J Neurosci

No-report diminishes the involvement of frontal areas!



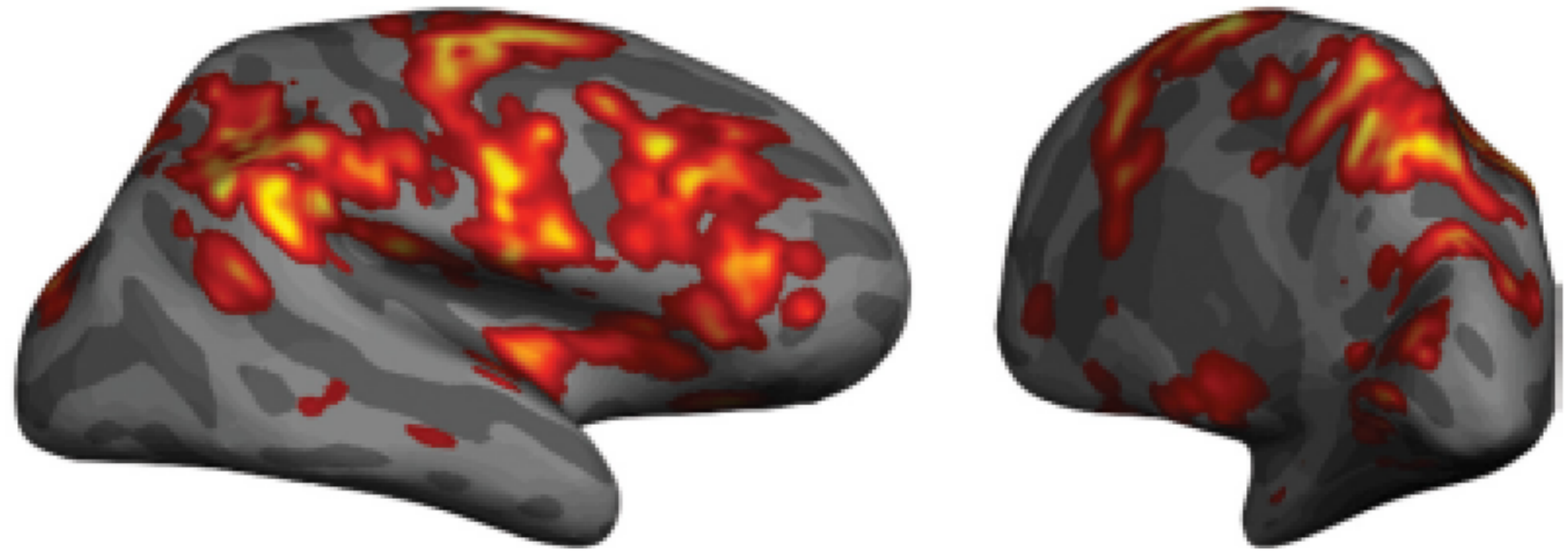
Frassle et al 2014 J Neurosci

What aspects of binocular rivalry do the frontal activity reflect?



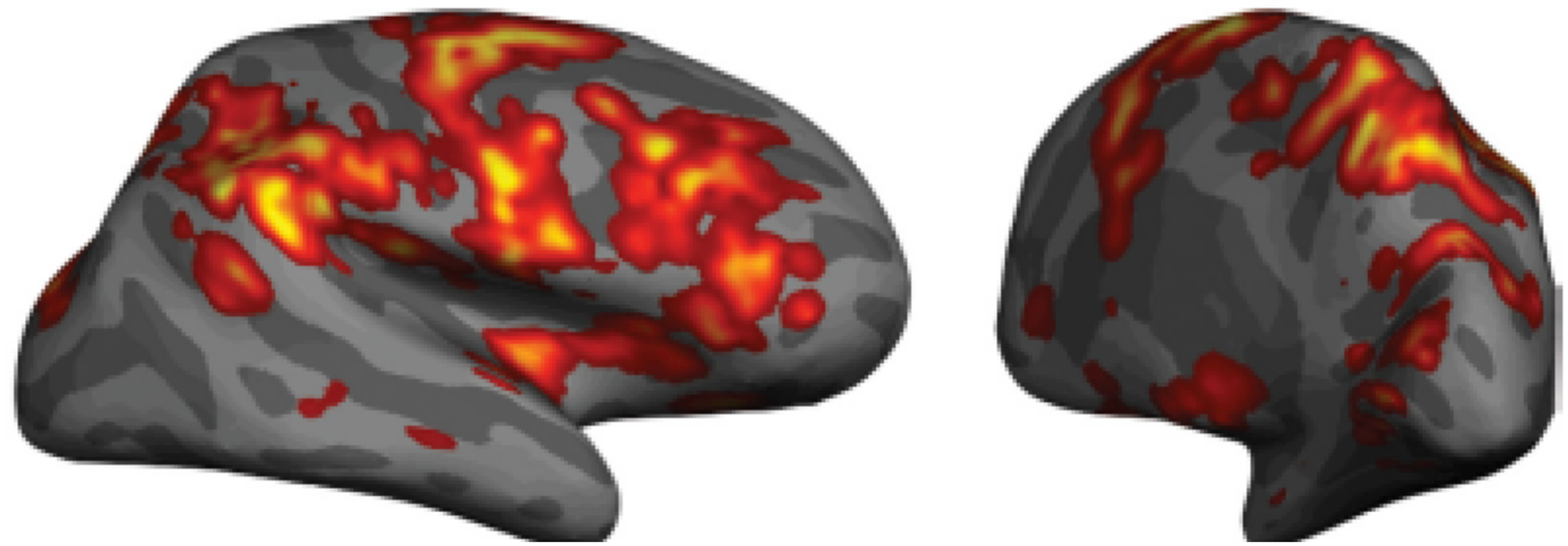
Knapen 2011 J Nsci

Genuine rivalry > Instantaneous (poor) replay



Knapen 2011 J Nsci

Genuine rivalry > Instantaneous (poor) replay



Genuine rivalry > Duration-matched (good) replay

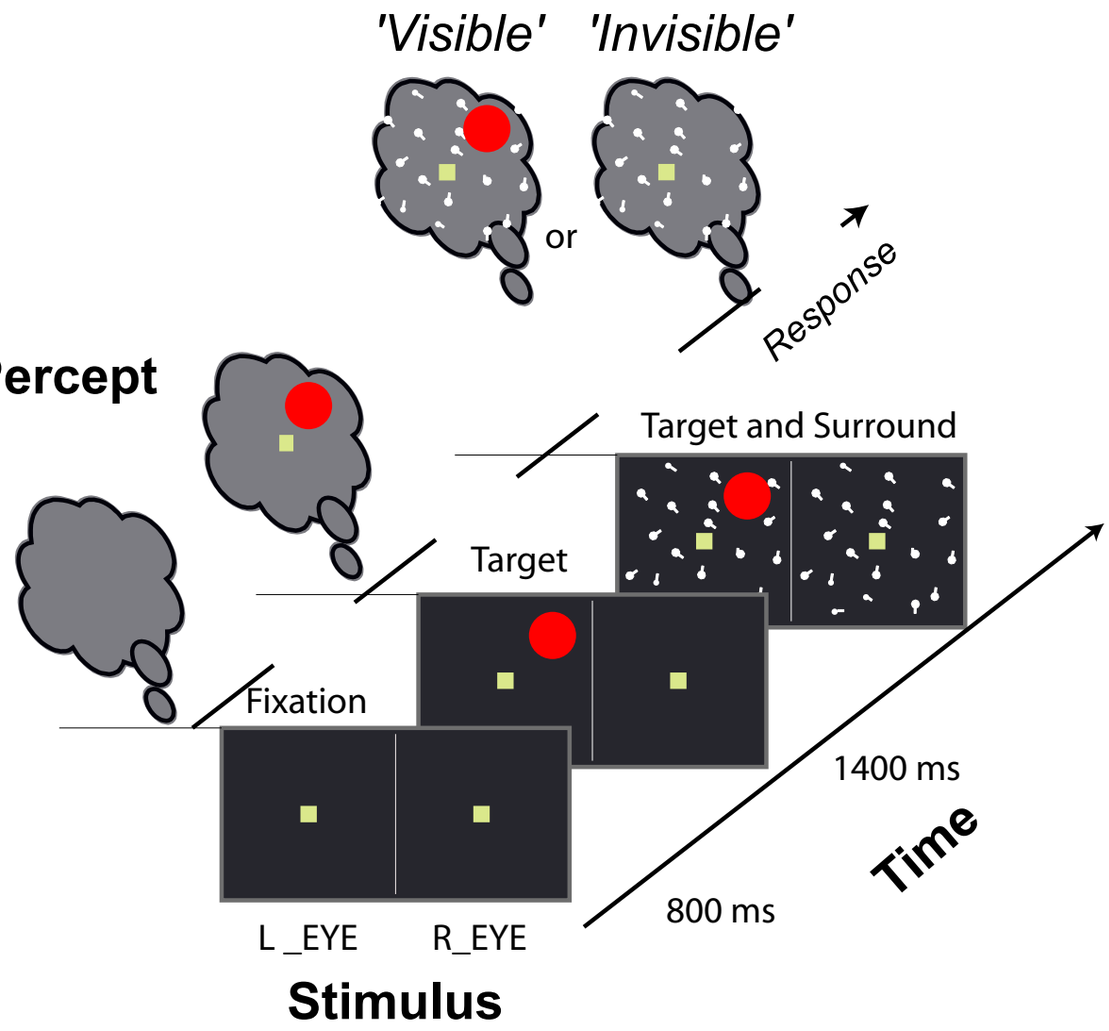
Knapen 2011 J Nsci

If reports are not required, or
if difficulty in reports are equated,
activity in frontal areas becomes similar
during binocular rivalry and replay.

Microscopic effects of report-related confound

A

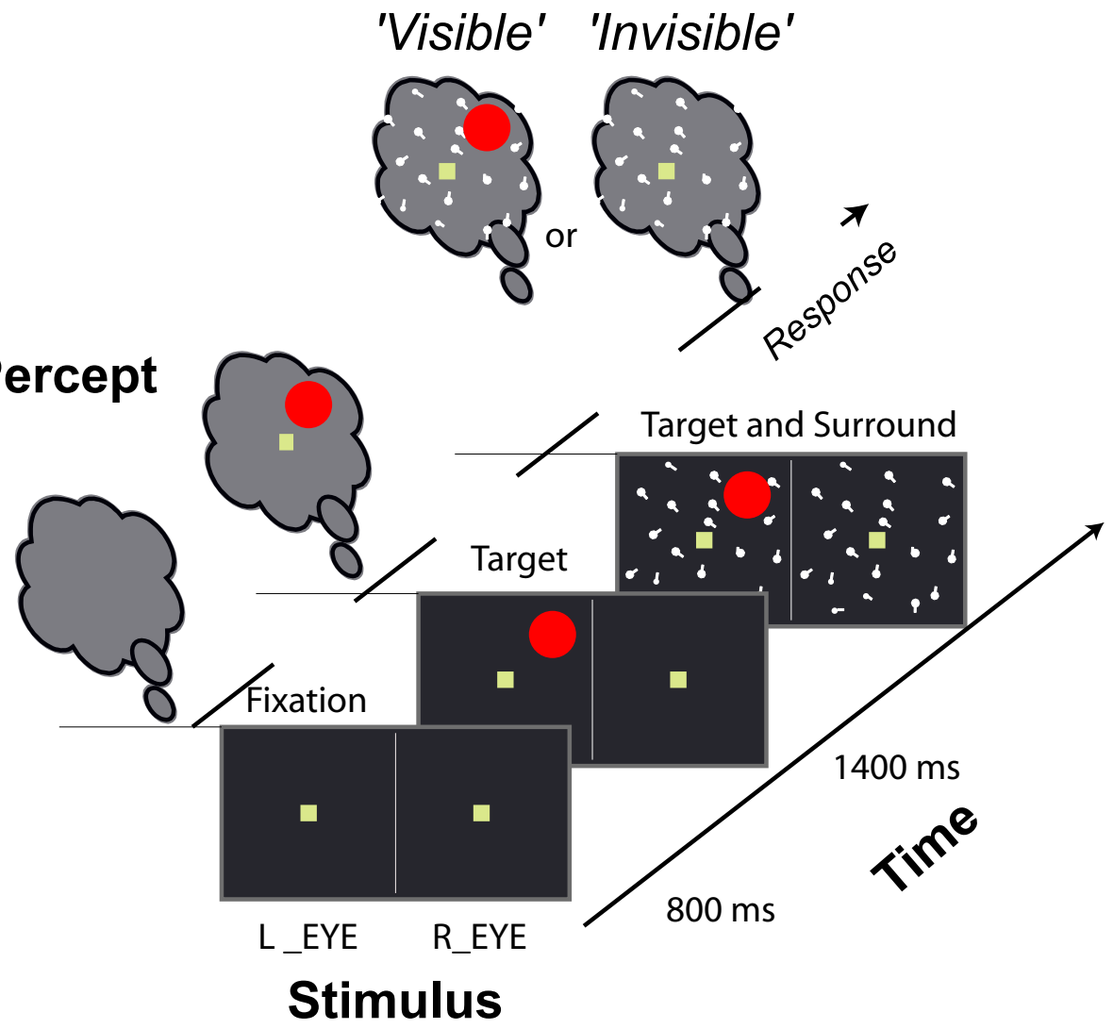
Generalized Flash Suppression Task



Wilke et al 2009 PNAS

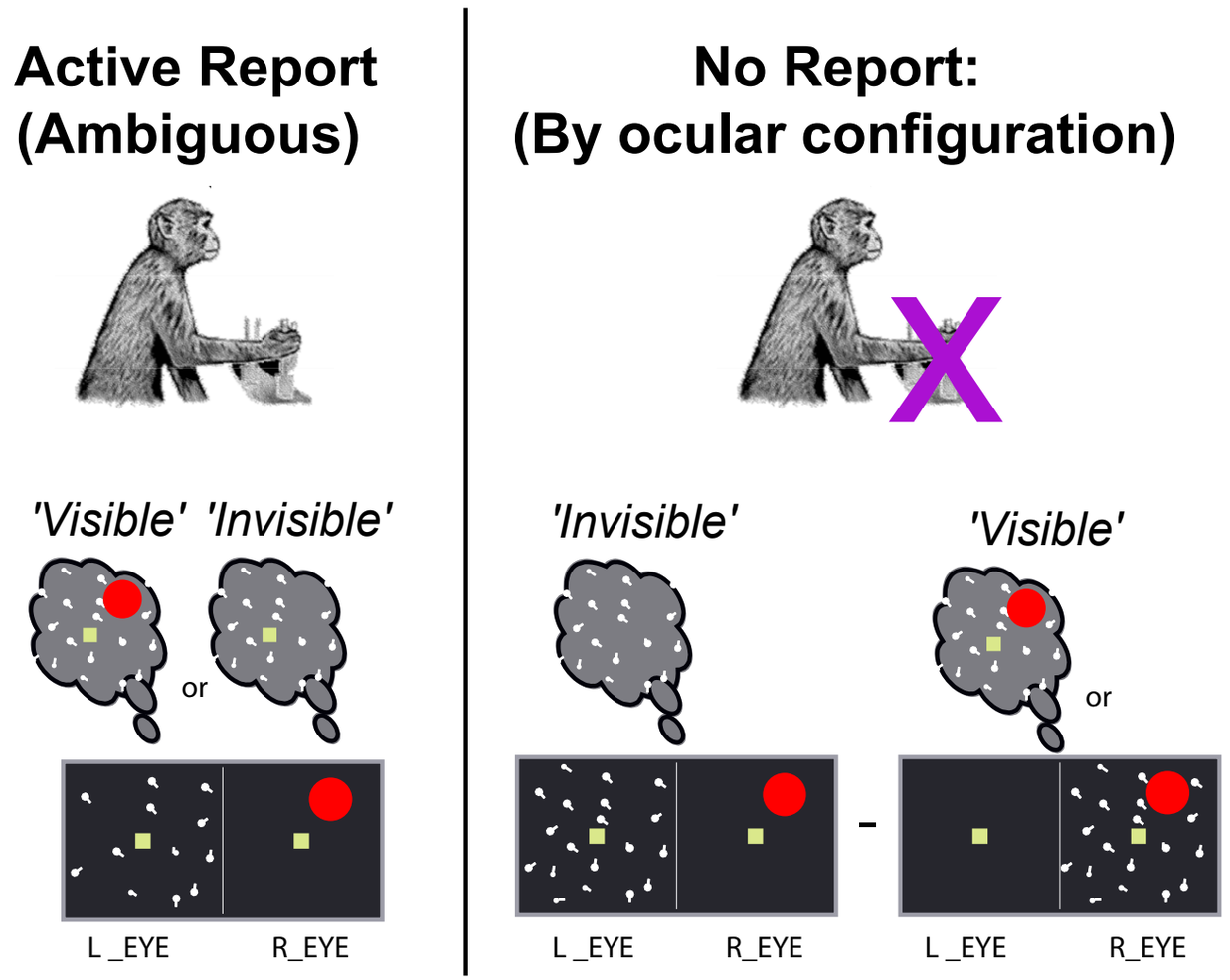
A

Generalized Flash Suppression Task



B

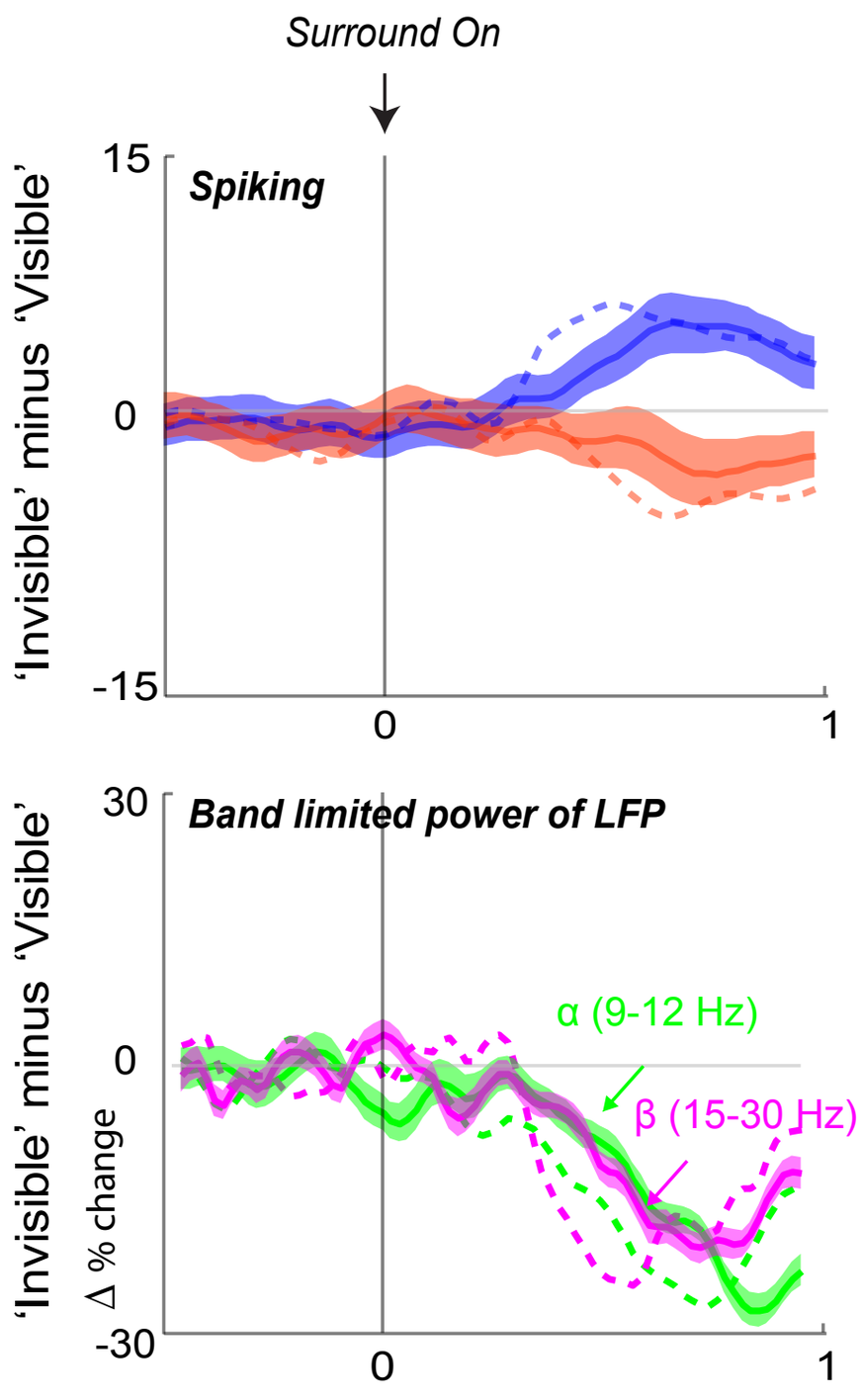
Experimental Conditions



Wilke et al 2009 PNAS

C

Active Report

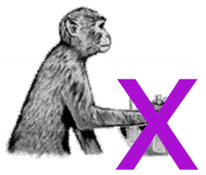


Wilke et al 2009 PNAS

Under the report-based condition,
alpha/beta range in LFPs (Pulvinar, V4, V2, V1)
& spikes (in Pulvinar & V4)
were identified as “the NCC”

C

Active Report



No report

Surround On

Surround On

'Invisible' minus 'Visible'

Spiking

15

0

-15

0

1

Spiking

60

0

-60

0

1

Band limited power of LFP

30

0

-30

Δ % change

α (9-12 Hz)

β (15-30 Hz)

0

1

Band limited power of LFP

α (9-12 Hz)

β (15-30 Hz)

0

1

Time since Surround Onset (ms)

Wilke et al 2009 PNAS

Under the report-based condition,
alpha/beta range in LFPs (pulvinar, V4, V2, V1)
& spikes (in pulvinar & V4)
were identified as “the NCC”

Under the no-report condition,
only spikes (in pulvinar & V4)
were identified as “the NCC”

	Report-based	No-report
Underestimation of NCC		
Overestimation of NCC	Prerequisites & consequences of NCC (Aru 2012)	

Tsuchiya, Wilke, Frassle, Lamme (under review)

	Report-based	No-report
Underestimation of NCC		Report- or attention-dependent experience
Overestimation of NCC	Prerequisites & consequences of NCC (Aru 2012)	Inclusion of non-conscious processing

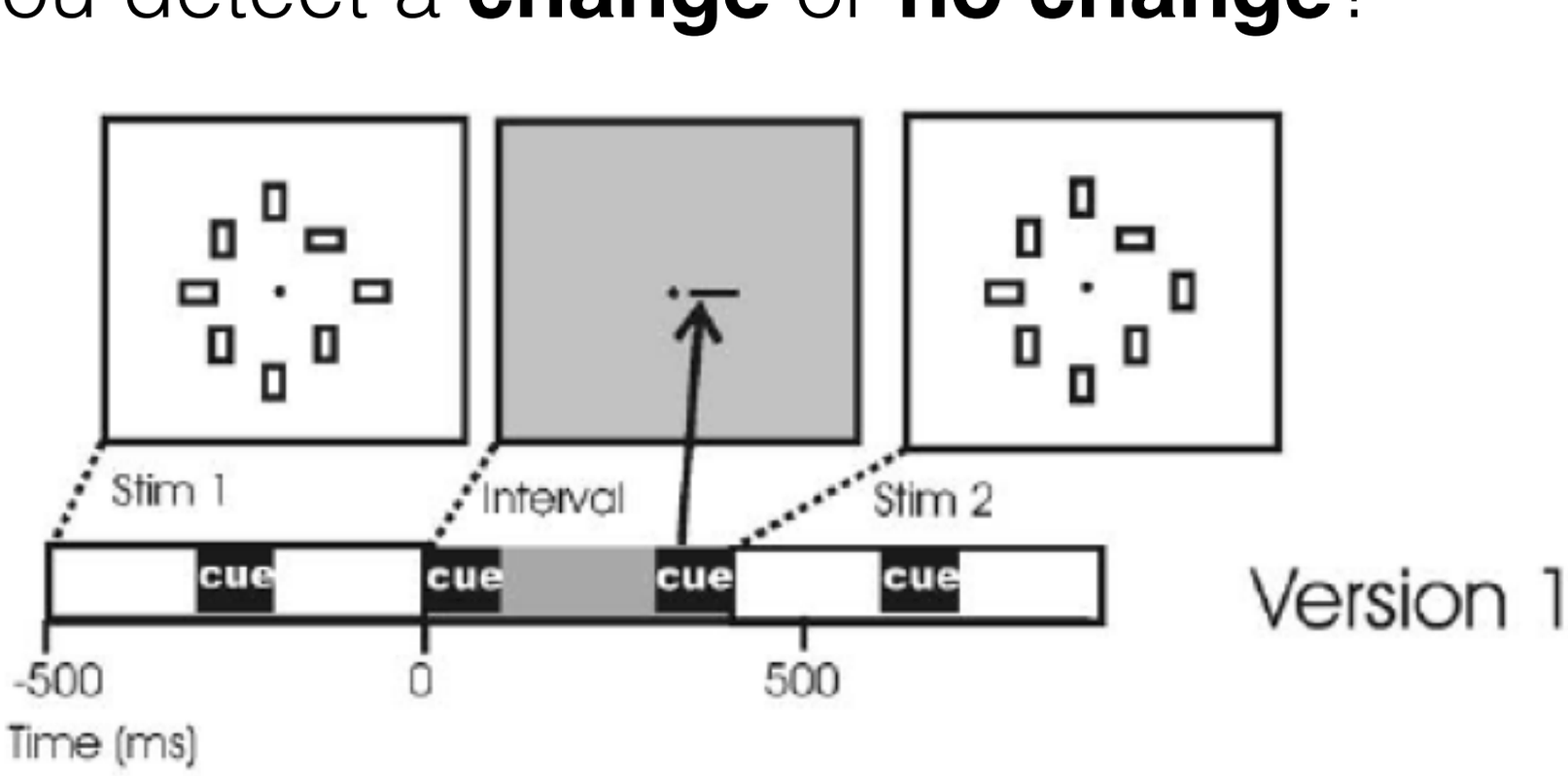
Tsuchiya, Wilke, Frassle, Lamme (under review)

	Report-based	No-report
Underestimation of NCC	???	Report-dependent experience (?)
Overestimation of NCC	Prerequisites & consequences of NCC (Aru 2012)	Inclusion of non-conscious processing

Tsuchiya, Wilke, Frassle, Lamme (under review)

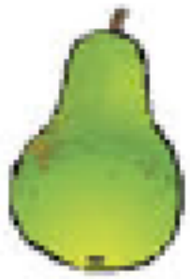
Can report accurately reflect what we consciously see?

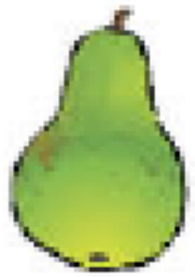
- Can you remember 8 objects in details?
- After a fixation, an array of 8 objects appear.
- Then, another array appears.
- Can you detect a **change** or **no change**?



Sligte et al 2010 Frontiers

Ready?

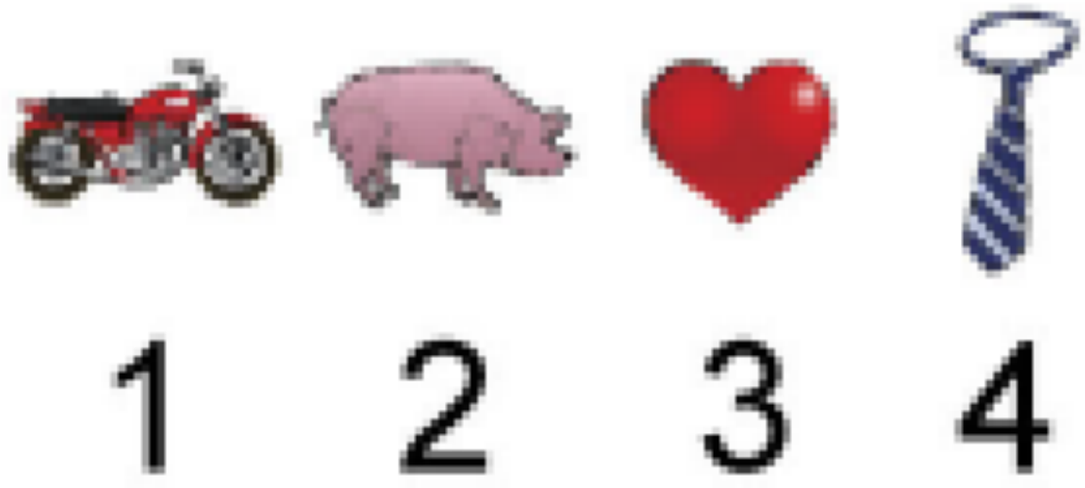




Was there a change in the cued location?

Yes or No!

What was the item before the change happened?

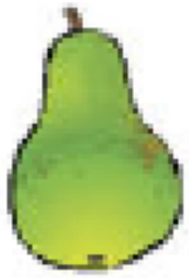


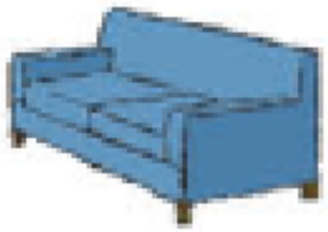
1 2 3 4

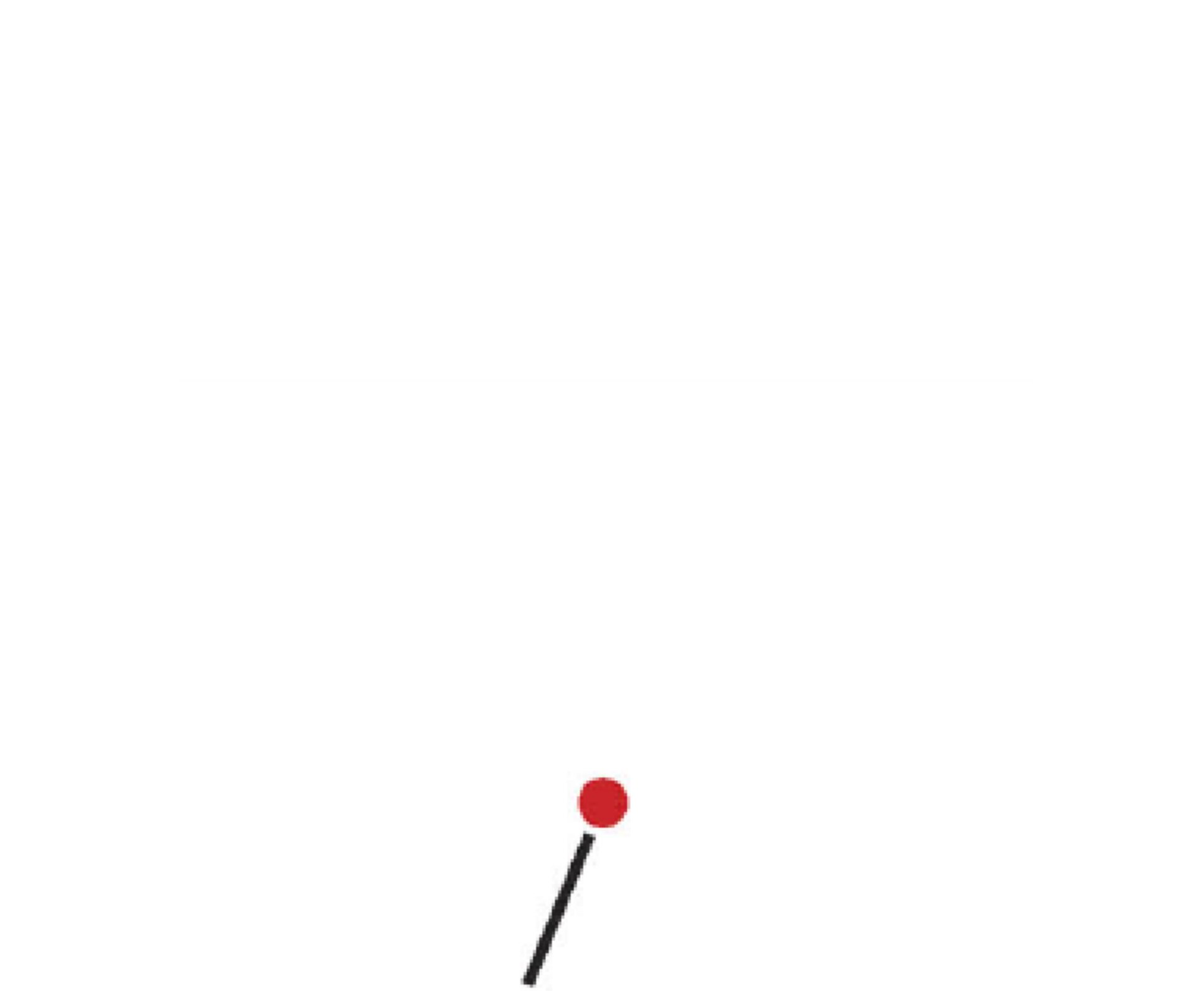
We feel like we saw an array of items vividly.

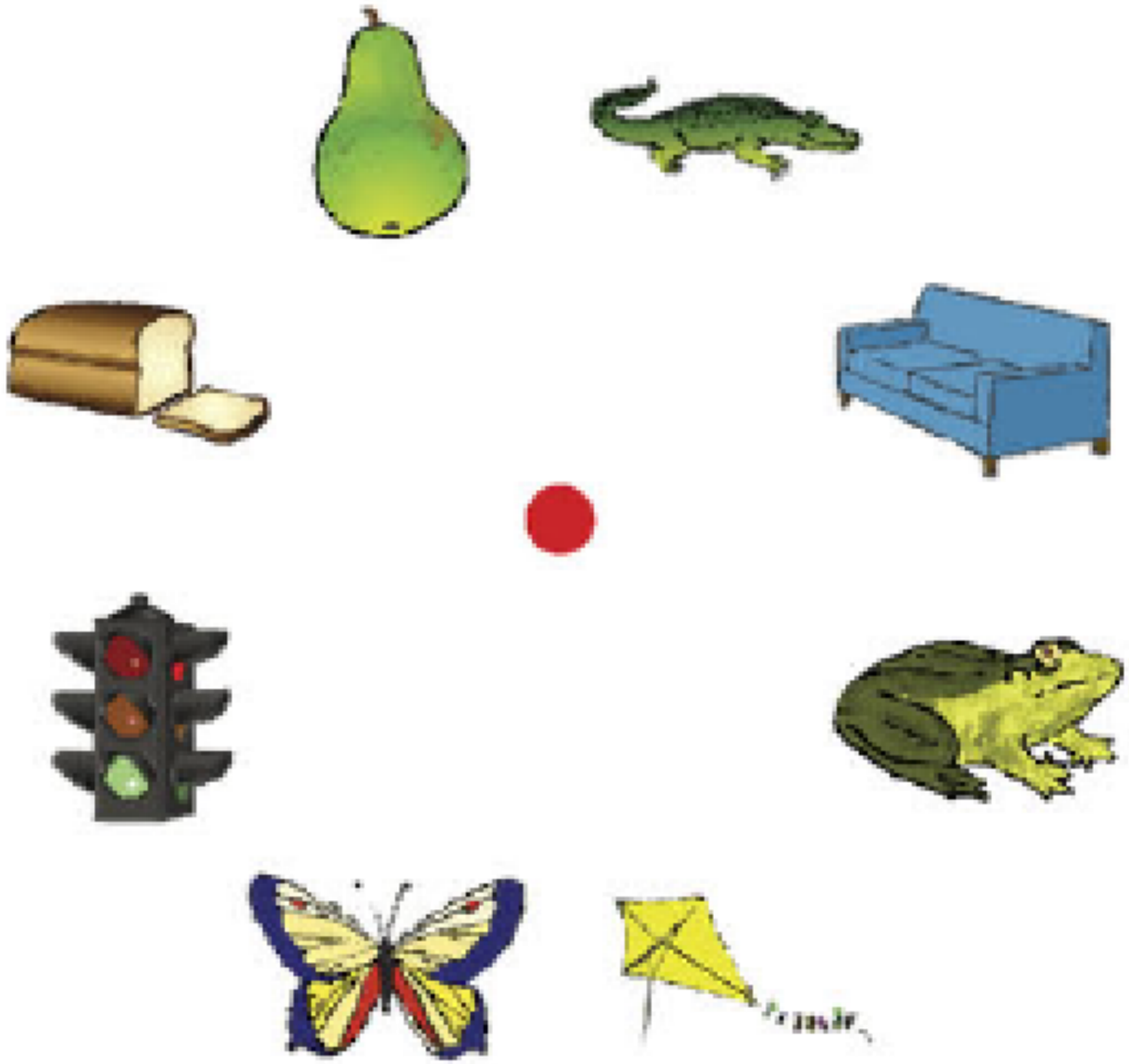
At the same time, we can’t remember and report what we saw.

-> Is it possible that we actually do NOT experience it consciously until proper attention and exceptions is allocated to an item so that it enters into working memory?









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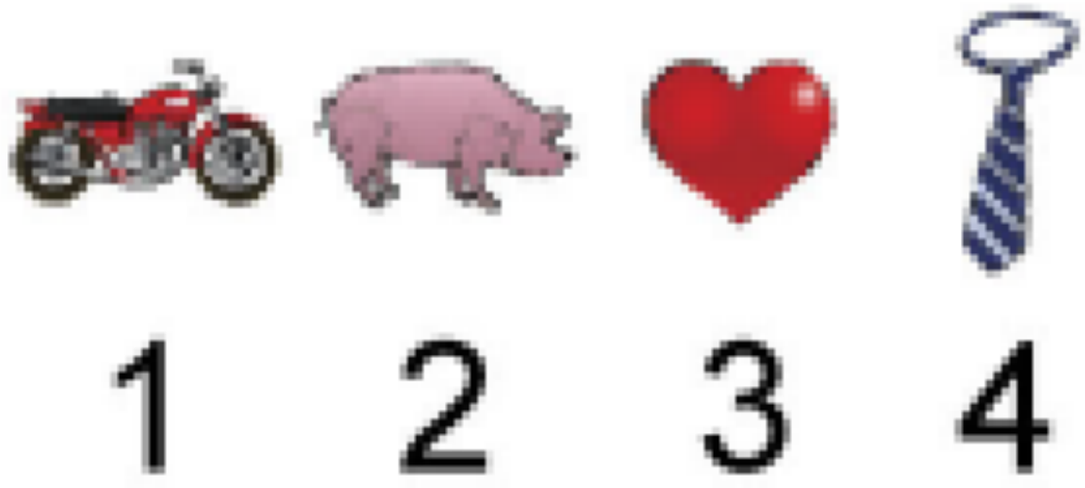
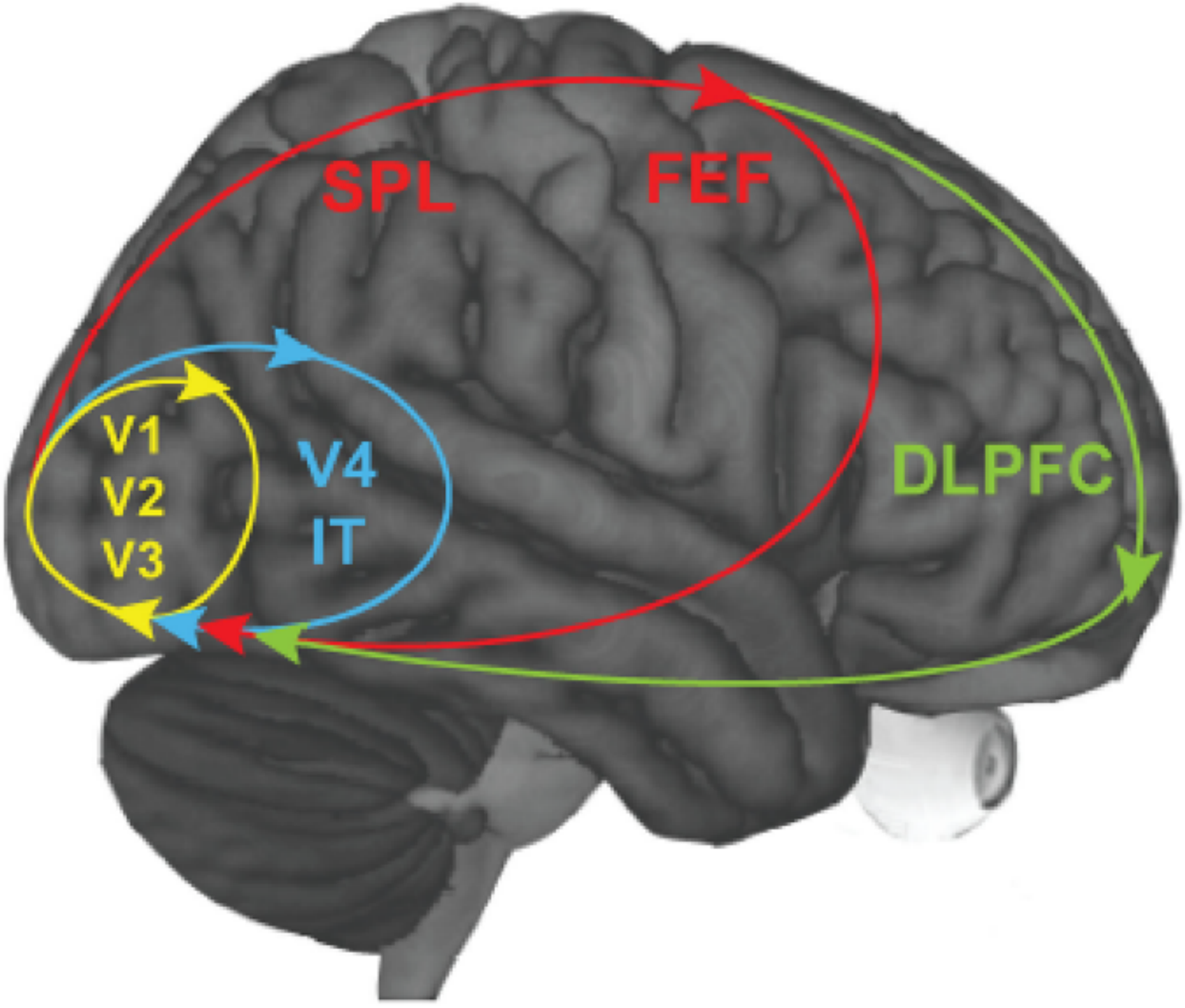
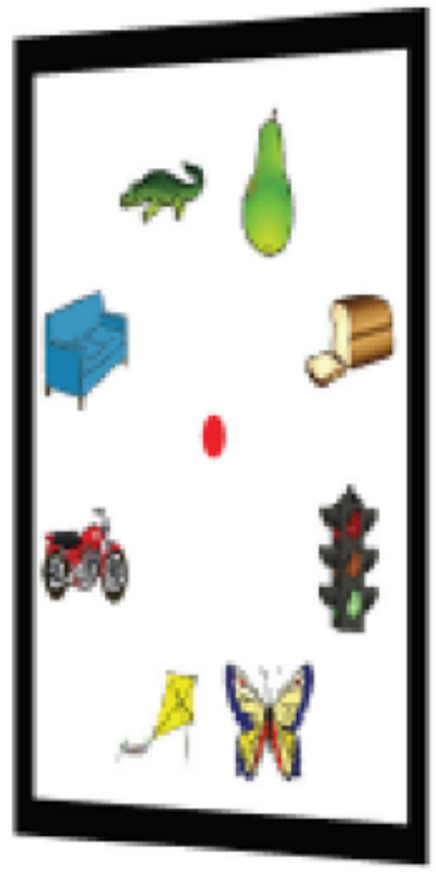
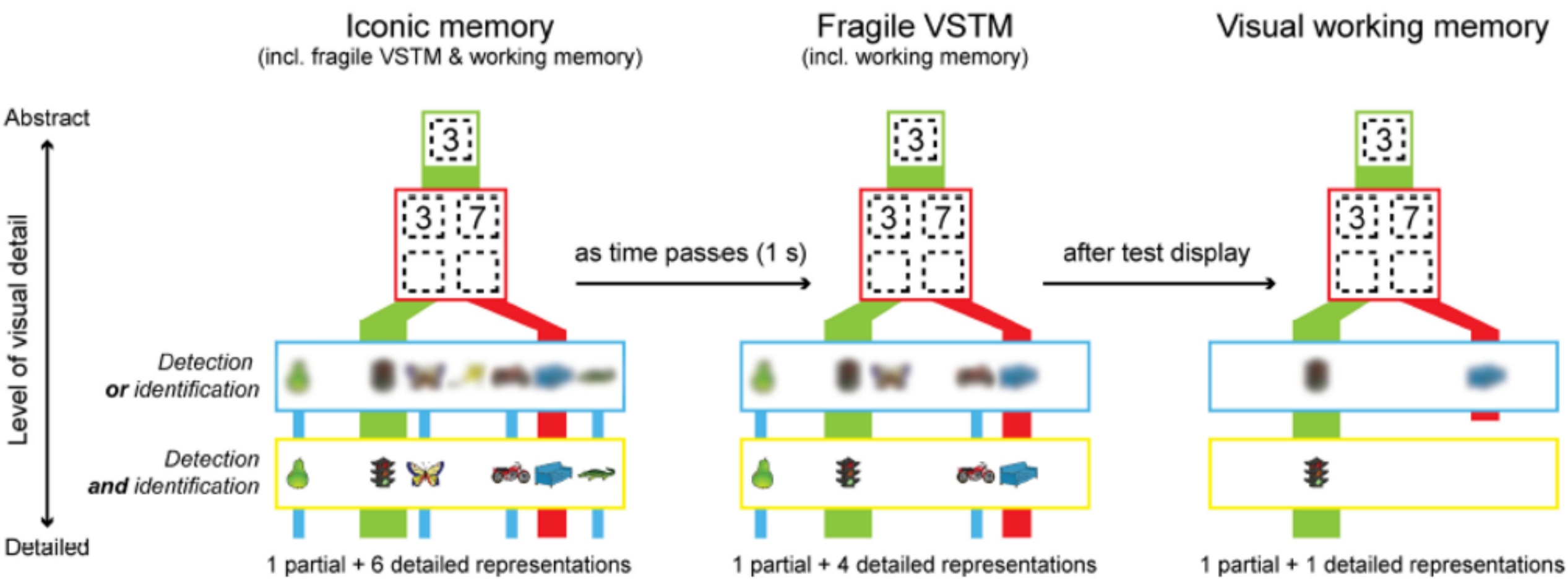
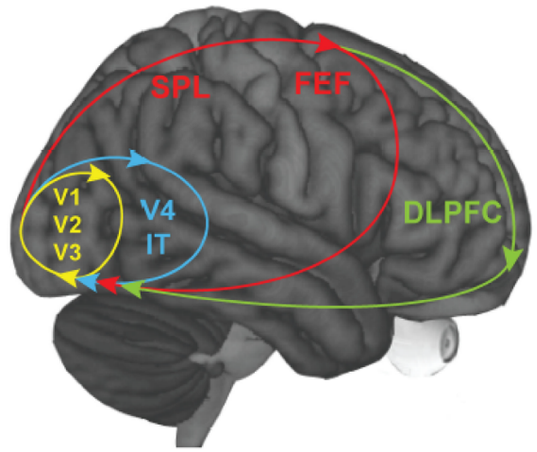


1 2 3 4


SPL
FEF
DLPFC
V1
V2
V3
V4
IT




Iconic memory
(incl. fragile VSTM & working memory)
Fragile VSTM
(incl. working memory)
Visual working memory
Abstract
Level of visual detail
Detailed
Detection
or identification
Detection
and identification
as time passes (1 s)
after test display
1 partial + 6 detailed representations
1 partial + 4 detailed representations
1 partial + 1 detailed representations


SPL
FEF
V1
V2
V3
V4
IT
DLPFC

- When we try to remember and report, only 1 item can be reported and its change detected. This leads to “impoverished” view of consciousness and “illusory” view of rich phenomenology.

- Partial report paradigm allows us to estimate more directly the capacity of initial phenomenology

- Failure of reports reflects visual interference (e.g., superposition of stimuli) that can be protected only with attention and working memory.

Conclusions

- No-report paradigms reveal over- and under-estimation of the neural correlates of consciousness

- This situation is largely due to a behavioristic thinking about conscious phenomenology from the functional perspective

- Need a revision of the way to attack the problem of neural basis of conscious phenomenology

- Starting from phenomenology, and search for the physical substrate that supports the central properties of phenomenology

- Combine no-report and report-based paradigms!

- With complete no-report paradigms, we can study …

  - Why do we lose consciousness under anesthesia and dreamless sleep? (are we really?) What aspects of neural activity are lost under loss of consciousness?

  - Why is our auditory qualia different from visual qualia? What neural substrate supports the difference? What are the critical phenomenological difference between the modalities?

6. integrated information theory

Integrated information theory of consciousness

- Starts from phenomenology, identifies five essential properties of conscious experience (1. existence, 2. composition, 3. information, 4. integration, 5. exclusion)
- Tries to translate the axioms into how these axioms can be supported by the physical mechanisms

Tononi 2004, 2008, Oizumi et al 2014 PLoS Comp Bio

Integrated information theory

I : information

O : integration

Φ (phi) : integrated information

Guilio Tononi

Integrated information theory

I : information

O : integration

Φ (phi) : integrated information

Guilio Tononi

Two kinds of information
Intrinsic
vs
Extrinsic

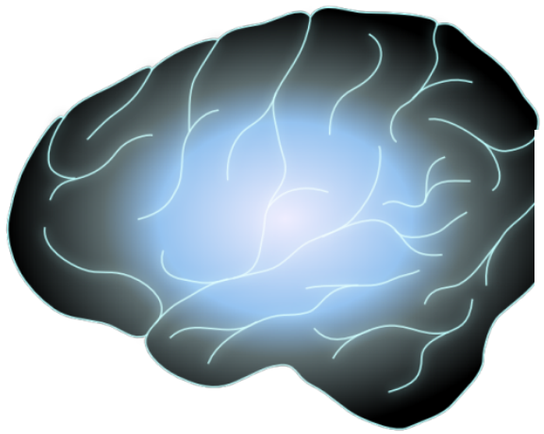
Tononi 2010 Acta Ital

Photodiode thought experiment

Unconscious (?)

Single photodiode

1 bit



Conscious

Brain

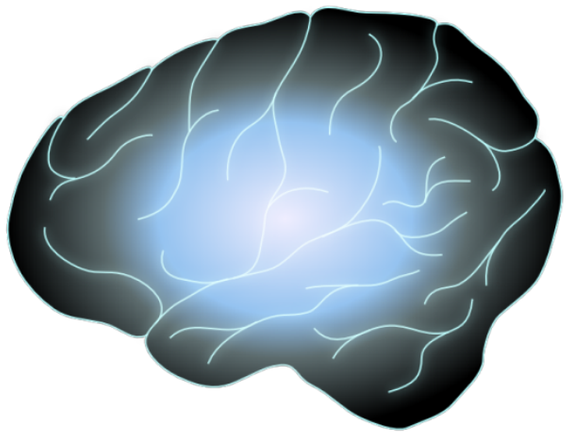
10^11 neurons - 10^11 bits

Information

Photodiode thought experiment

Unconscious (?)

Digital camera



Conscious

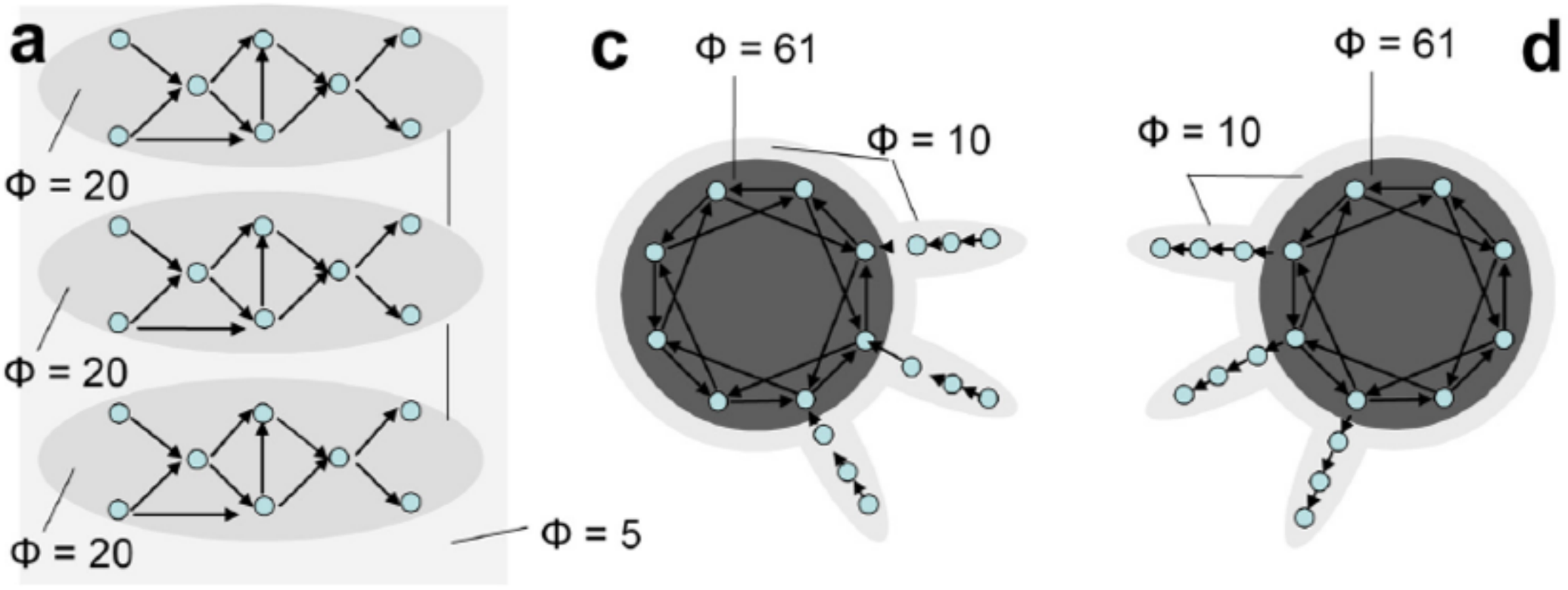
Brain

Integrated information

(Balduzzi and Tononi, 2008)

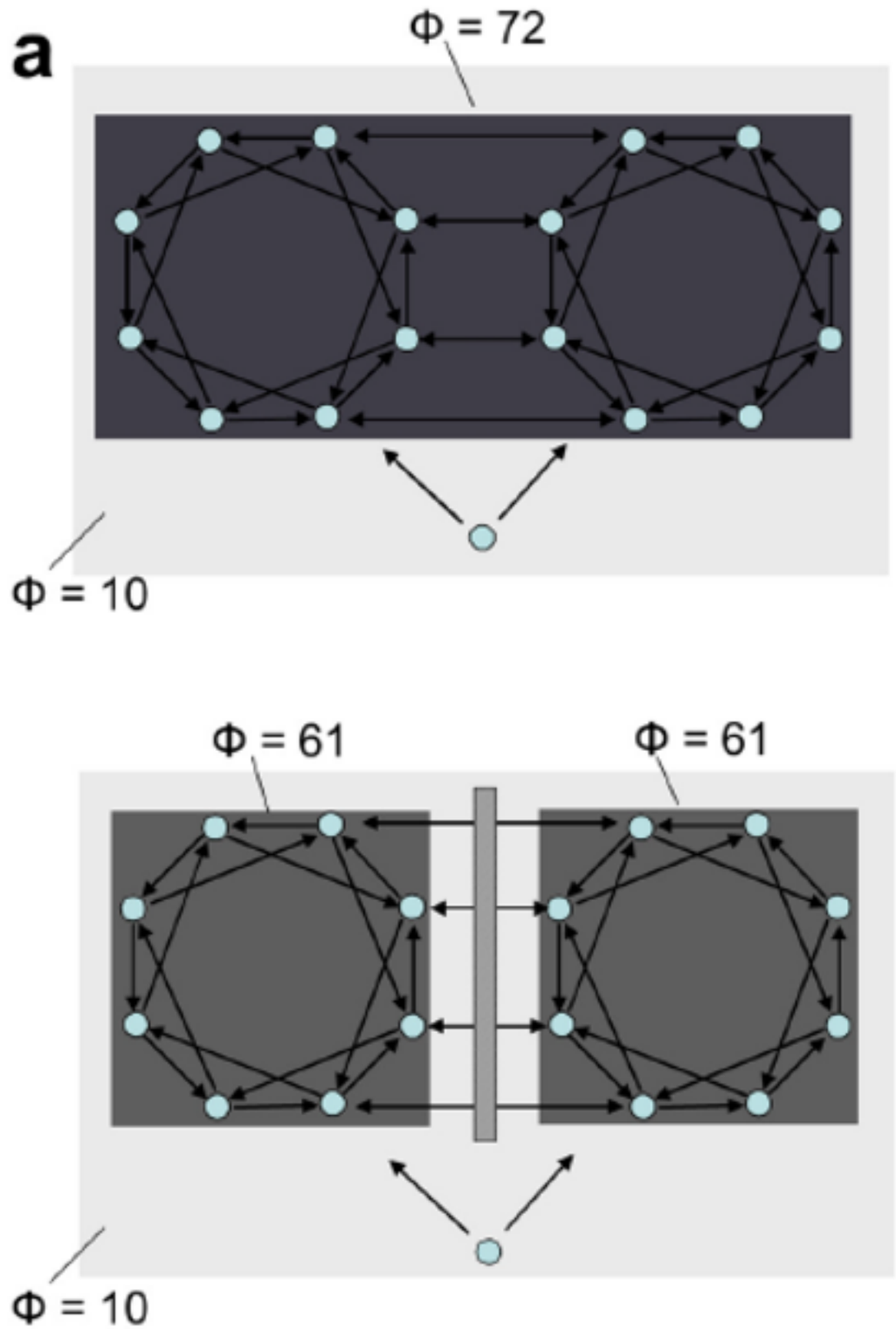
IIT explains…

- why a thalamo-cortical system generates consciousness while cerebellum, retina (afferent), and motor systems (efferent) do not



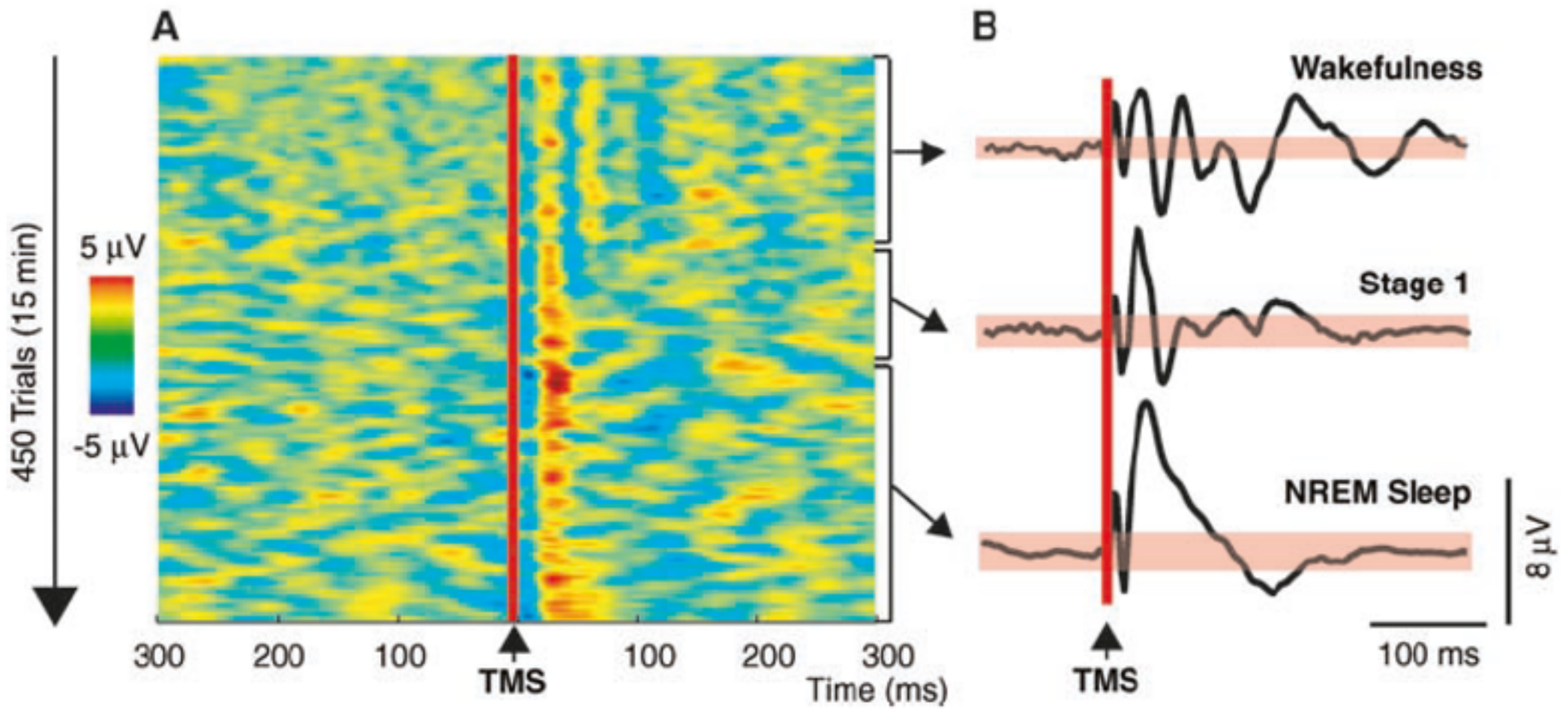
IIT explains…

- why two consciousness emerge when a brain is split into two.

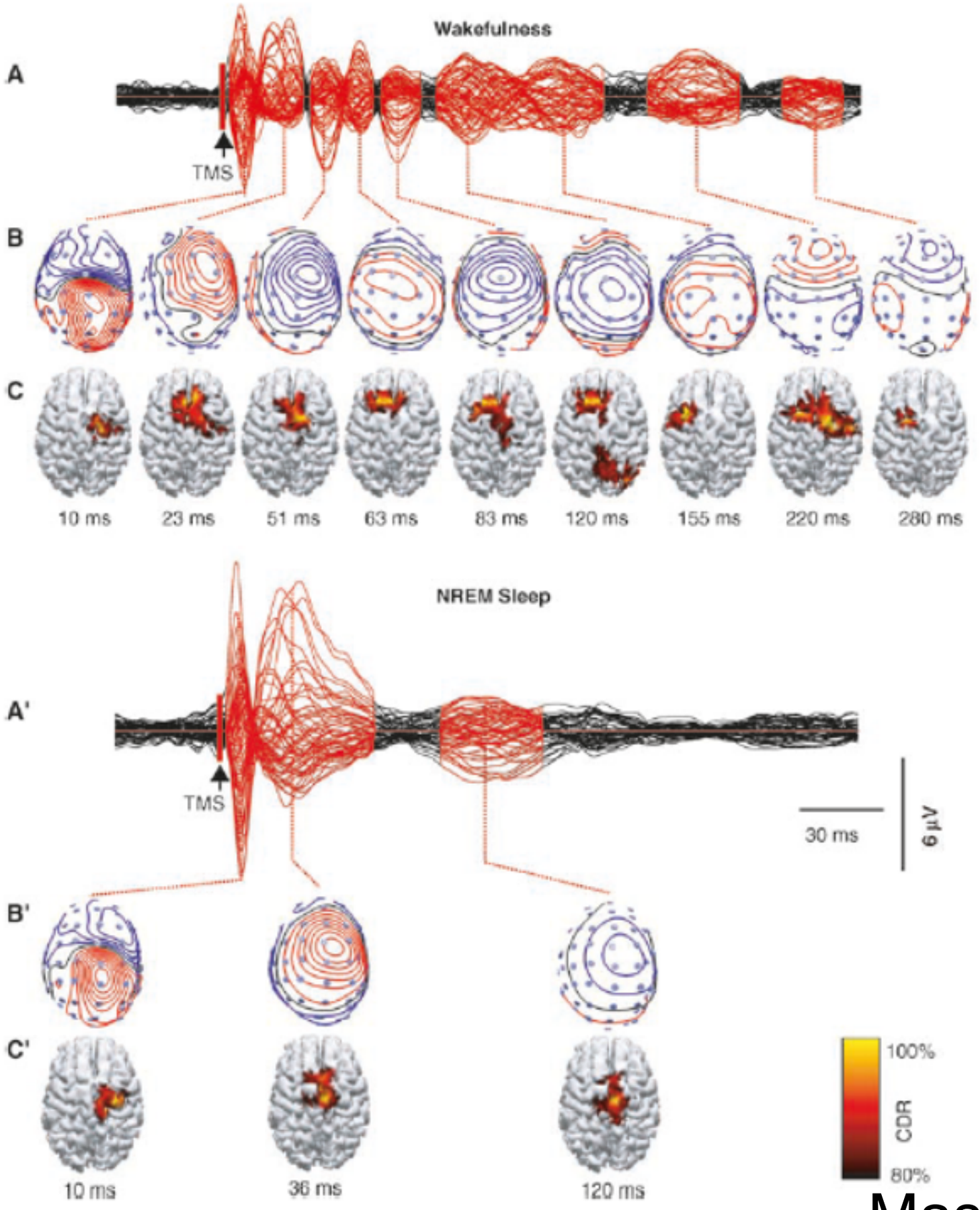


IIT predicts …

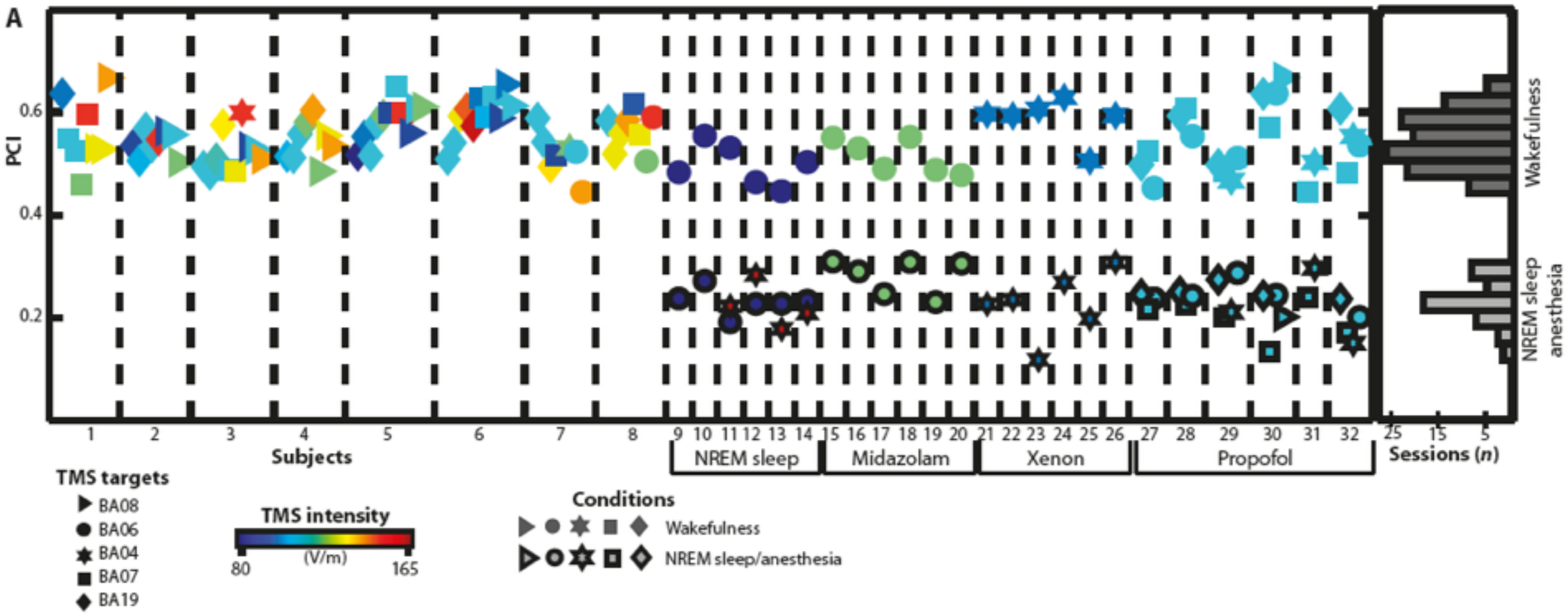
- waking brains would maximally integrate information (indirectly supported by TMS-EEG experiments)



Massimini et al 2005 Science

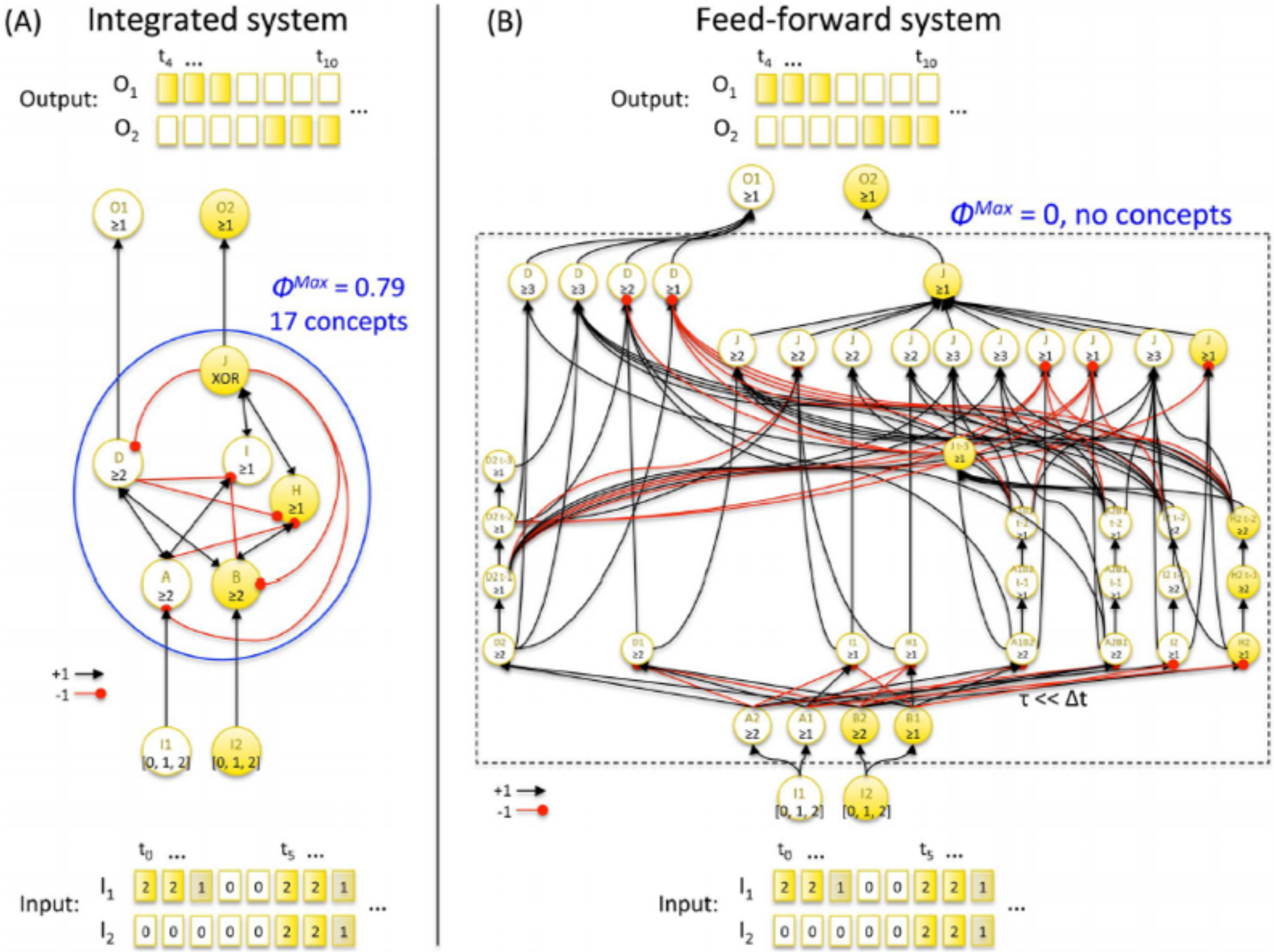


Massimini et al 2005 Science



Casali et al 2013 Science Trans Medicine

Advantages of conscious system with phi>0?



IIT predicts …

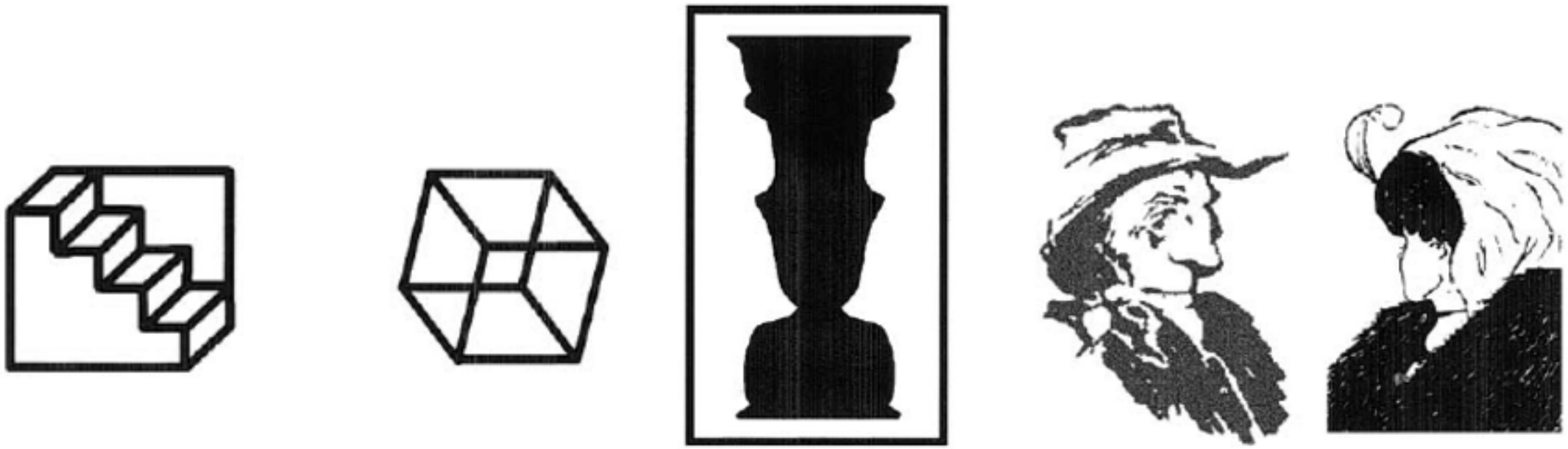
- that **overall amount of integrated information (phi) corresponds to levels** of consciousness
  - Oizumi et al ASSC 2011 under review
  - Cohen et al ASSC 2013, in preparation
- that that **a collection of phi's** computed from local neuronal populations maps onto **contents** of consciousness (phenomenology)
- **>>> Compute phi to directly test these predictions!**

Conclusion

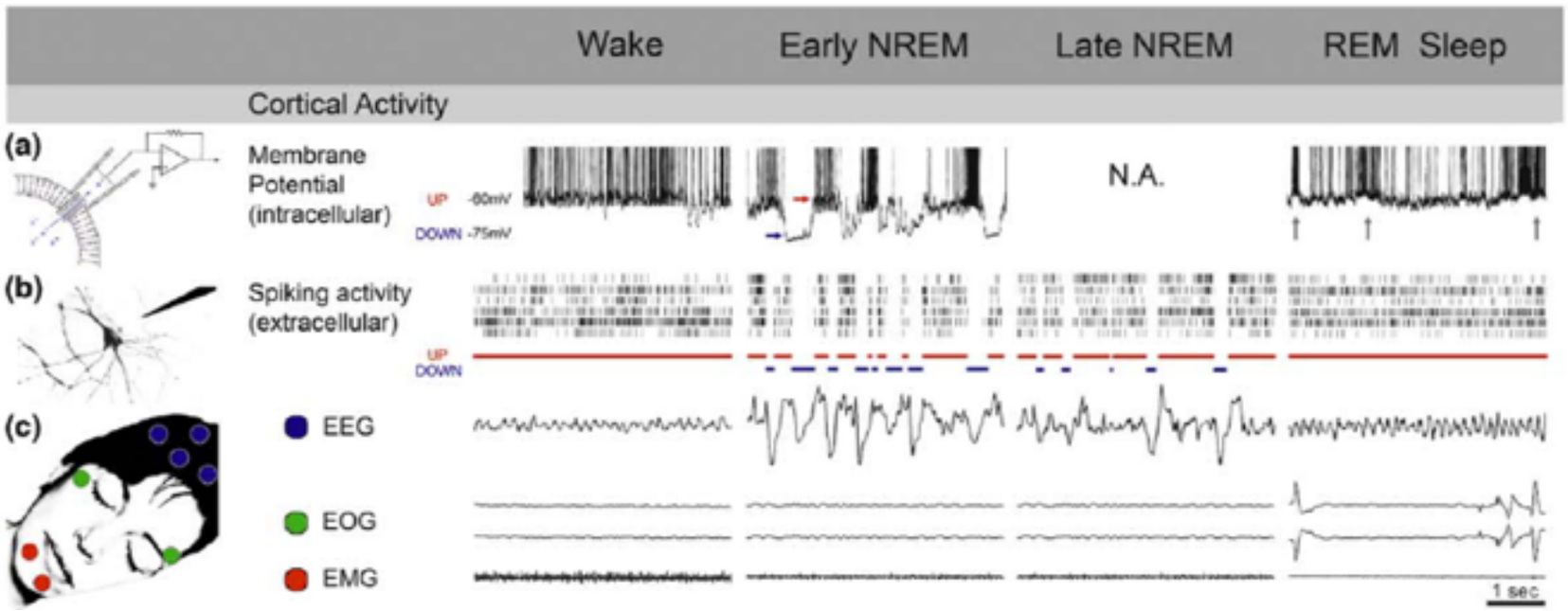
- New measure for integrated information based on mismatched decoder
- Integrated information computed from ECoG data filtered around 8-24 Hz show decrease at the onset of anesthesia and increase at the recovery

What kind of physical mechanisms can support conscious phenomenology?

consciousness is intrinsic



Leopold & Logothetis 1999 TICS



Nir & Tononi 2010 TICS

consciousness is informative

consciousness is integrated and composed of various aspects

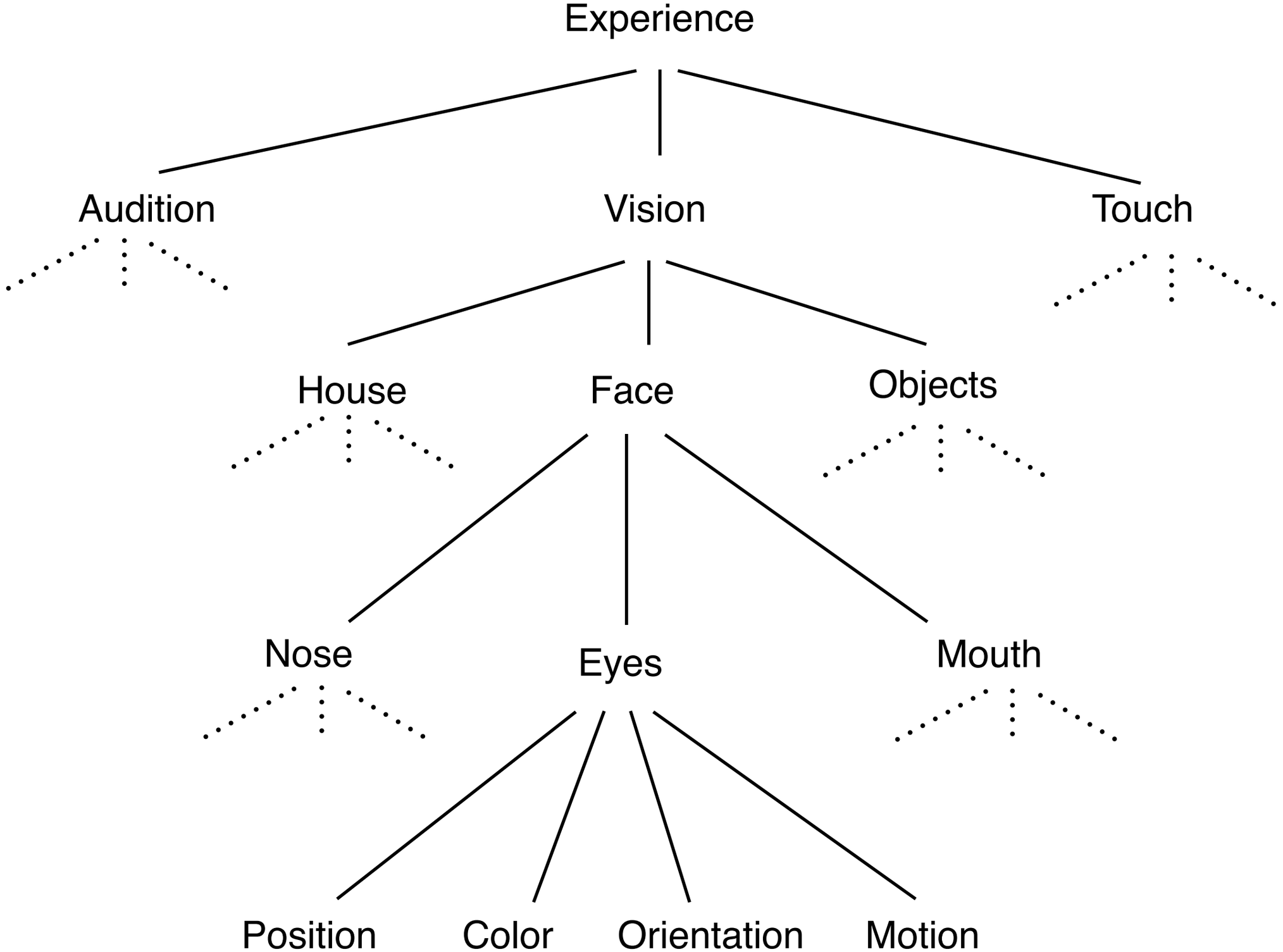
Essential properties of conscious phenomenology

- **Intrinsic**
- **informative**
- **integrated**
- **Compositional**
- Exclusion

What kind of neural mechanisms can support these properties?

Conscious experience : Hierarchical structure?

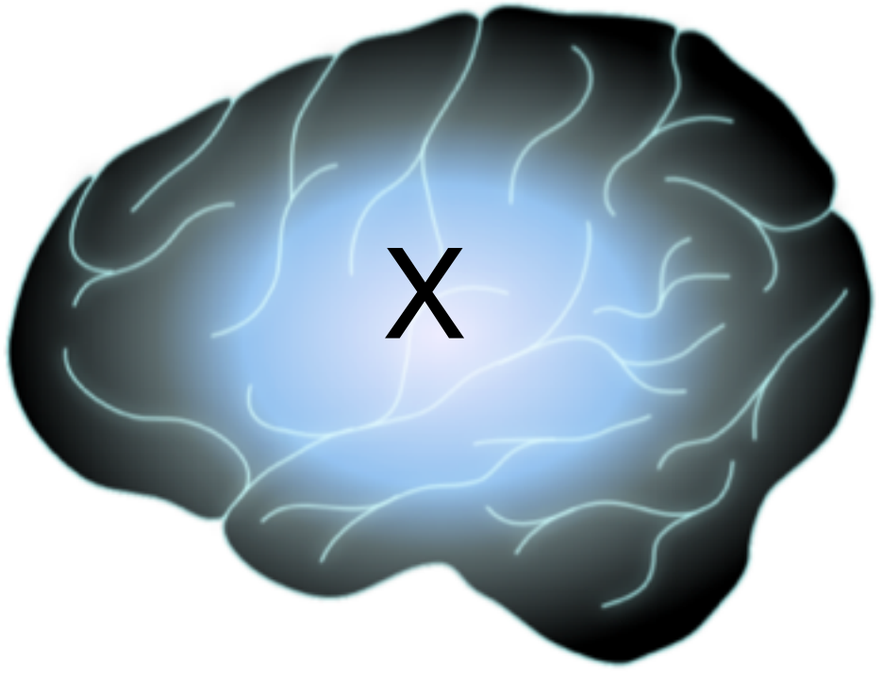
Note: each level is not reducible to lower levels!



Previous related approaches in neuroscience

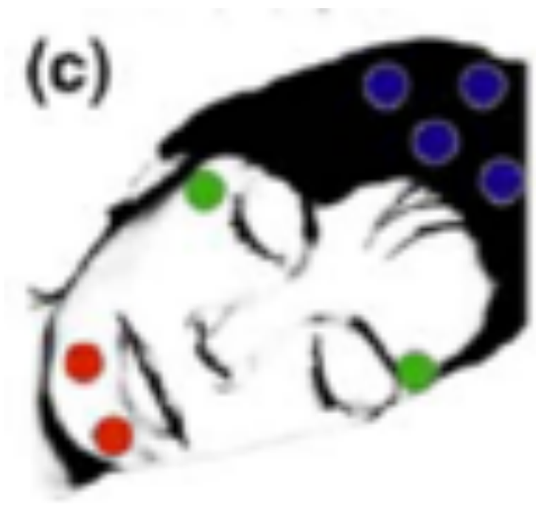
- "Extrinsic information" approach in neuroscience
  - I(X;S) = H(S) - H(S|X)

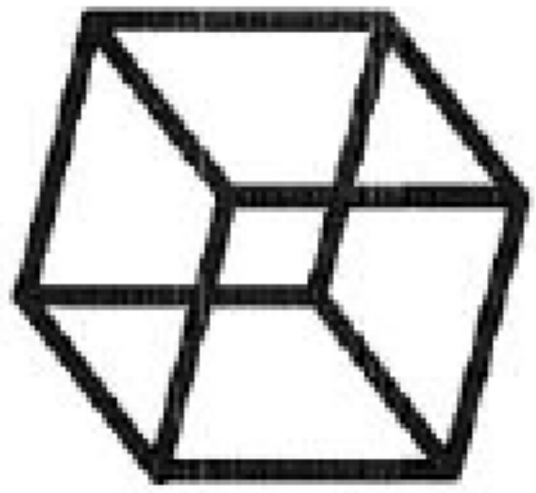
S



Previous related approaches in neuroscience

- But, concsiousness is "intrinsic"!



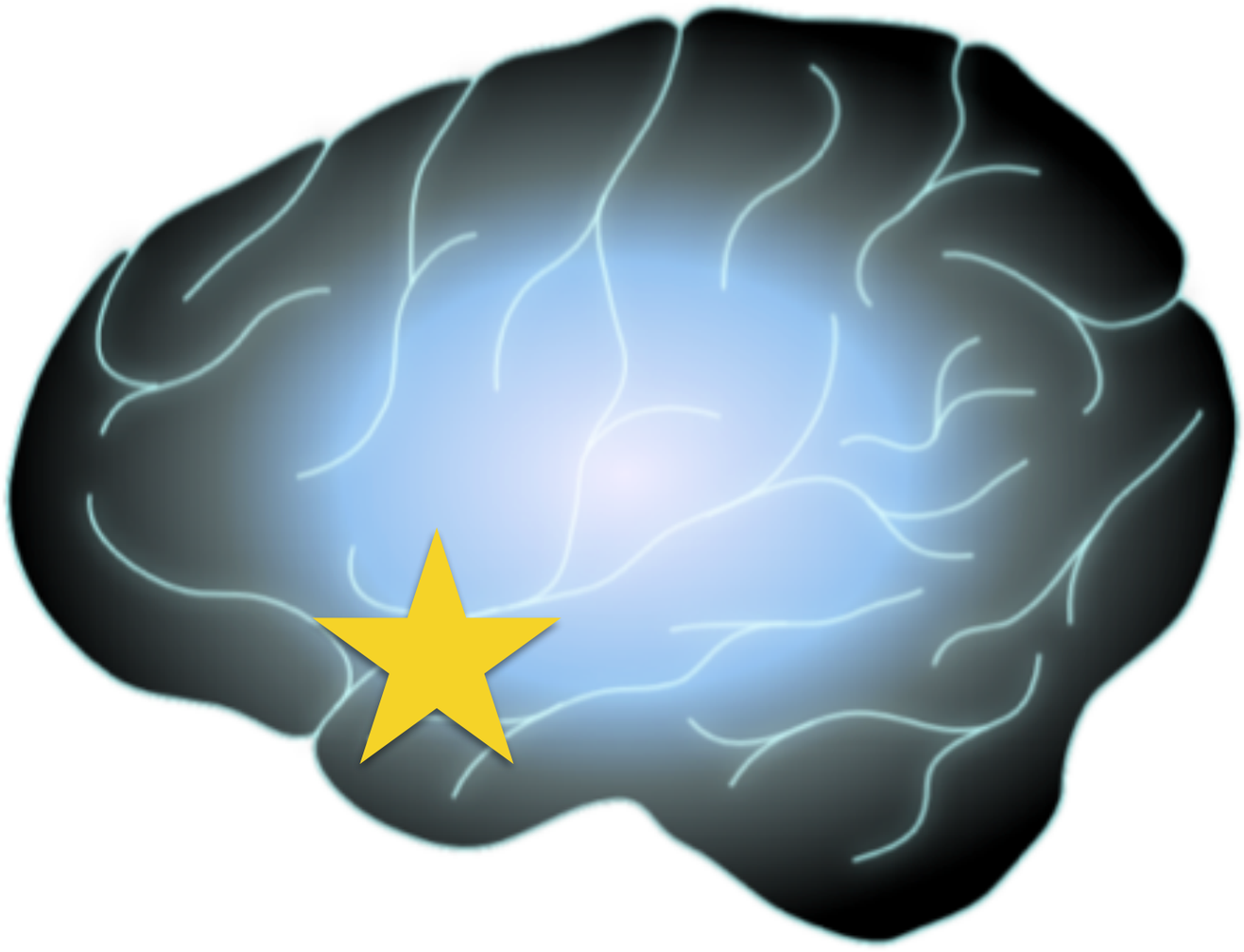


Previous related approaches in neuroscience

- Composition and integration
  - Distributed representation. Bounded percept and unified experience
  - Synchrony, coherence, oscillation, etc

Integrated information theory

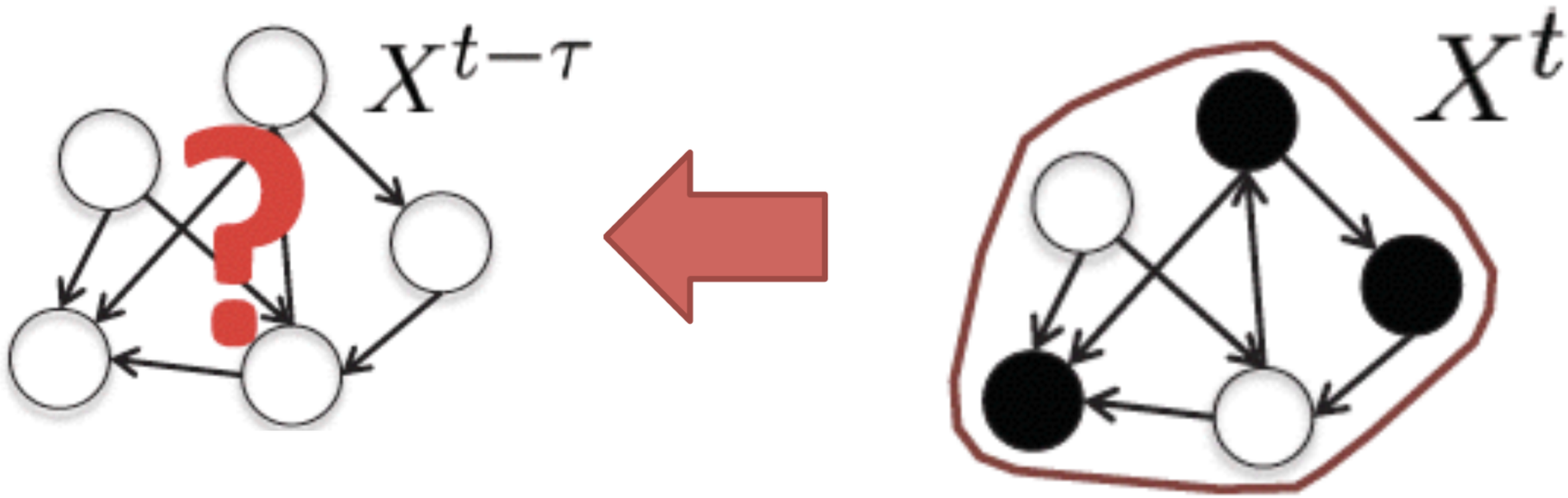
- Intrinsic information:
- Integration:
- Composition:
- Exclusion



Tononi 2004, 2008, 2012, Balduzzi & Tononi 2008, Oizumi et al 2014

What is *intrinsic* information?

: firing : silent



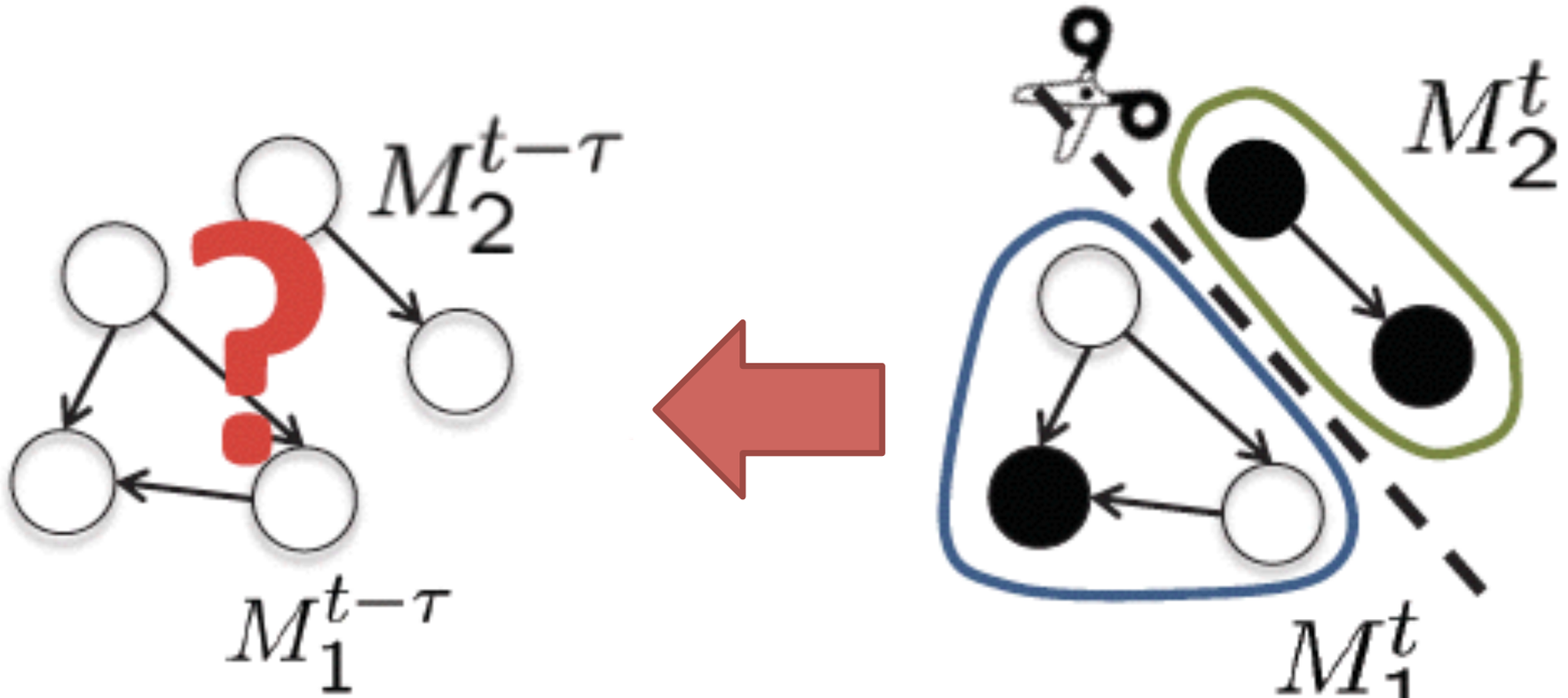
Infer the **previous** state from the knowledge of the **present** state.

$$I(X^{t-\tau}; X^t) = H(X^{t-\tau}) - H(X^{t-\tau} | X^t)$$

mutual information — entropy — conditional entropy

(Balduzzi and Tononi, 2008)

What is *intrinsic* integrated information?



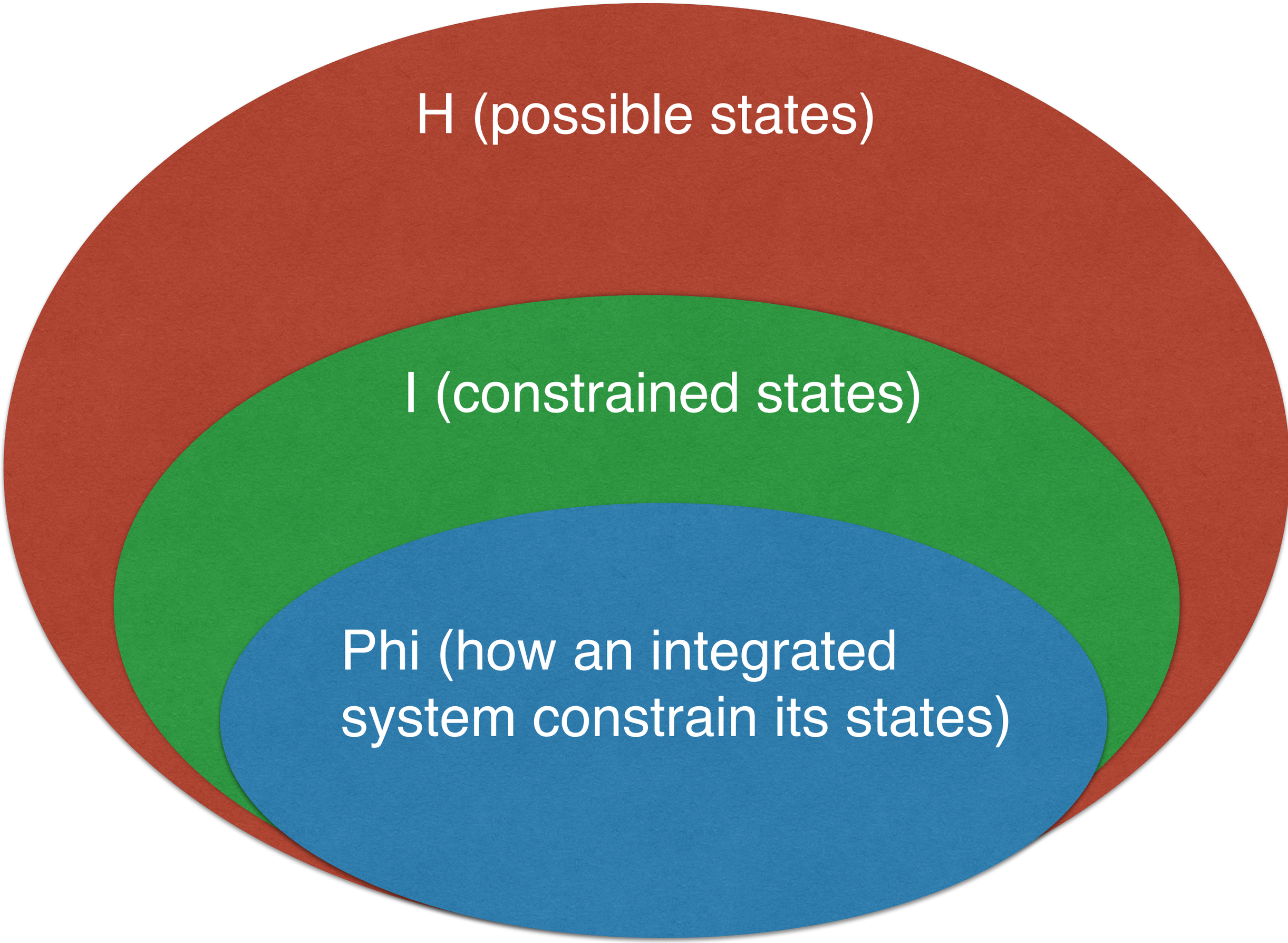
Infer the **previous** state from the knowledge of the **present** state.

$$I(X^{t-\tau}; X^t) = H(X^{t-\tau}) - H(X^{t-\tau} | X^t)$$

H**ow much information would be lost** when we infer the previous state **based only on the knowledge of the parts**.

$$\phi = I(X^{t-\tau}; X^t) - \sum_i I(M_i^{t-\tau}; M_i^t)$$

Balduzzi & Tononi 2008, Barrett & Seth 2011, Oizumi et al 2015 Arxiv

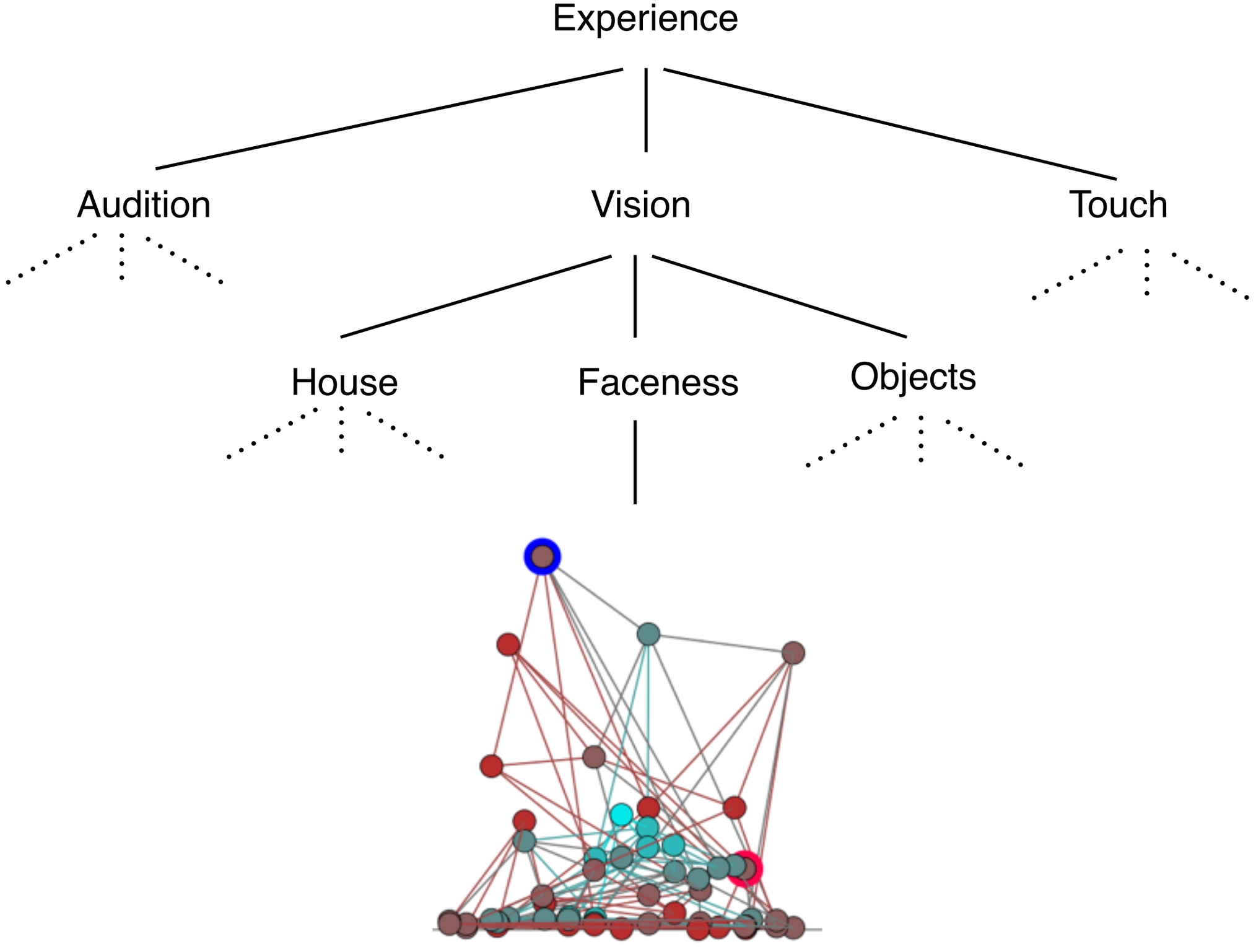

H (possible states)
I (constrained states)
Phi (how an integrated system constrain its states)

- Hypothesis:
  - **Structure of integrated information should reflect phenomenology rather than physical input to the system.**

- Can structure of integrated information discriminates different percepts given the same stimulus?
  - Use visual illusions (e.g., backward masking & continuous flash suppression)

Conscious experience : Hierarchical structure?

Note: each level is not reducible to lower levels



Conclusions

- Information structure computed from the ECoG electrodes in the FFA areas naturally categorizes conscious phenomenology of faces in masked and unmasked conditions
- Information structure based on phi* (based on either partitions or magnitudes) outperforms those based on I or H (matched in dimensionality).

Speculations

- Structure of integrated information =~ qualia?
- Can be compared between sensory modalities
  - Across individuals
  - Across species
- Why does vision feel different from audition?
- What is it like to be a bat?
- Dissolution of the Hard Problem?