

fMRI Paradigm Designs and Processing Methods

Peter A. Bandettini, Ph.D.

**Section on Functional Imaging Methods
Laboratory of Brain and Cognition**

<http://fim.nimh.nih.gov>

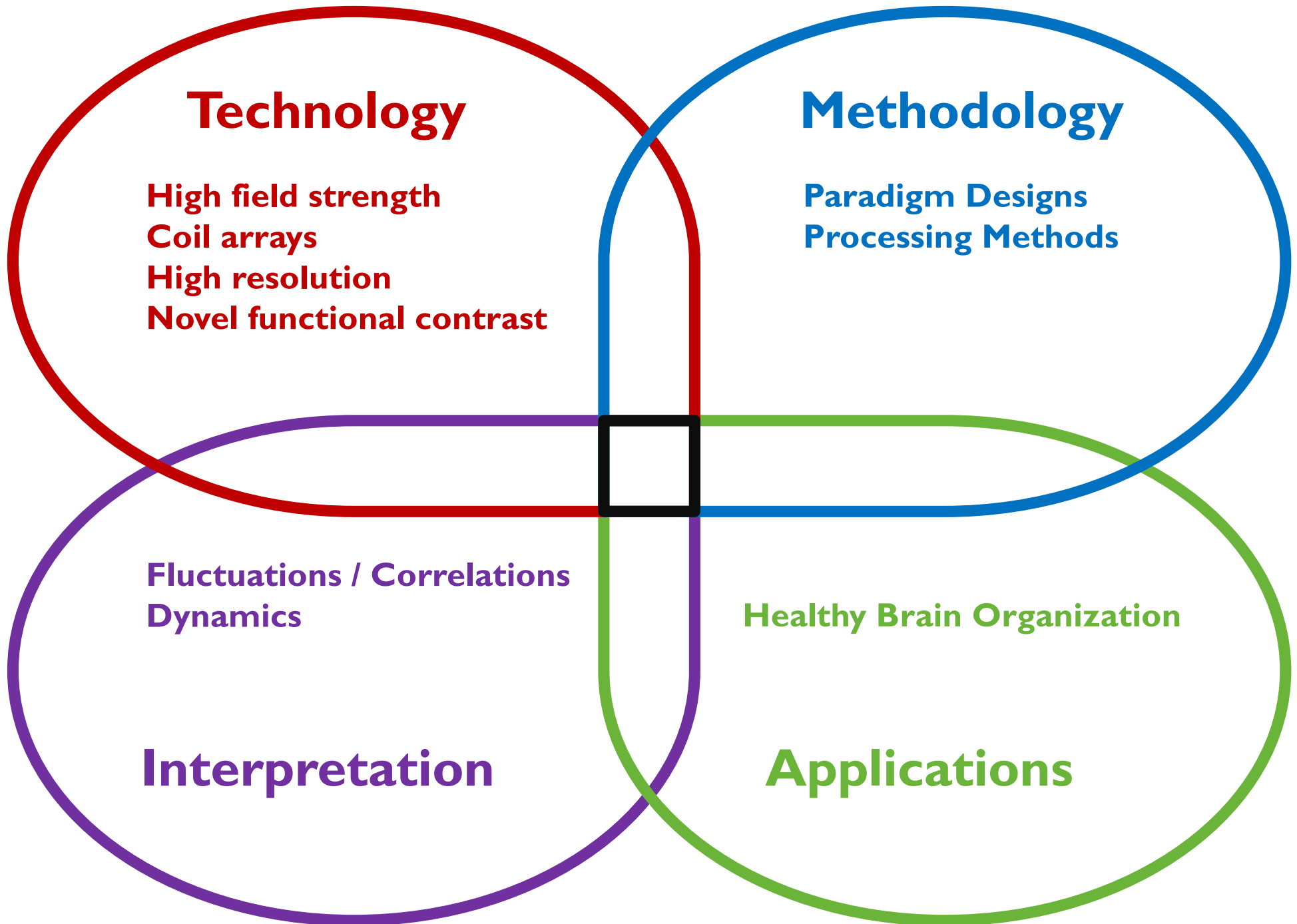
&

Functional MRI Facility

<http://fmrif.nimh.nih.gov>



Focus of this lecture

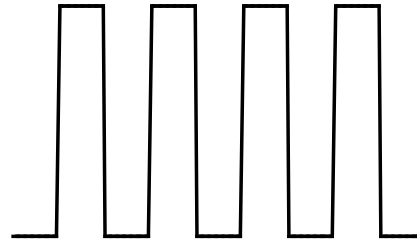


fMRI Paradigm Designs and Processing Strategies

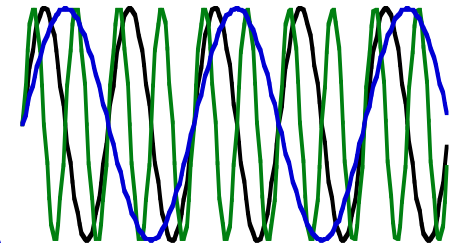
- 1. Neuronal Activation Input Strategies**
- 2. Resting State fMRI**
- 3. fMRI Decoding**

Neuronal Activation Input Strategies

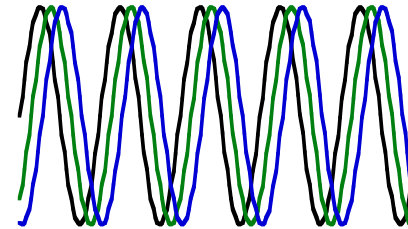
1. Block Design



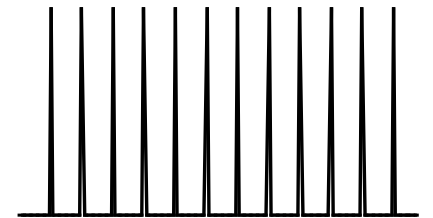
2. Frequency Encoding



3. Phase Encoding

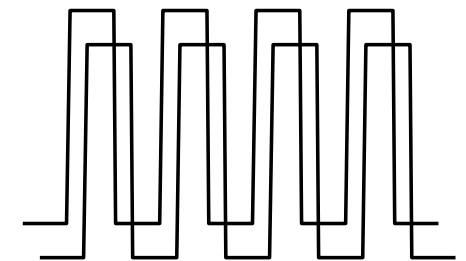


4. Event-Related



5. fMRI adaptation

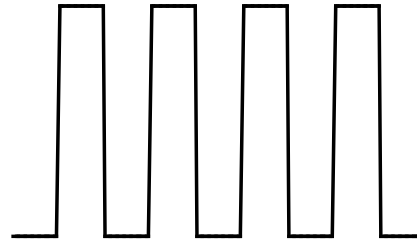
6. Orthogonal Block Design



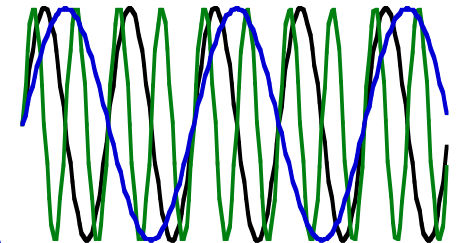
7. Free Behavior Design.

Neuronal Activation Input Strategies

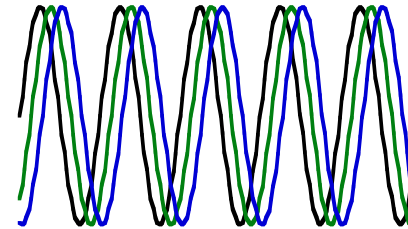
1. Block Design



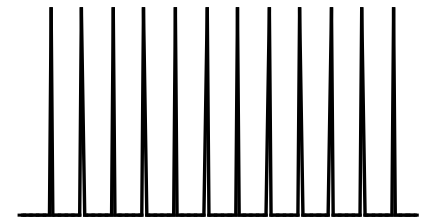
2. Frequency Encoding



3. Phase Encoding

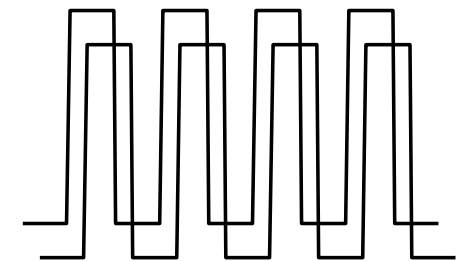


4. Event-Related

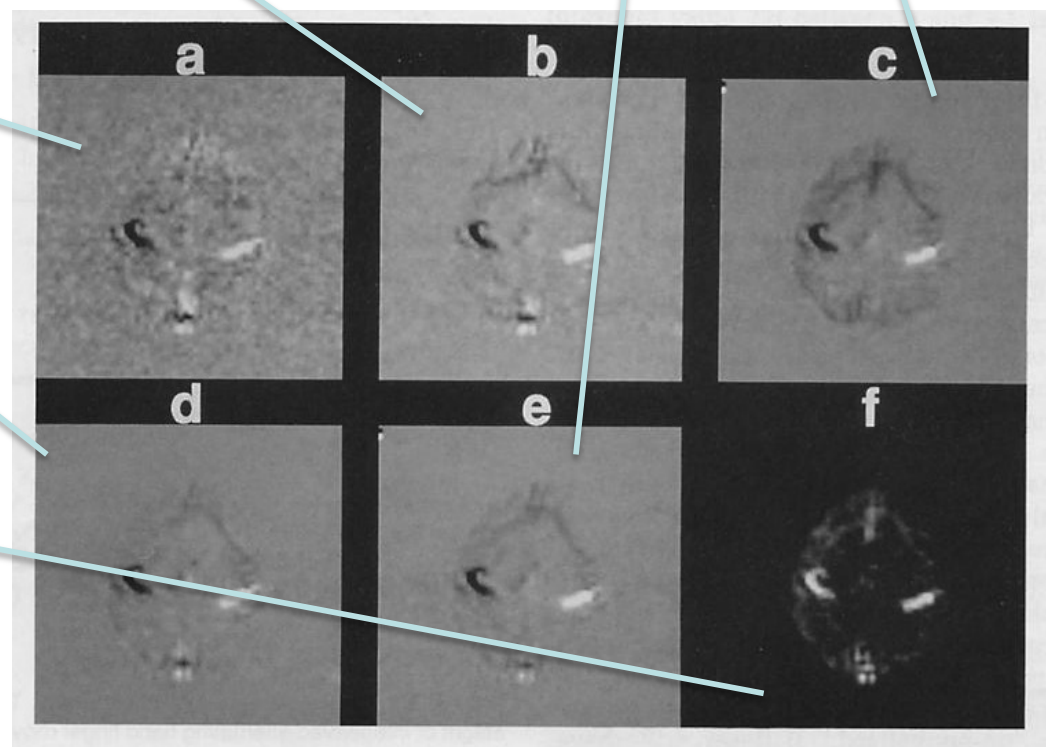
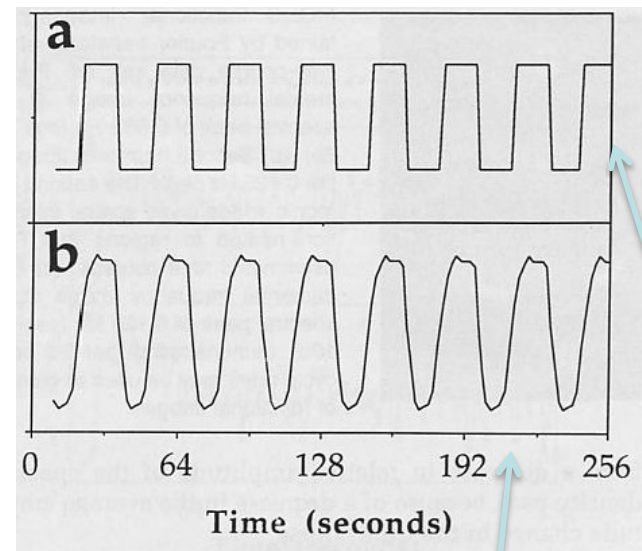
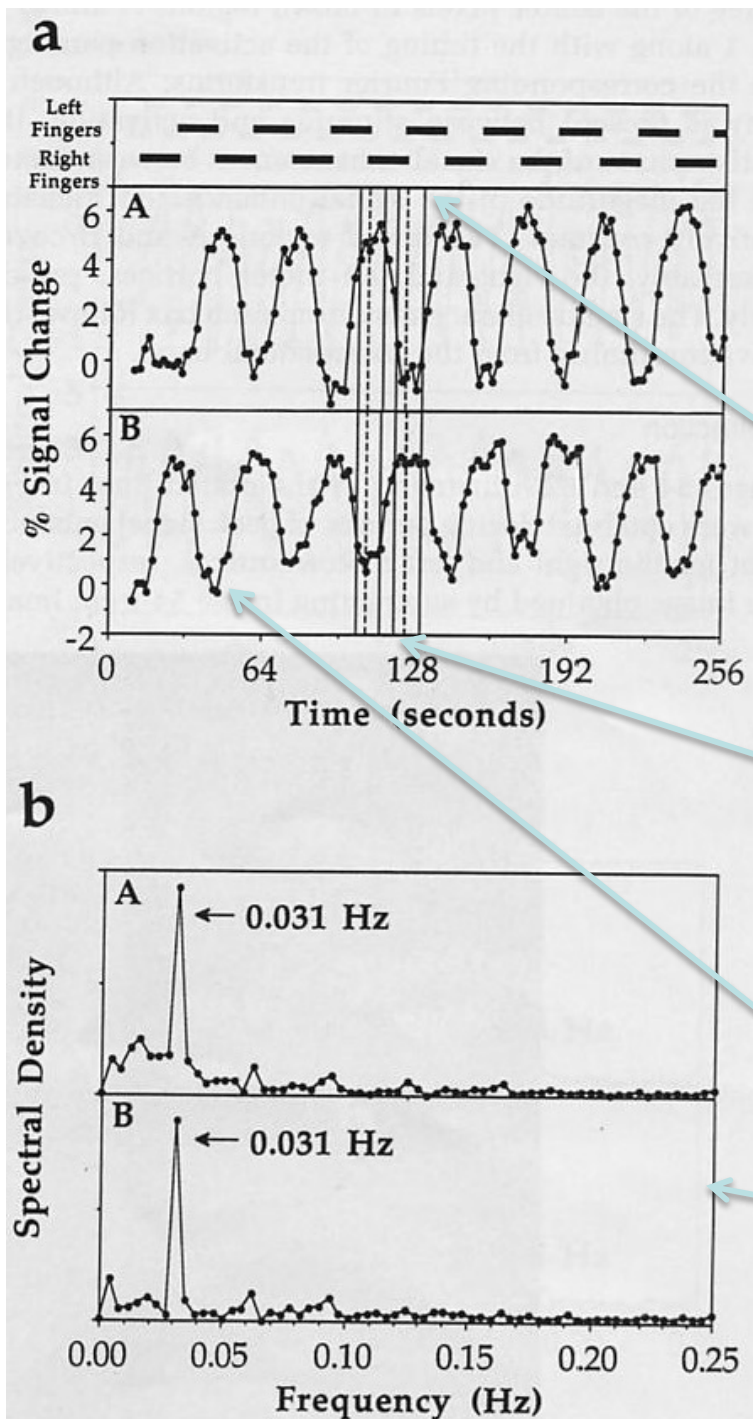


5. fMRI adaptation

6. Orthogonal Block Design

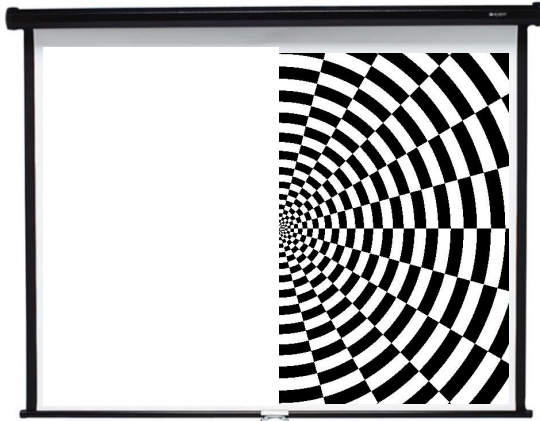


7. Free Behavior Design.

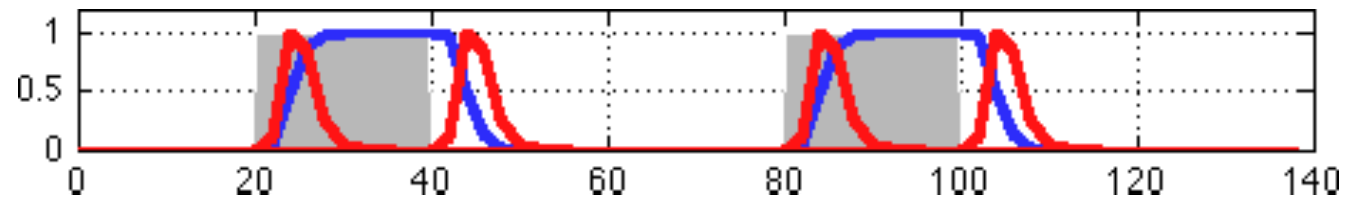


P. A. Bandettini, A. Jesmanowicz, E. C. Wong, J. S. Hyde, Processing strategies for time-course data sets in functional MRI of the human brain. *Magn. Reson. Med.* 30, 161-173 (1993).

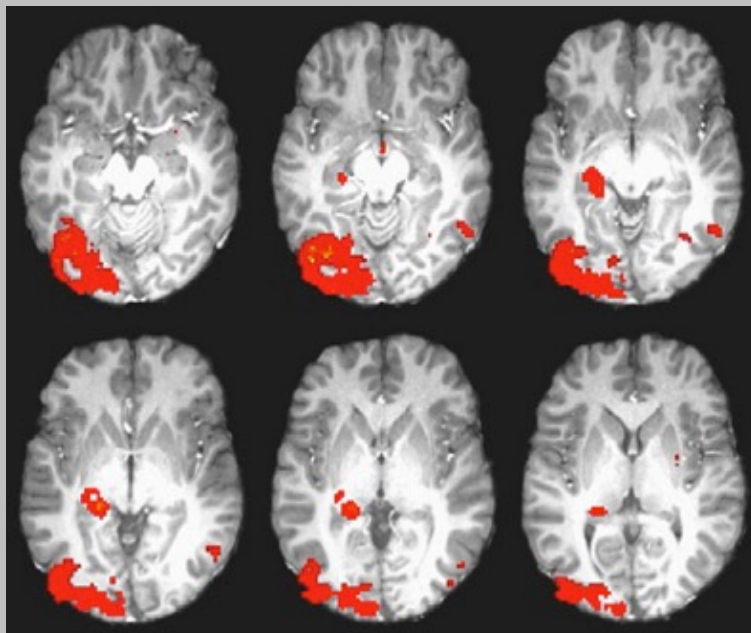
Predictive Response Model effect on fMRI Results (III)



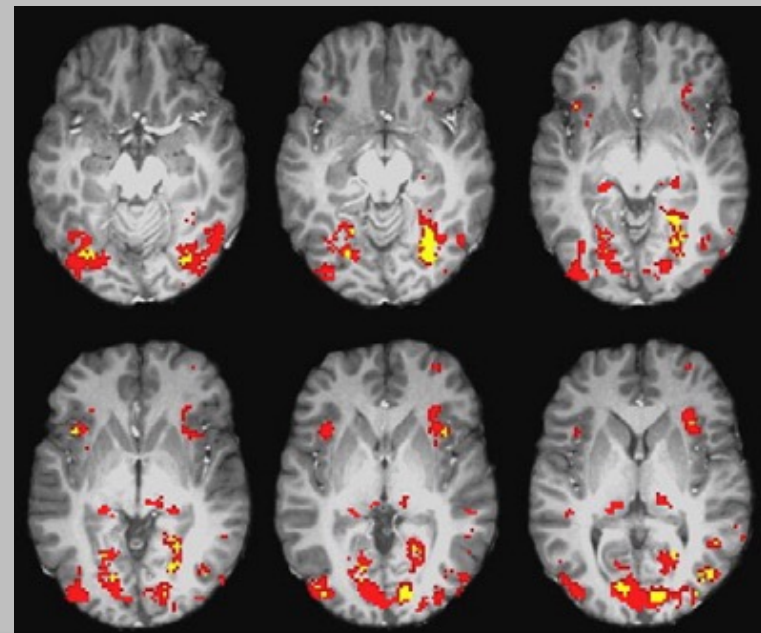
BLOCK DESIGN & HEMIFIELD VISUAL STIMULATION



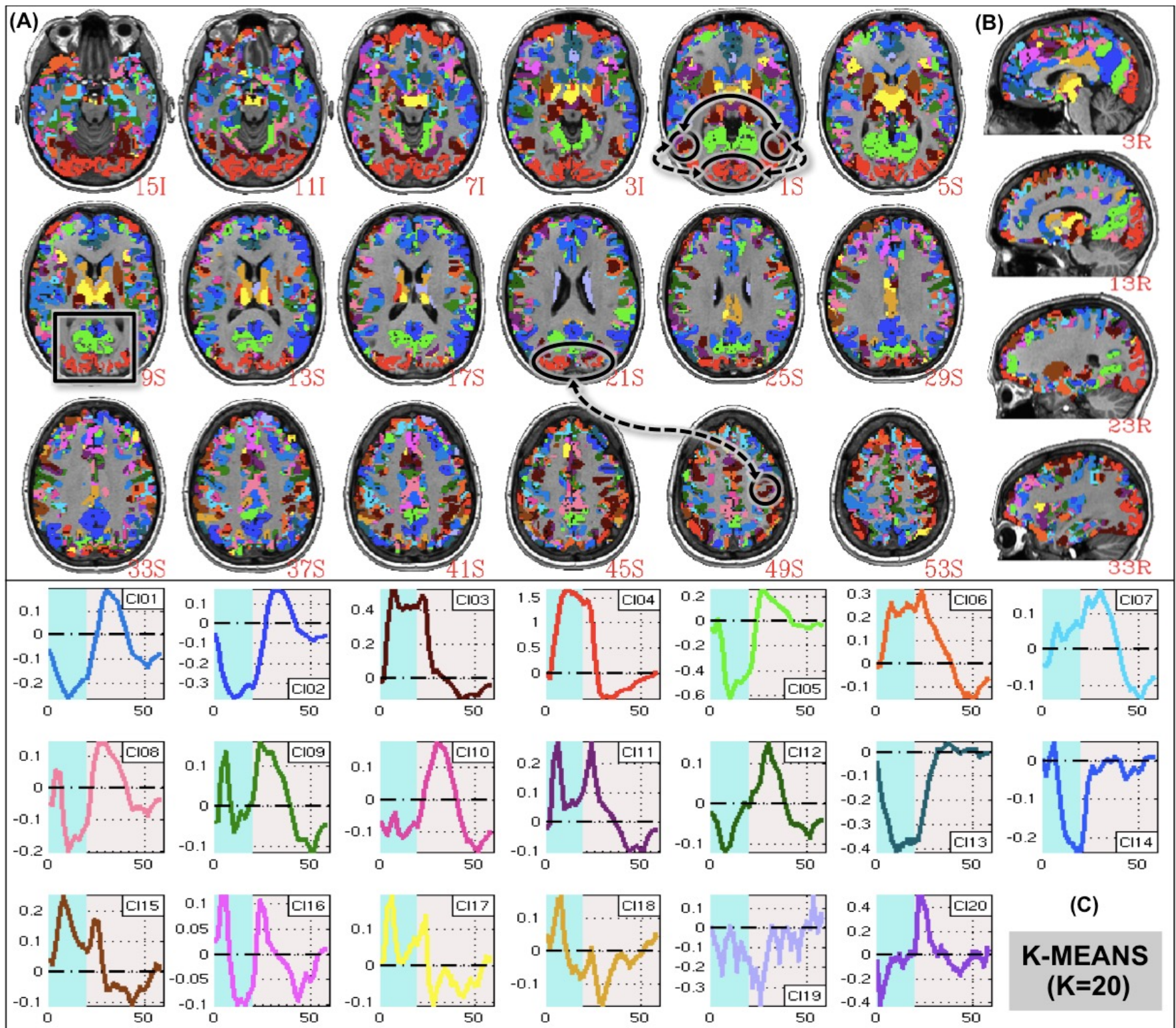
SUSTAINED RESPONSE MODEL



ONSET/OFFSET RESPONSE MODEL

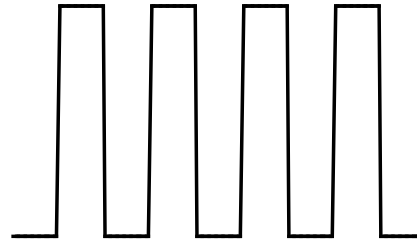


DIFFERENT RESPONSE SHAPES ARE PRESENT ACROSS DIFFERENT REGIONS OF THE BRAIN FOR A SINGLE STIMULUS TYPE

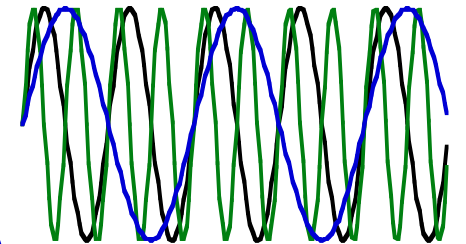


Neuronal Activation Input Strategies

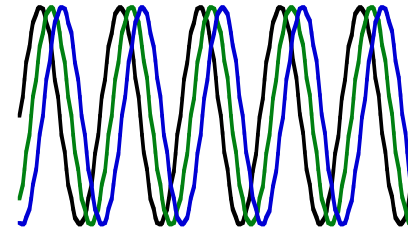
1. Block Design



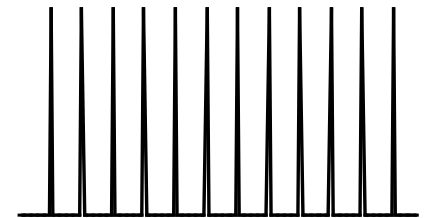
2. Frequency Encoding



3. Phase Encoding

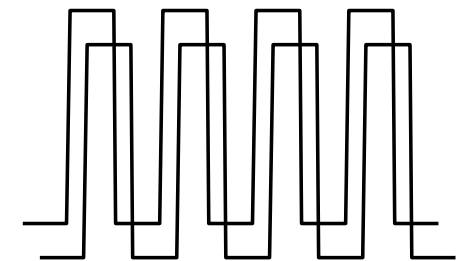


4. Event-Related

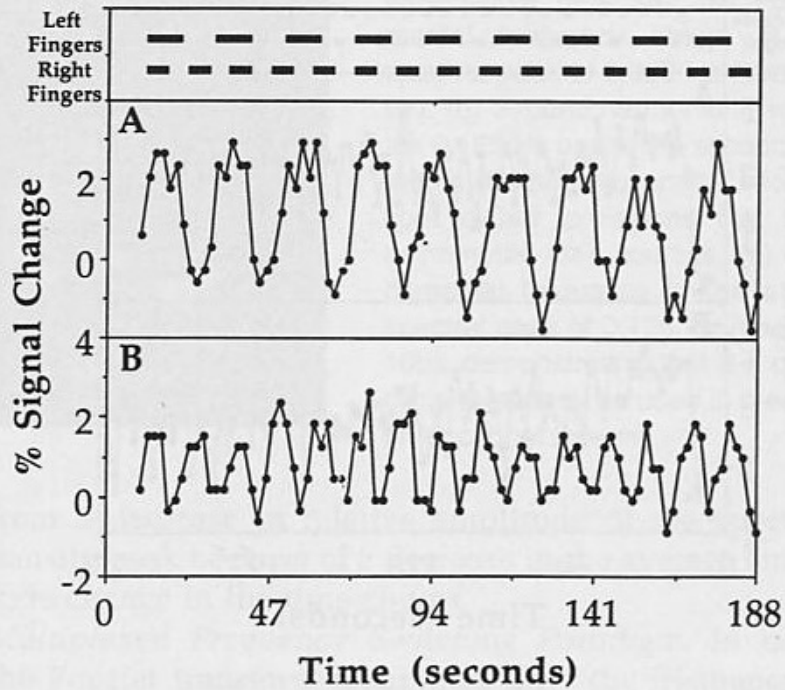


5. fMRI adaptation

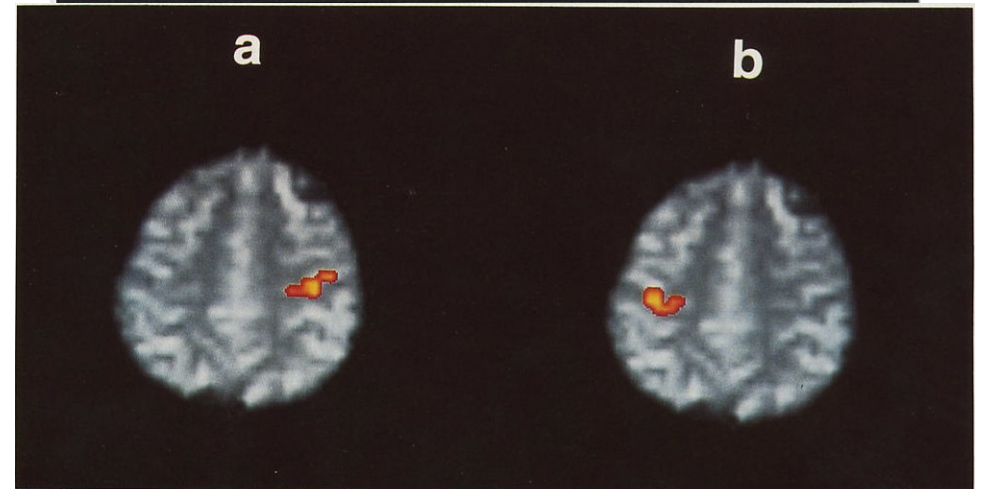
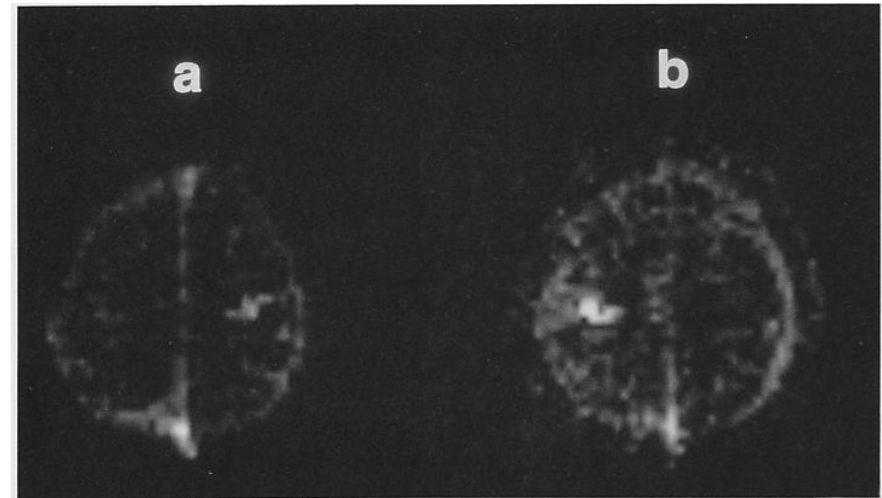
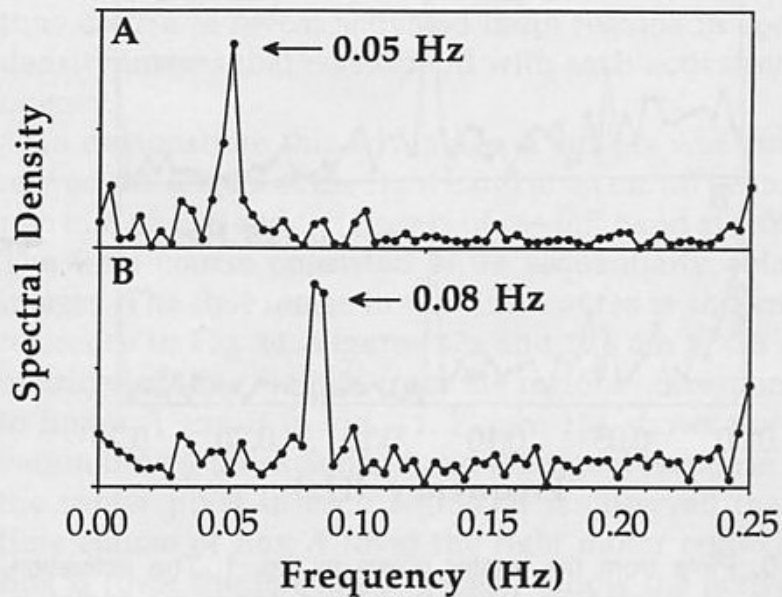
6. Orthogonal Block Design



7. Free Behavior Design.

a

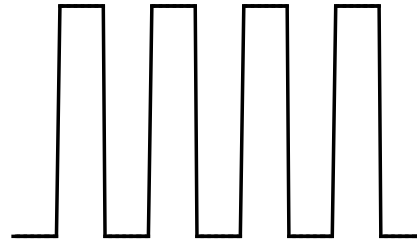
Tapping left and right fingers at two different “on/off” frequencies

**b**

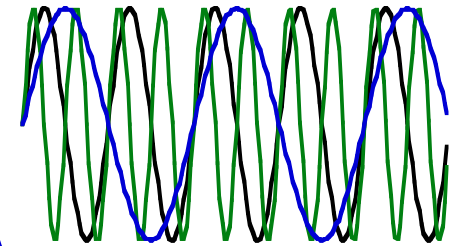
P. A. Bandettini, A. Jesmanowicz, E. C. Wong, J. S. Hyde, Processing strategies for time-course data sets in functional MRI of the human brain. *Magn. Reson. Med.* 30, 161-173 (1993).

Neuronal Activation Input Strategies

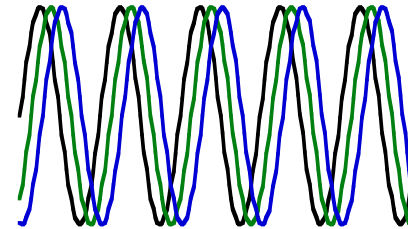
1. Block Design



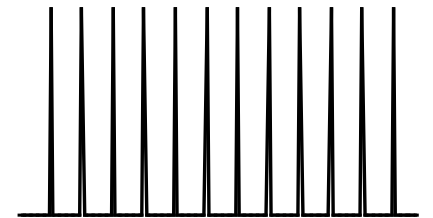
2. Frequency Encoding



3. Phase Encoding

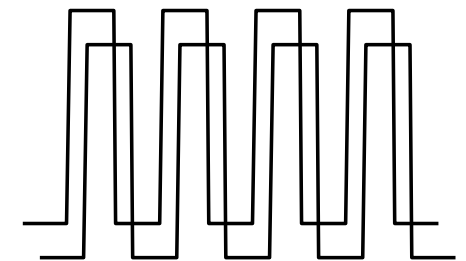


4. Event-Related

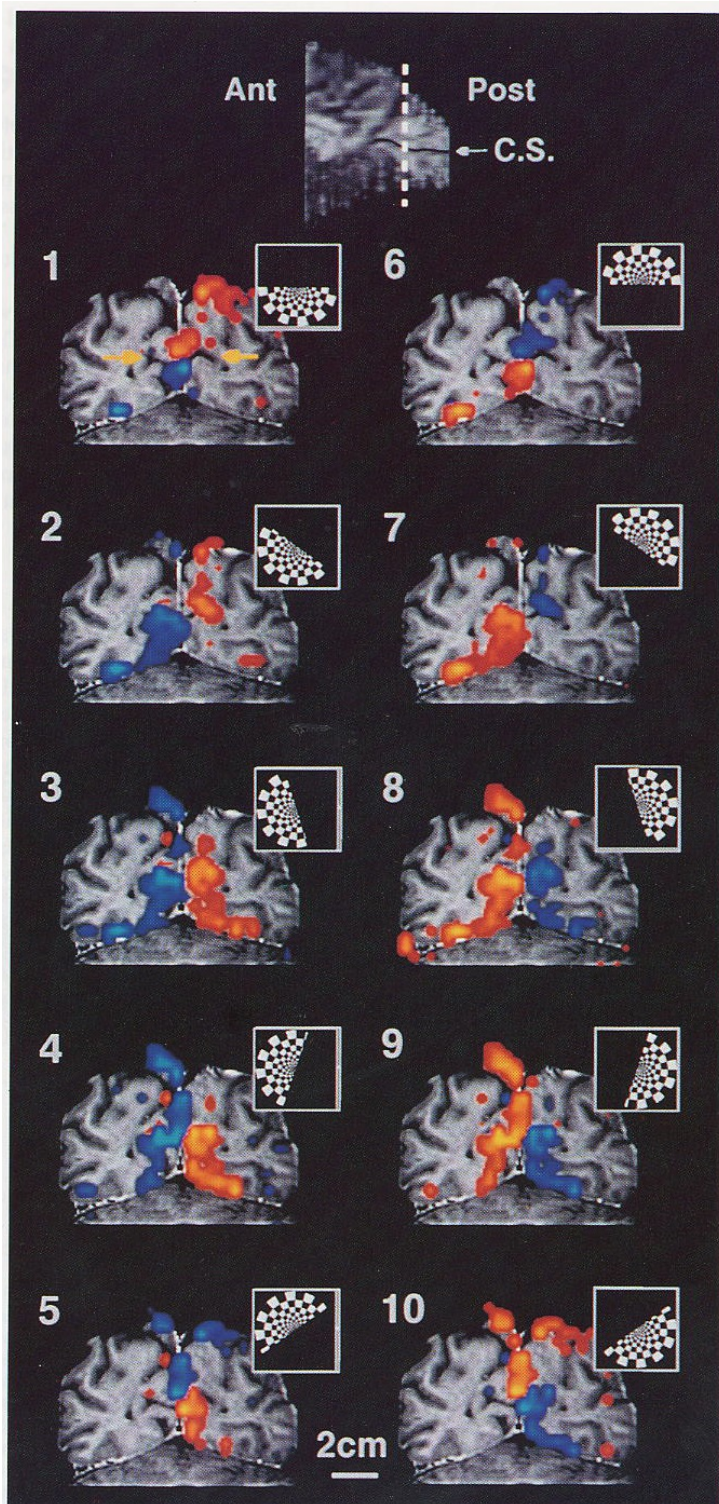


5. fMRI adaptation

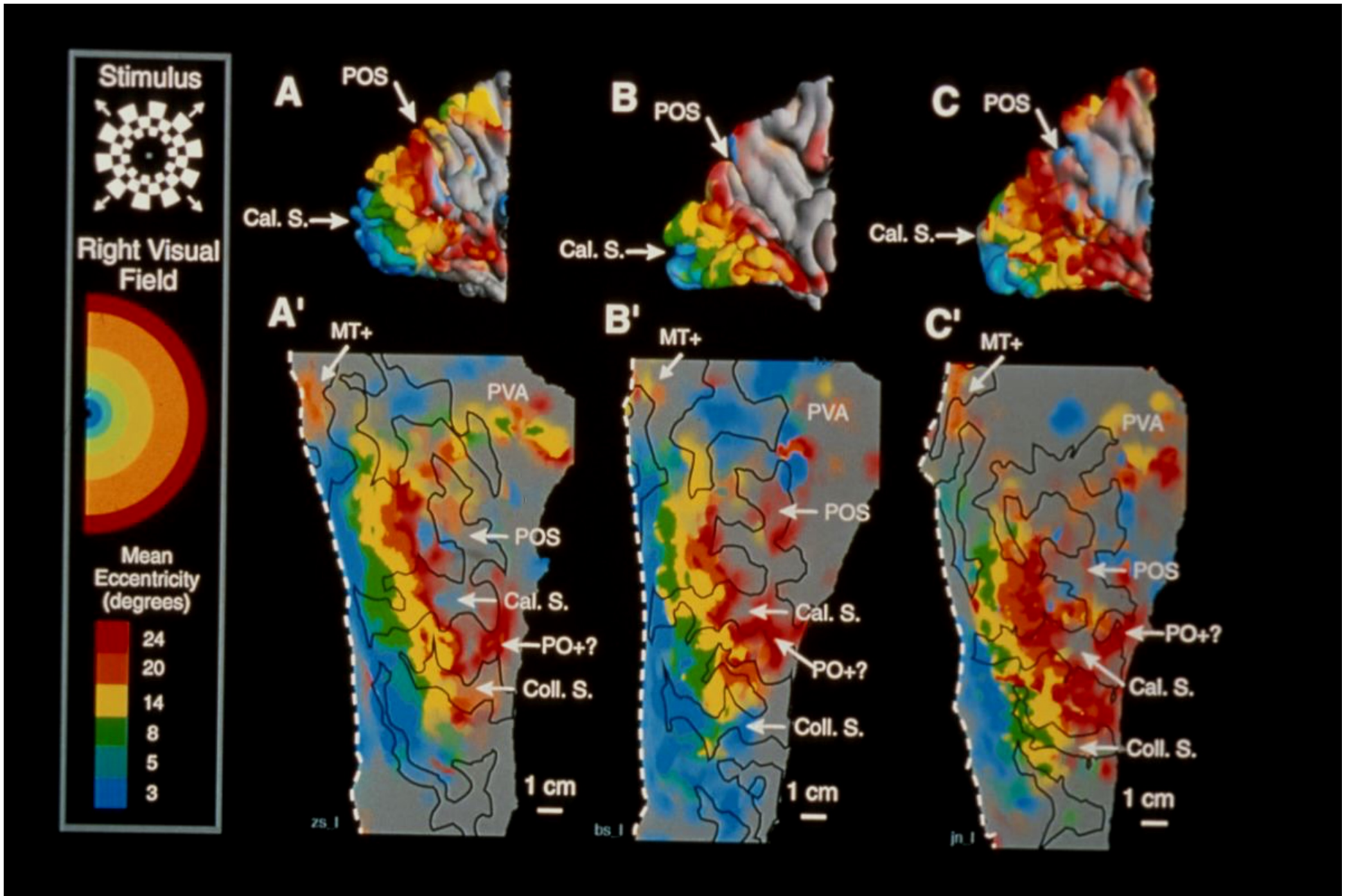
6. Orthogonal Block Design



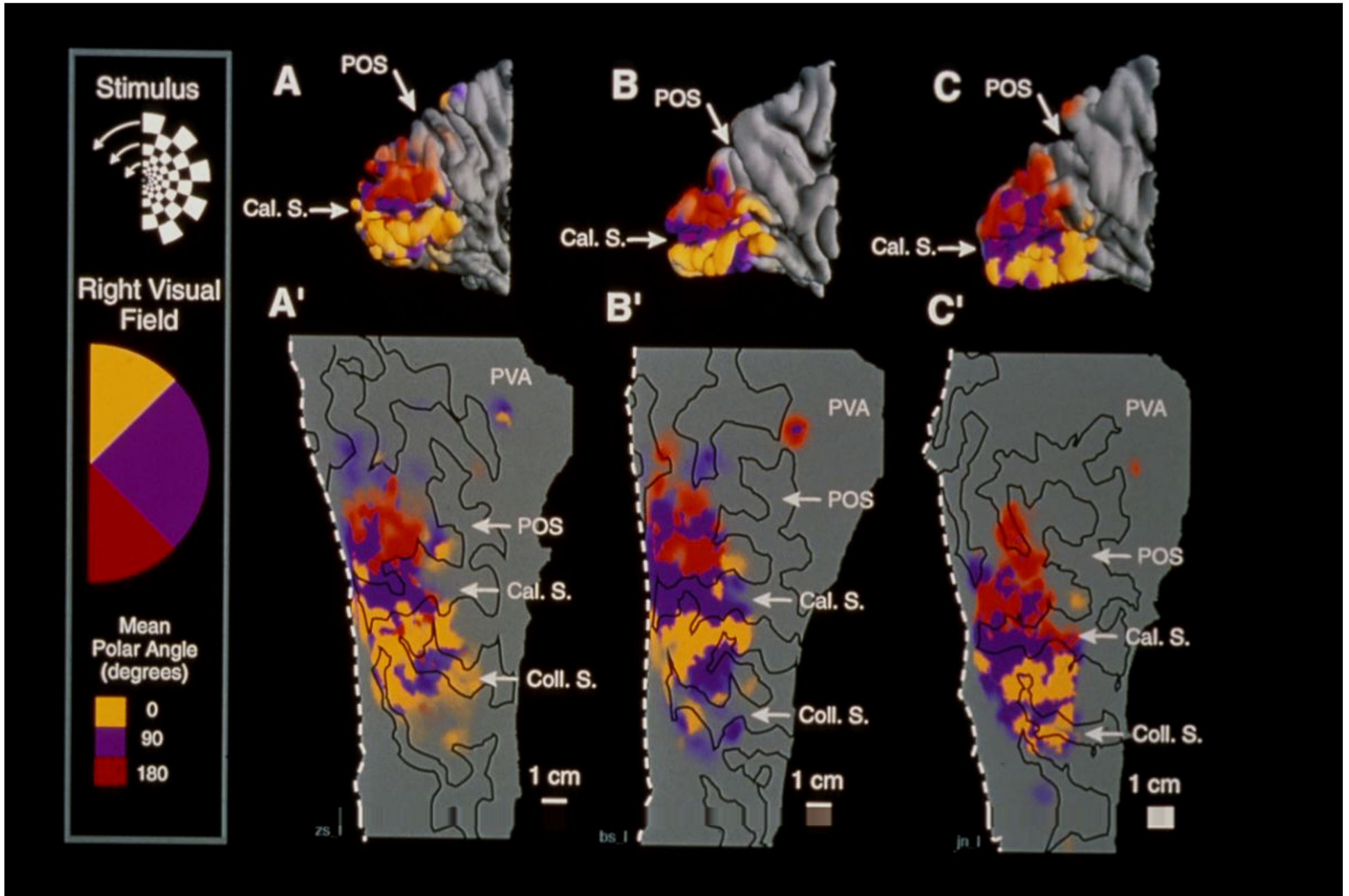
7. Free Behavior Design.



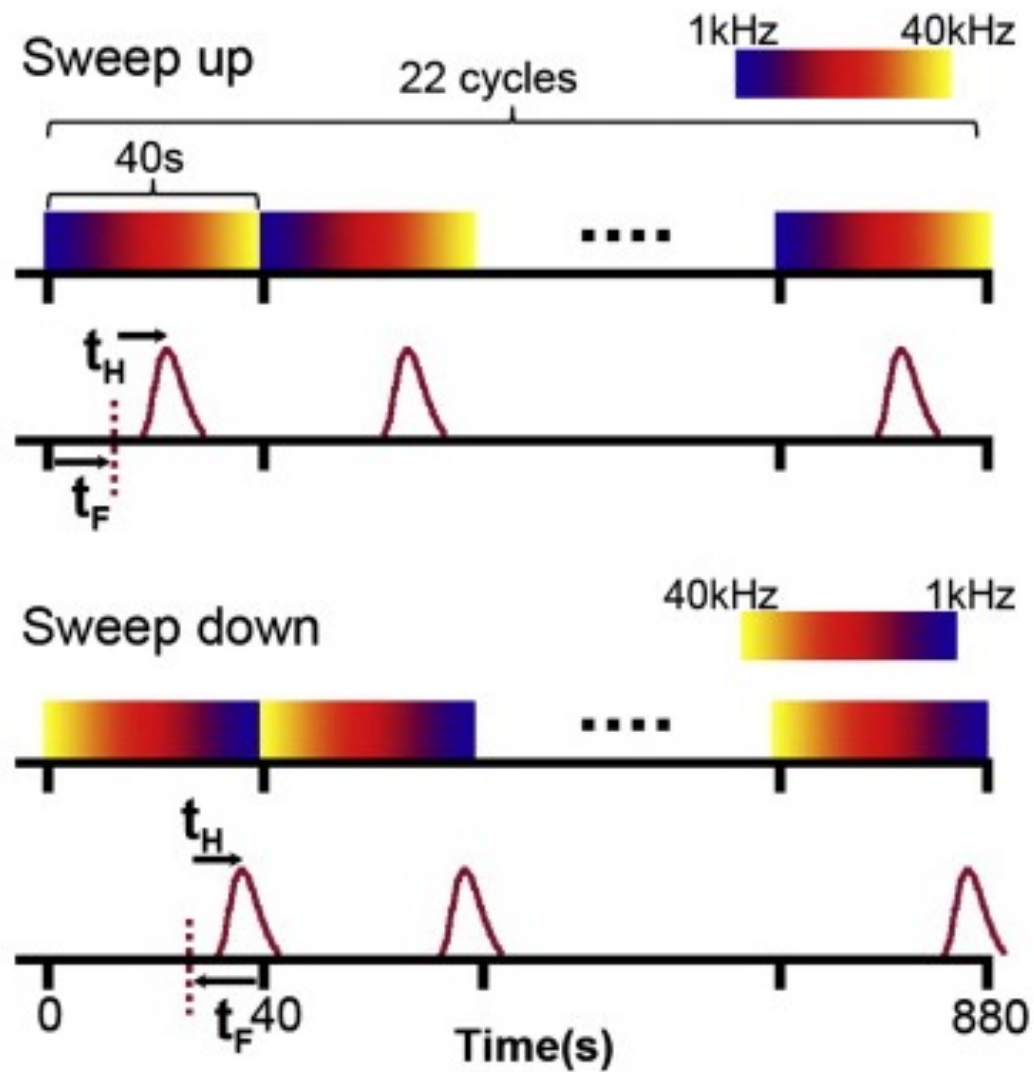
E. A. DeYoe, P. A. Bandettini, J. Nietz, D. Miller, P. Winas, Functional magnetic resonance imaging (fMRI) of the human brain. *J. Neuroscience Methods* 54, 171-187 (1994).



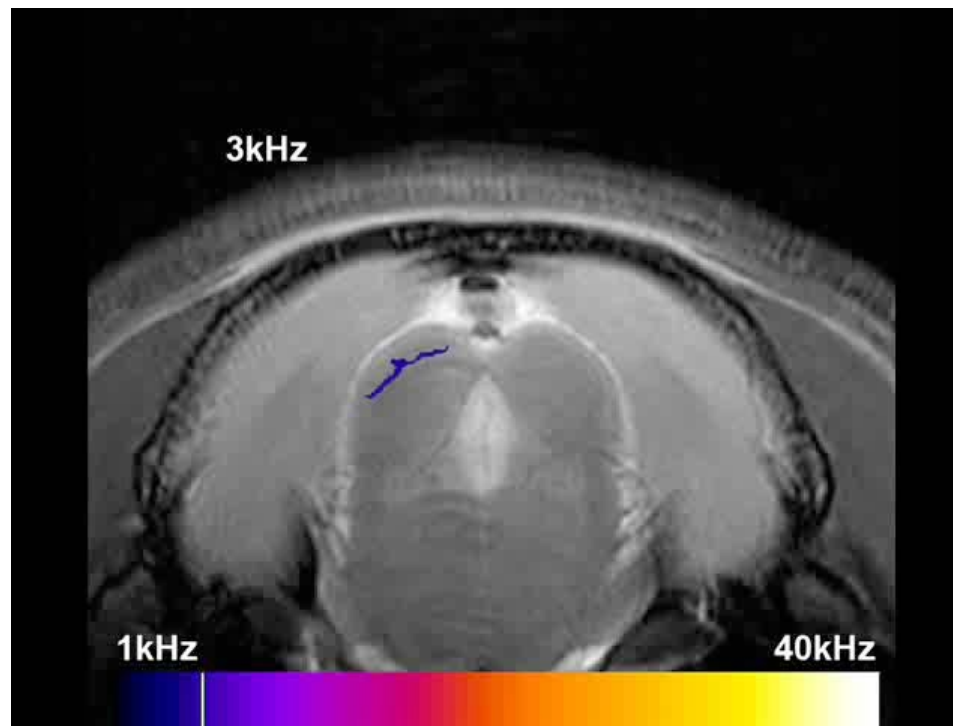
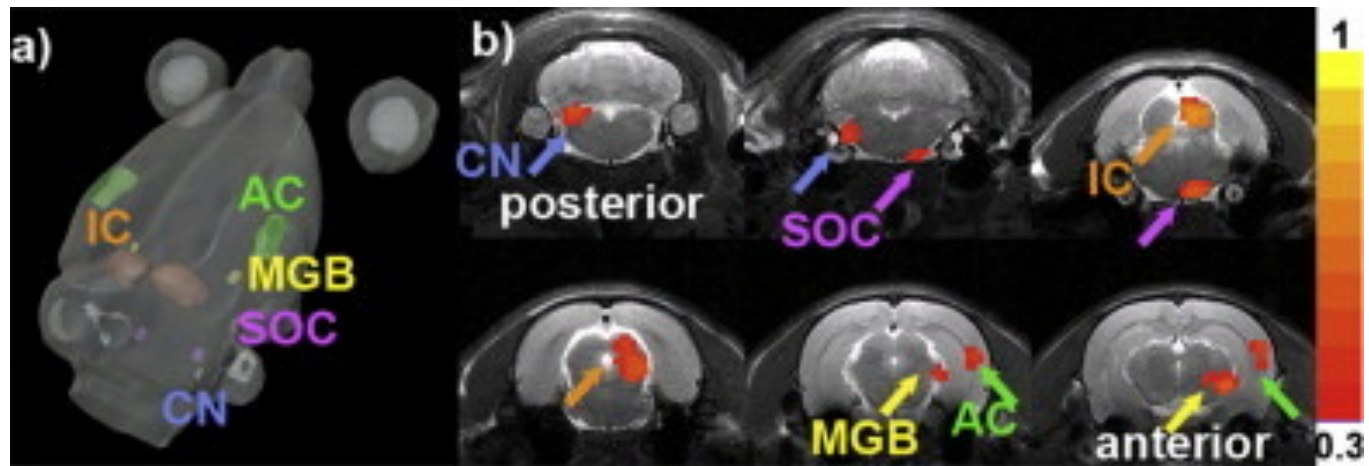
E. A. DeYoe, G. Carman, P. Bandettini, G. S., W. J., R. Cox, D. Miller, J. Neitz, Mapping striate and extrastriate visual areas in human cerebral cortex. *Proc. Nat'l. Acad. Sci.* 93, 2282-2386 (1996).



E. A. DeYoe, G. Carman, P. Bandettini, G. S., W. J., R. Cox, D. Miller, J. Neitz, Mapping striate and extrastriate visual areas in human cerebral cortex. *Proc. Nat'l. Acad. Sci.* 93, 2282-2386 (1996).

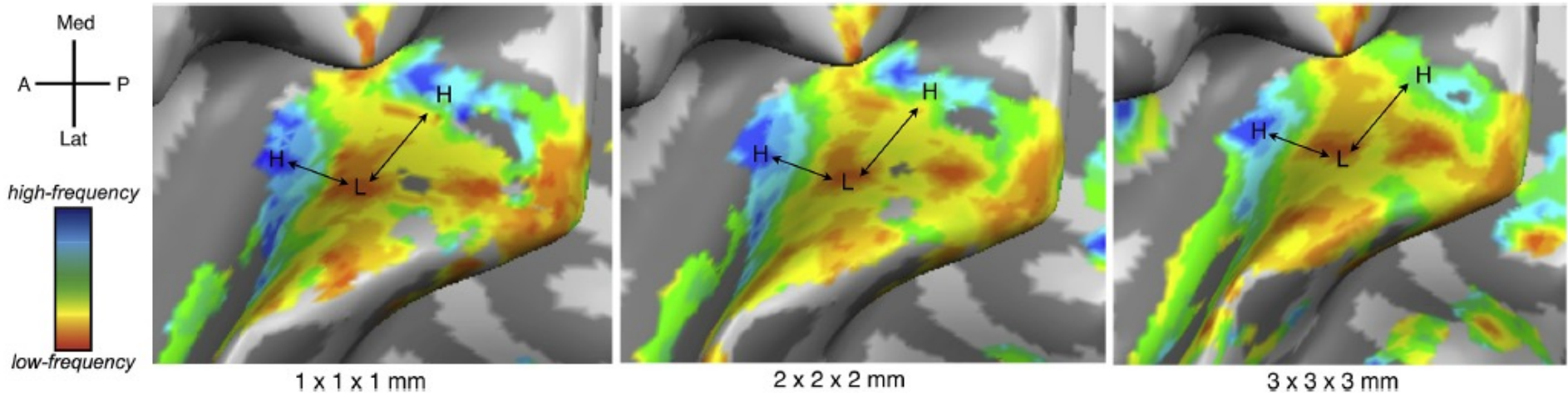
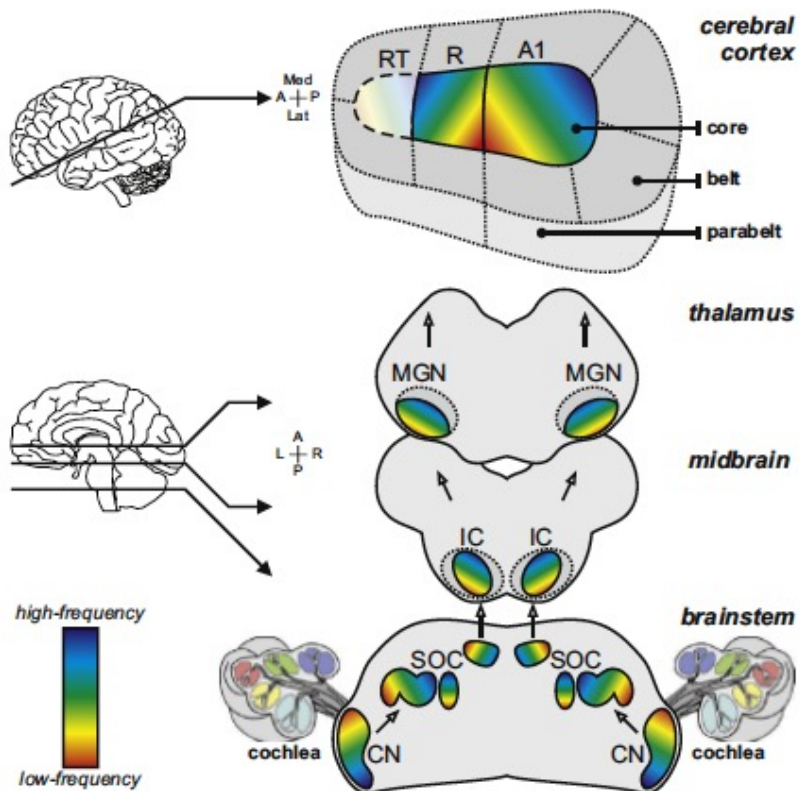


High fidelity tonotopic mapping using swept source functional magnetic resonance imaging, MM Cheung et al. NeuroImage Volume 61, Issue 4, 16 July 2012, Pages 978-986

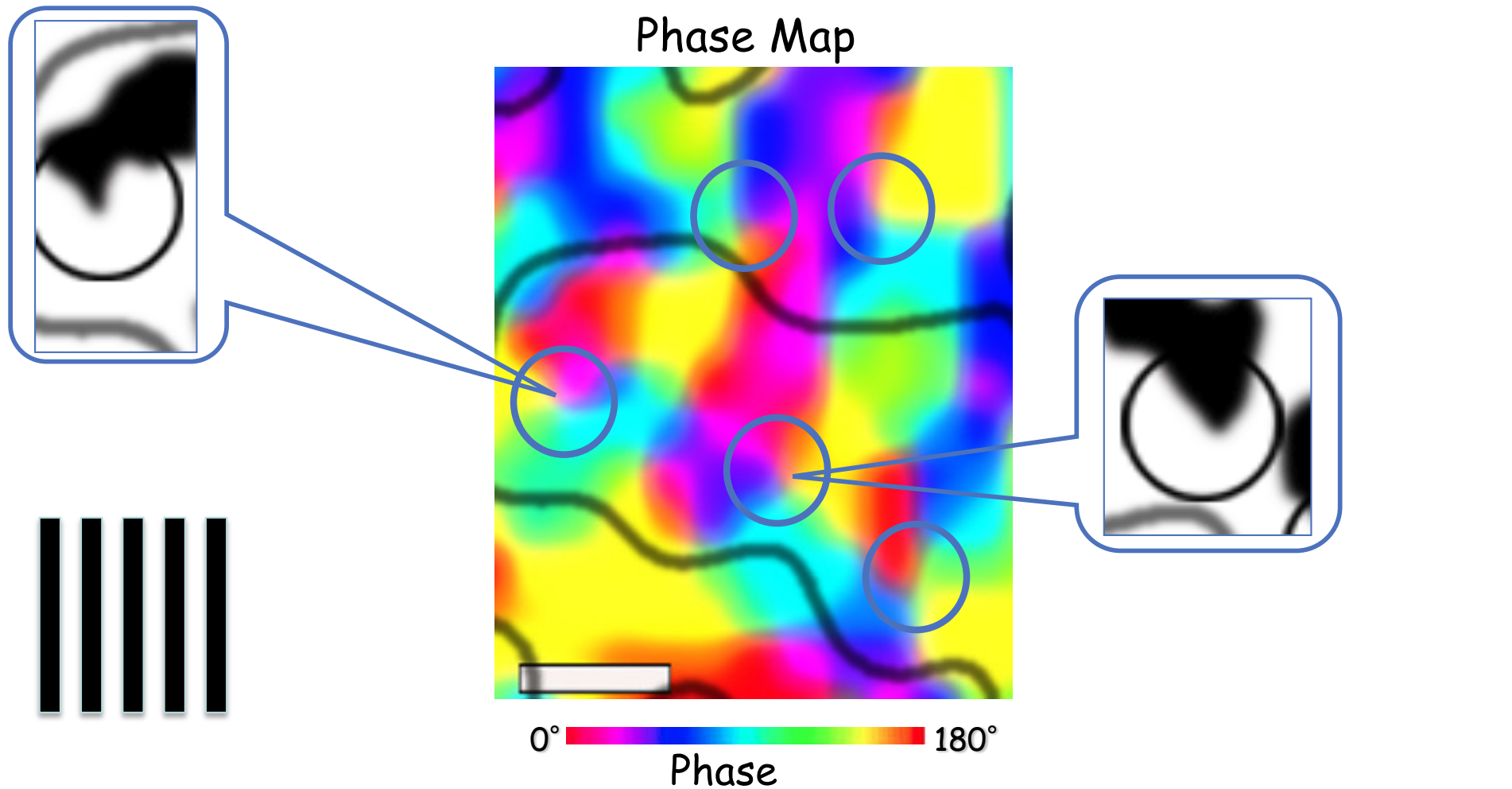


High fidelity tonotopic mapping using swept source functional magnetic resonance imaging, MM Cheung et al. NeuroImage Volume 61, Issue 4, 16 July 2012, Pages 978-986

Tonotopic mapping of human auditory cortex
 Melissa Saenz, Dave R.M. Langers,
 Hearing Research, 307, 42-52
 (2014)



Orientation Columns in Human V1 as Revealed by fMRI at 7T

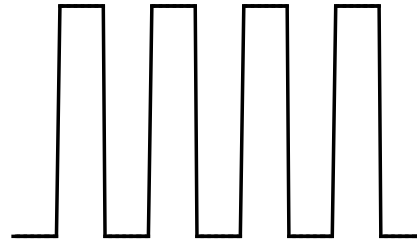


Scalebar = 0.5 mm

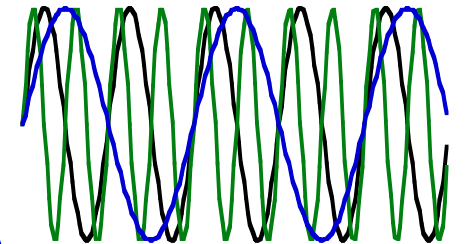
High-field fMRI unveils orientation columns in humans,
E. Yacoub, N. Harel, K. Ugurbil, **PNAS**, vol 105, pp. 10607-10612

Neuronal Activation Input Strategies

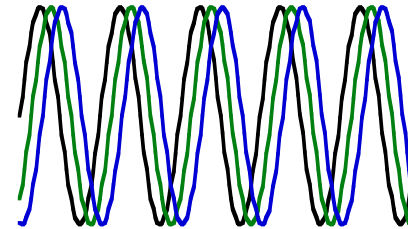
1. Block Design



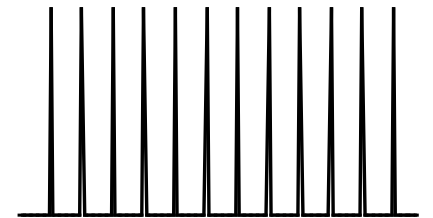
2. Frequency Encoding



3. Phase Encoding

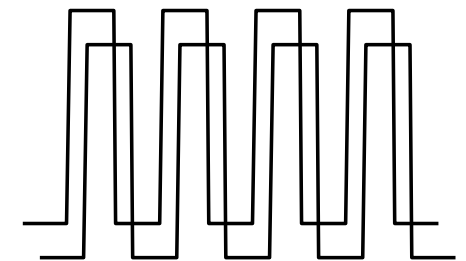


4. Event-Related



5. fMRI adaptation

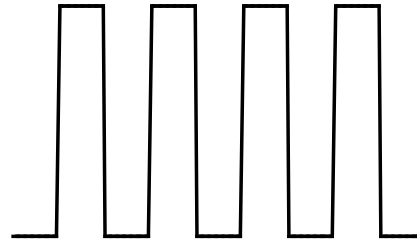
6. Orthogonal Block Design



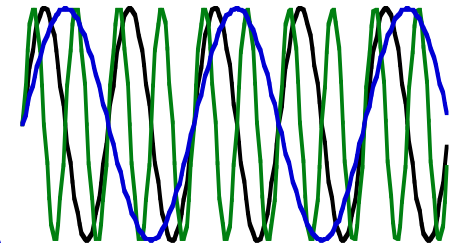
7. Free Behavior Design.

Neuronal Activation Input Strategies

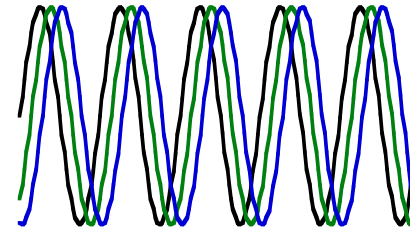
1. Block Design



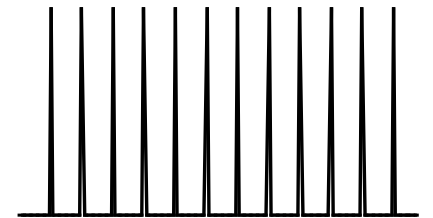
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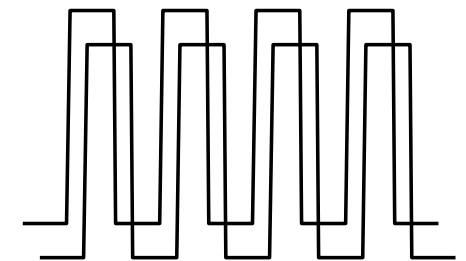


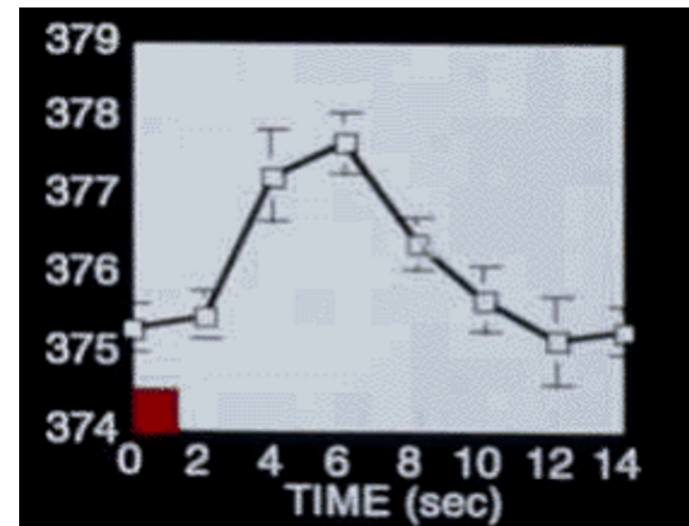
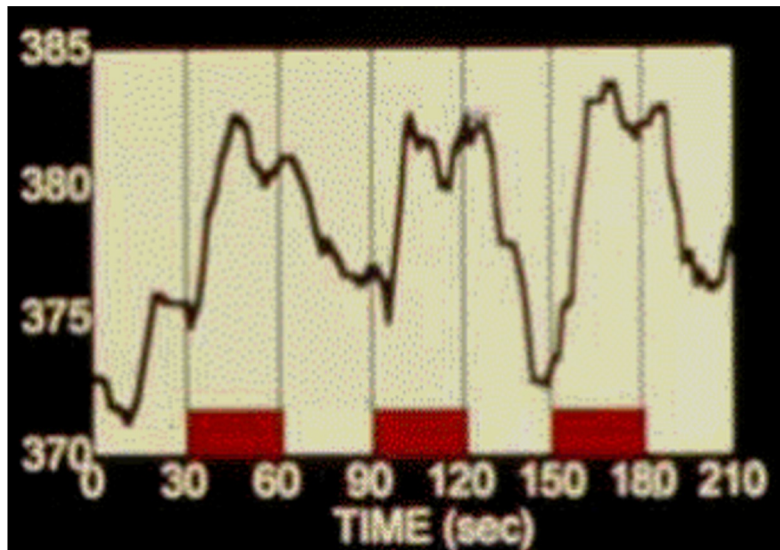
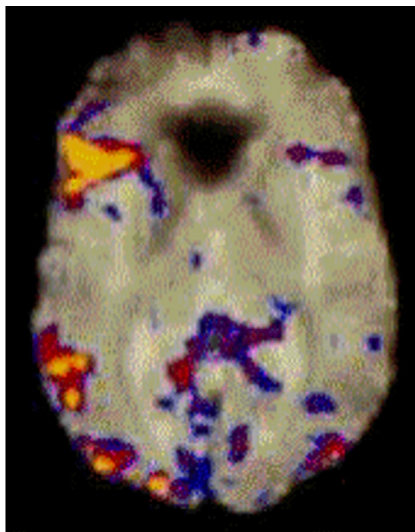
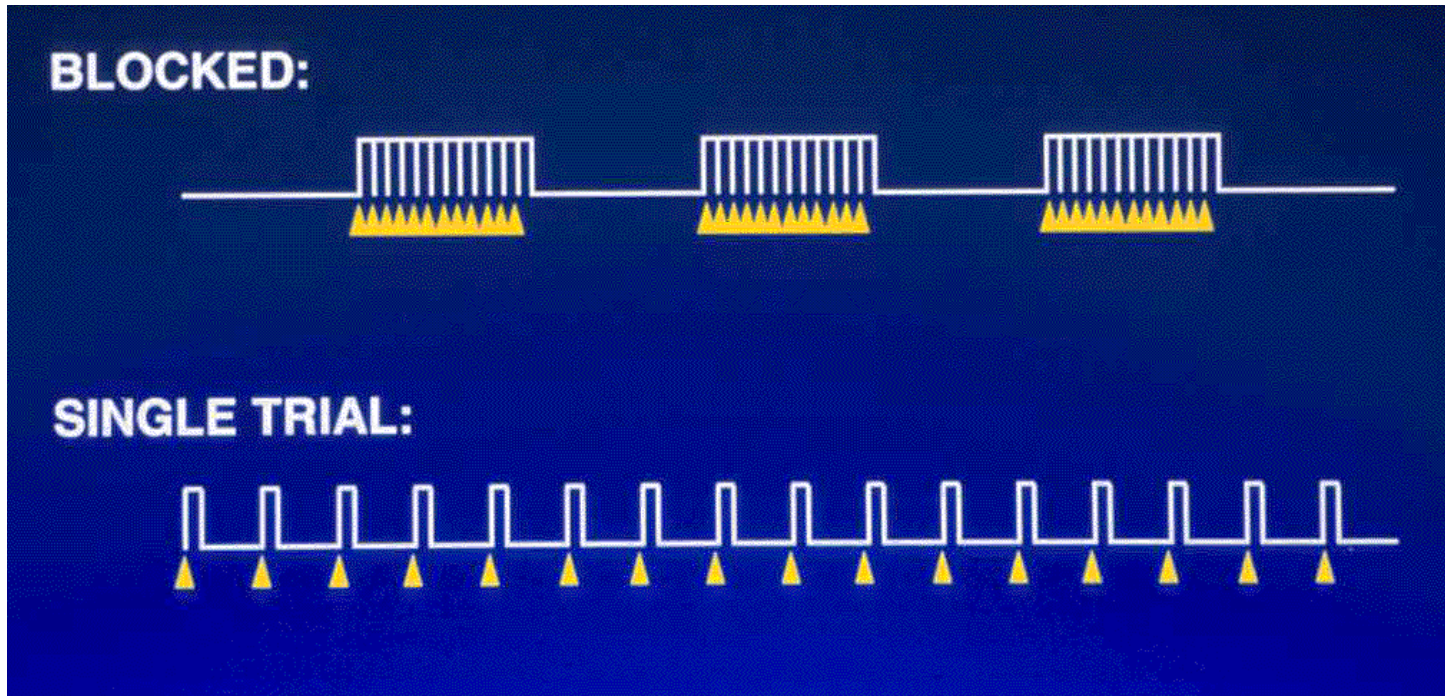
4. Event-Related



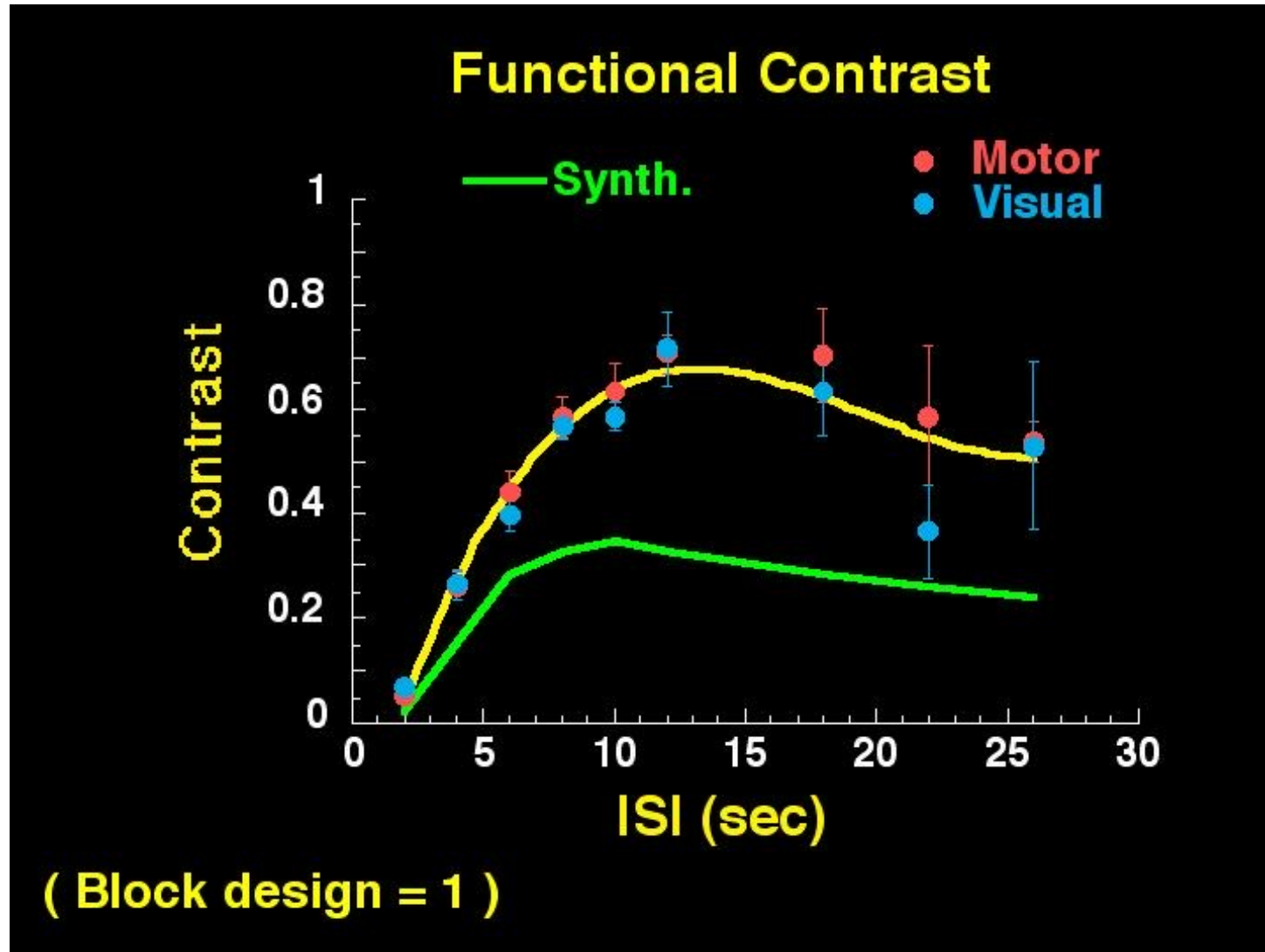
5. Orthogonal Block Design

6. Free Behavior Design.





R. L. Buckner, P. A. Bandettini, K. M. O'Craven, R. L. Savoy, S. E. Peterson, M. E. Raichle, T. L. Brady, B. R. Rosen, fMRI detection and time course of distributed cortical activations during single trials of a cognitive task. *Proc. Nat'l. Acad. Sci. USA* 93, 14878-14883 (1996).



P. A. Bandettini, R. W. Cox. Functional contrast in constant interstimulus interval event - related fMRI: theory and experiment. *Magn. Reson. Med.* 43: 540-548 (2000).

Contrast to Noise Images

(ISI, SD)

20, 20

12, 2

10, 2

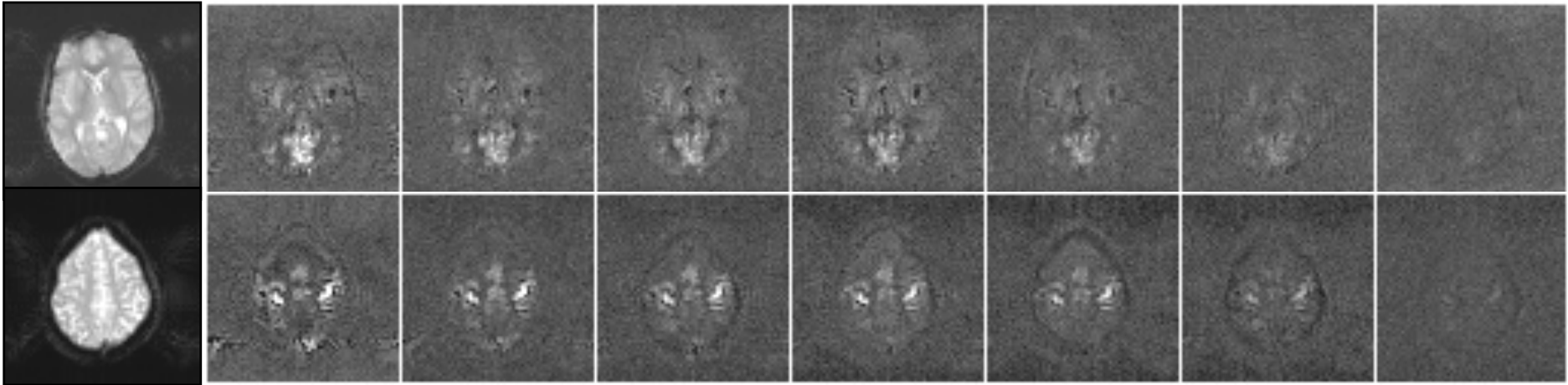
8, 2

6, 2

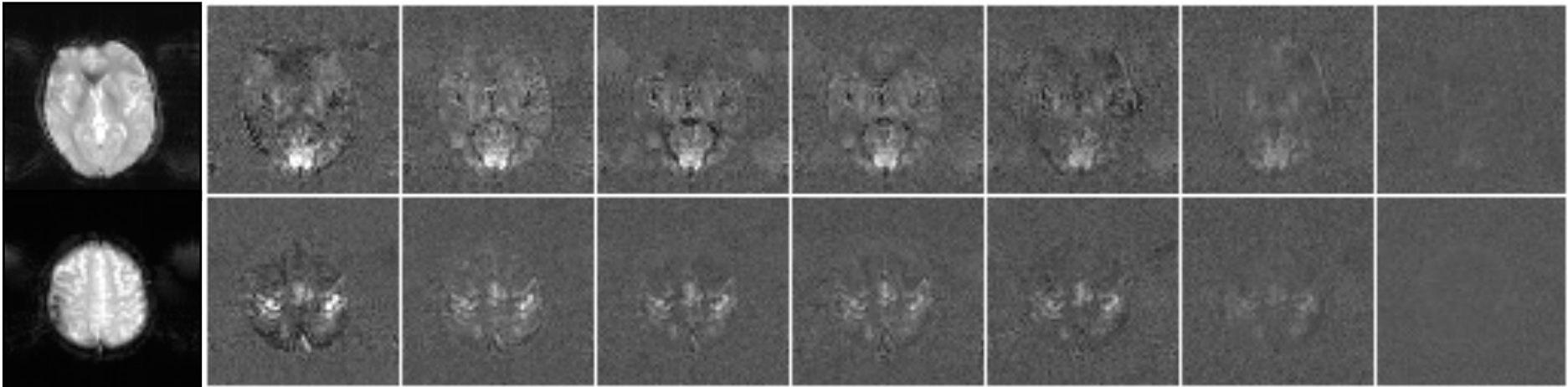
4, 2

2, 2

S1



S2

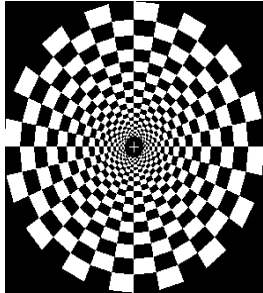


P. A. Bandettini, R. W. Cox. Functional contrast in constant interstimulus interval event - related fMRI: theory and experiment. *Magn. Reson. Med.* 43: 540-548 (2000).

Selective Averaging of Rapidly Presented Individual Trials Using fMRI

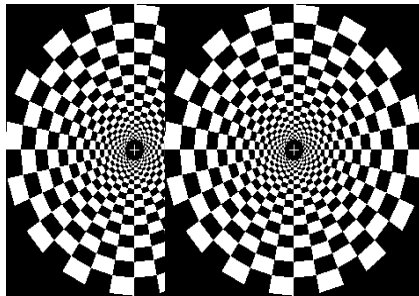
Anders M. Dale* and Randy L. Buckner

*Massachusetts General Hospital Nuclear Magnetic Resonance Center and the Department of Radiology,
Harvard Medical School, Boston, Massachusetts 02129*



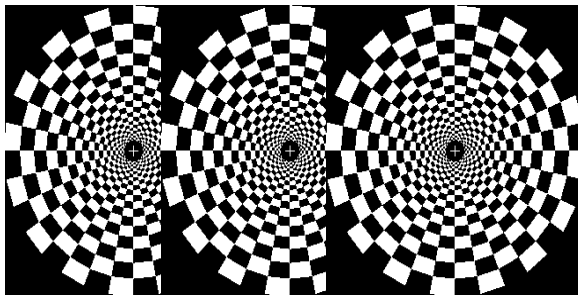
0 sec

20 sec



0 sec 2 sec

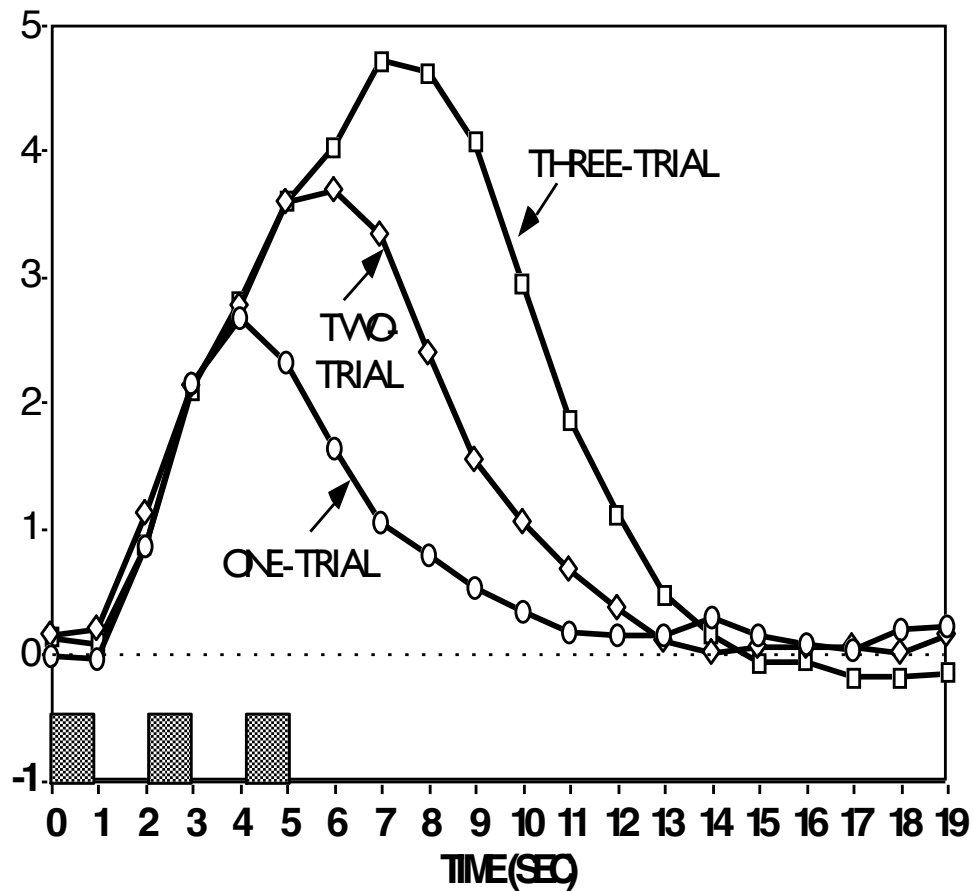
20 sec



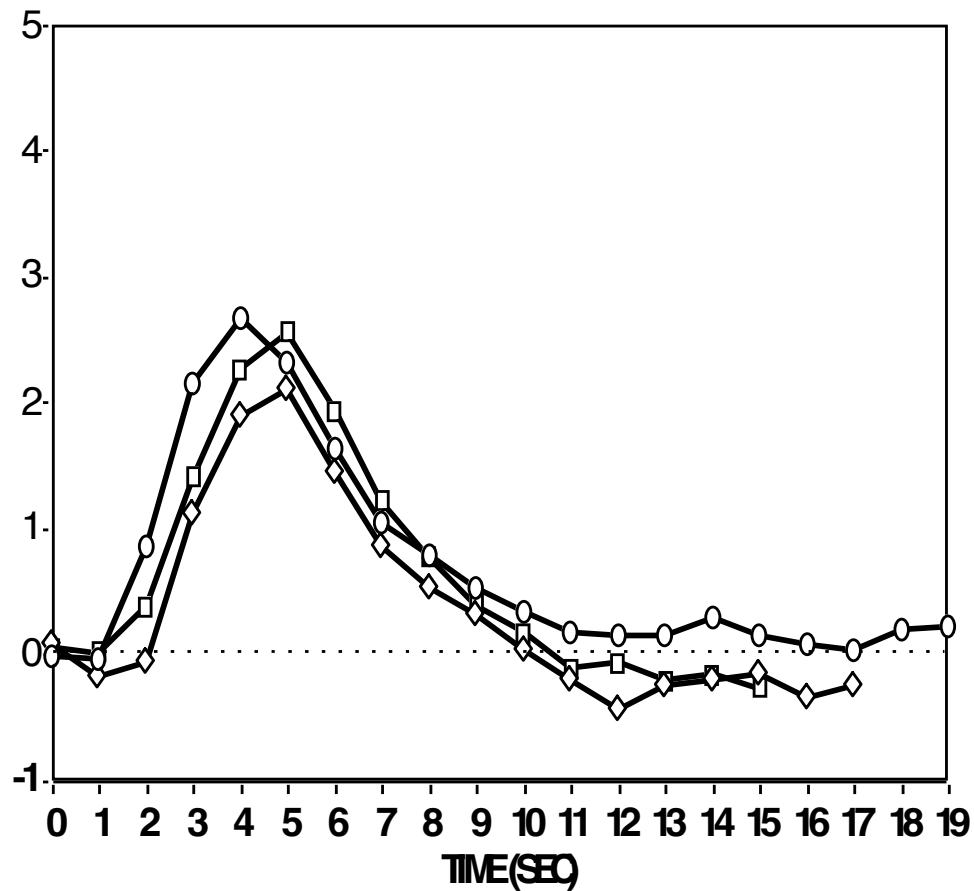
0 sec 2 sec 4 sec

20 sec

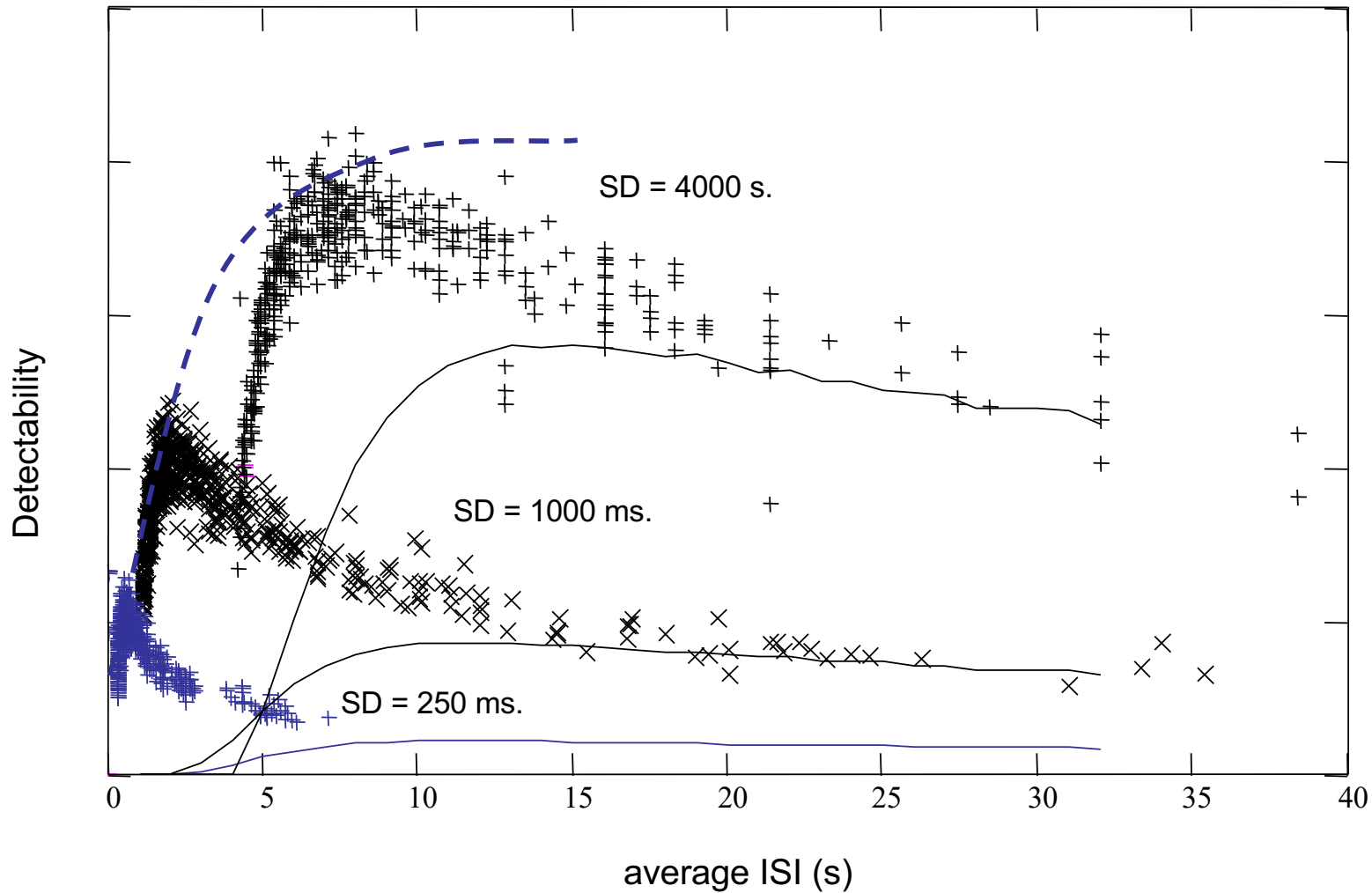
RAW DATA



ESTIMATED RESPONSES

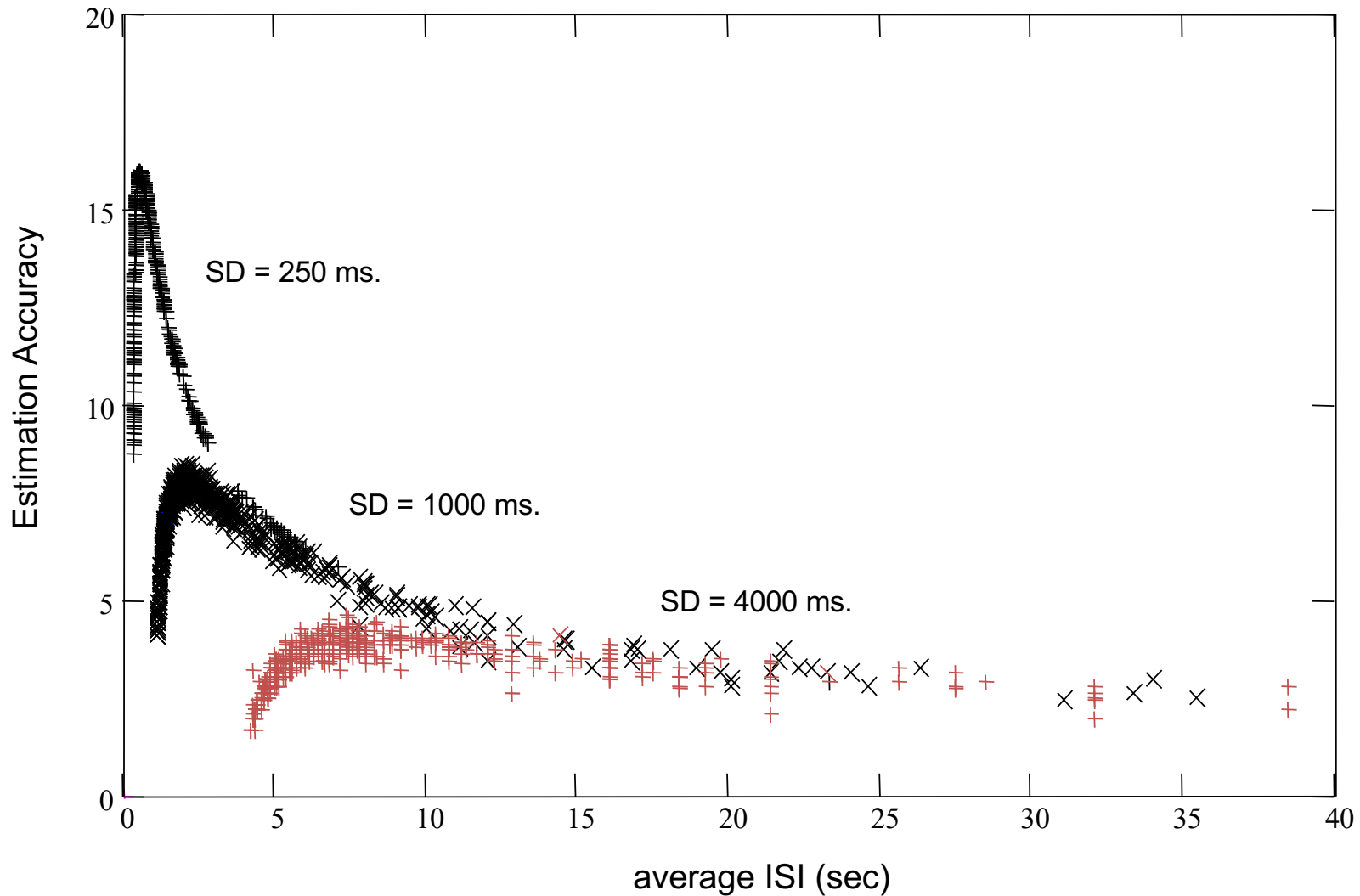


Detectability vs. Average ISI



R. M. Birn, R. W. Cox, P. A. Bandettini, Detection versus estimation in Event-Related fMRI: choosing the optimal stimulus timing. *NeuroImage* 15: 262-264, (2002).

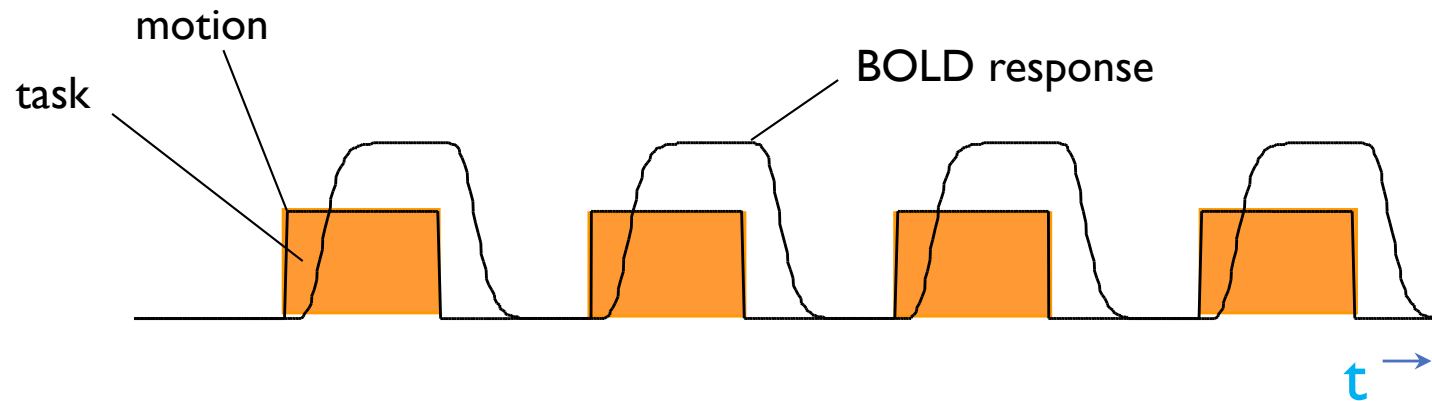
Estimation accuracy vs. average ISI



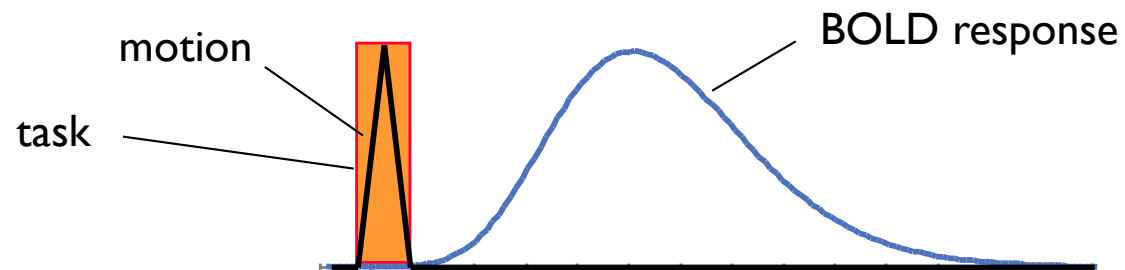
R. M. Birn, R. W. Cox, P. A. Bandettini, Detection versus estimation in Event-Related fMRI: choosing the optimal stimulus timing. *NeuroImage* 15: 262-264, (2002).

fMRI during tasks that involve brief motion

Blocked Design

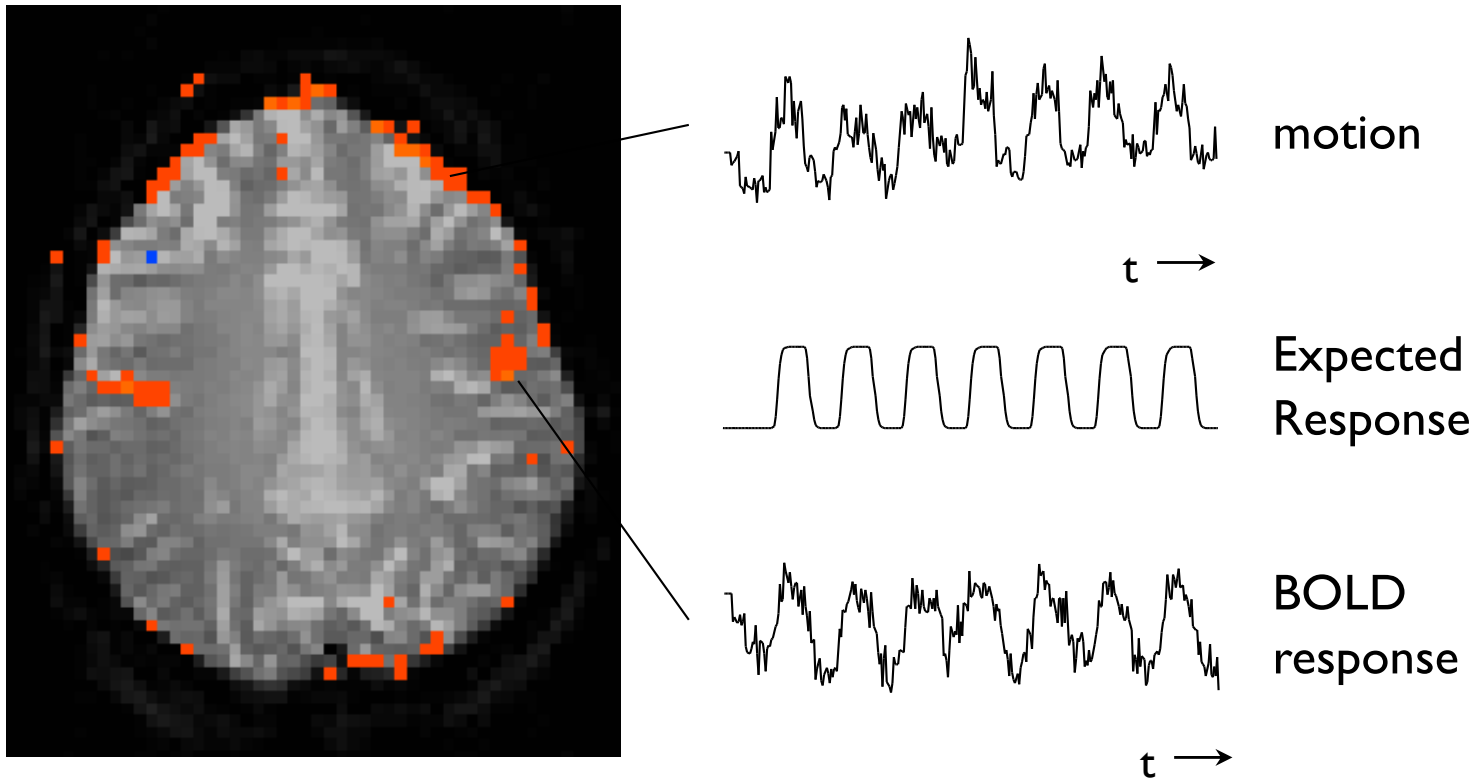


Event-Related Design



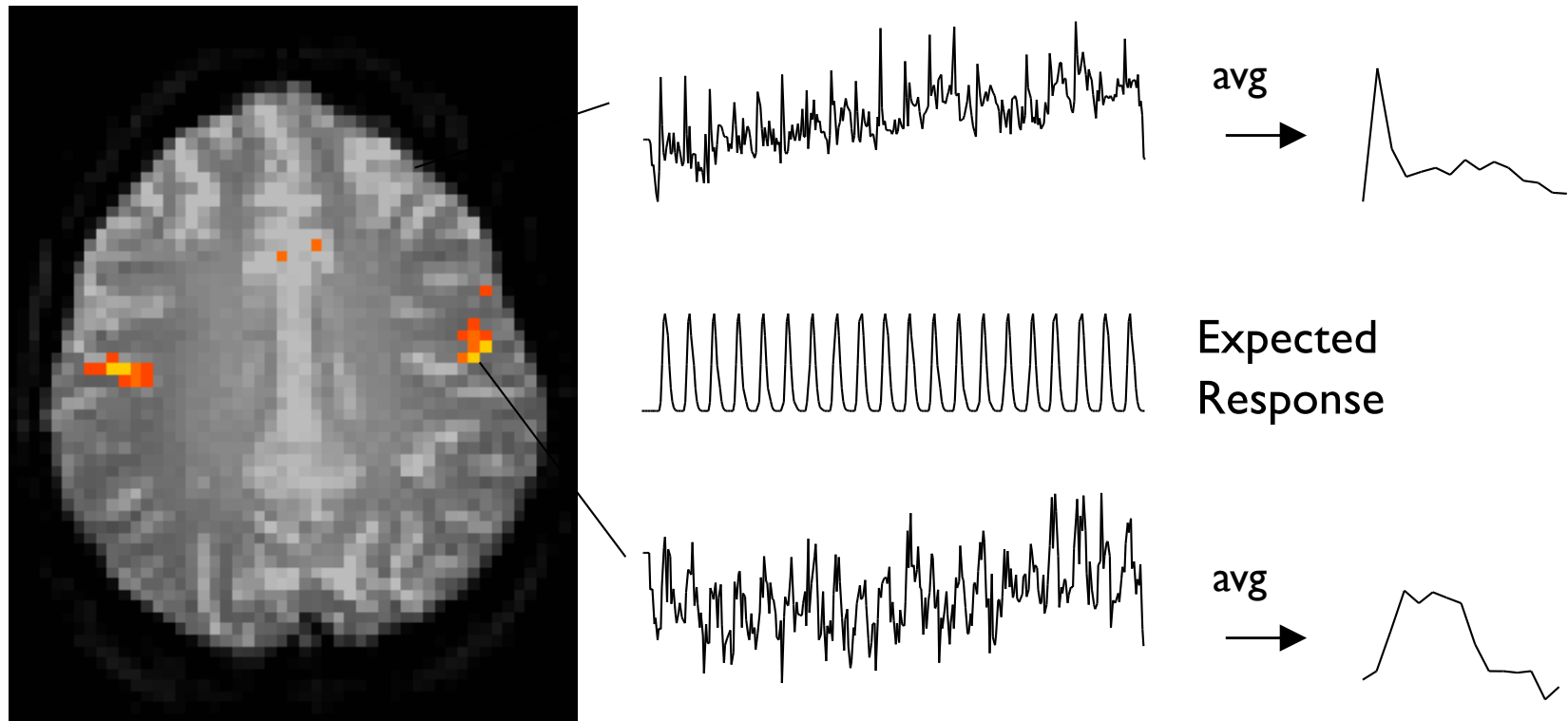
R. M. Birn, P. A. Bandettini, R. W. Cox, R. Shaker, Event - related fMRI of tasks involving brief motion. *Human Brain Mapping* 7: 106-114 (1999).

Speaking - Blocked Trial



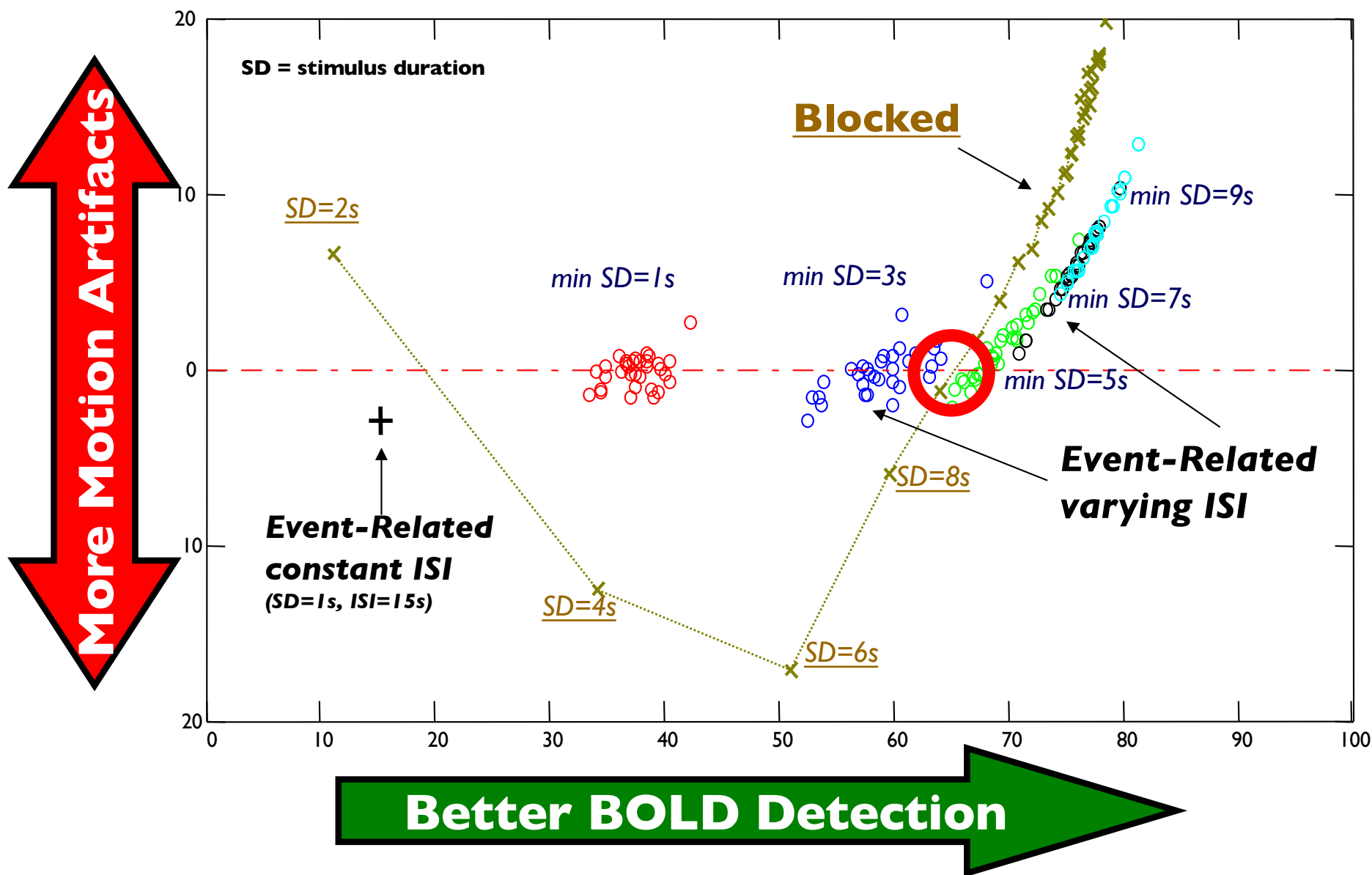
R. M. Birn, P. A. Bandettini, R. W. Cox, R. Shaker, Event - related fMRI of tasks involving brief motion. *Human Brain Mapping* 7: 106-114 (1999).

Speaking - ER-fMRI

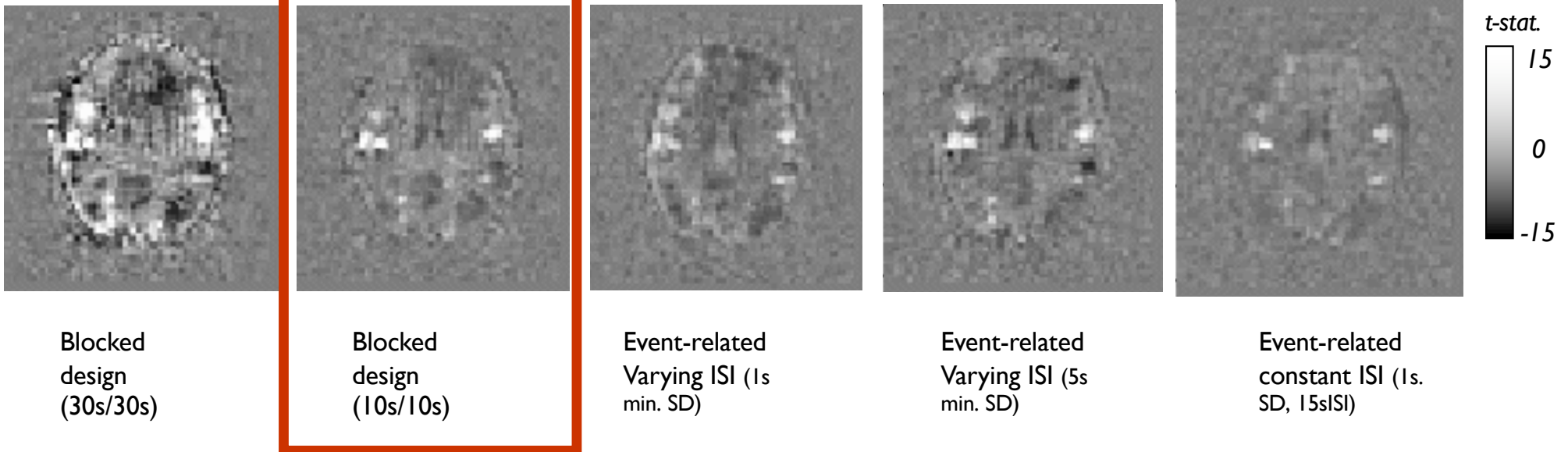


R. M. Birn, P. A. Bandettini, R. W. Cox, R. Shaker, Event - related fMRI of tasks involving brief motion. *Human Brain Mapping* 7: 106-114 (1999).

Overt Responses - Simulations



Overt Responses



Blocked design (30s/30s)

Blocked design (10s/10s)

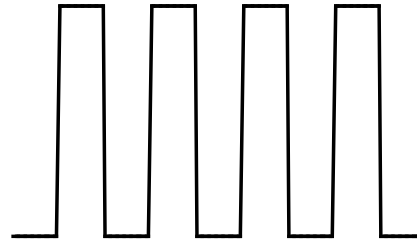
Event-related Varying ISI (1s min. SD)

Event-related Varying ISI (5s min. SD)

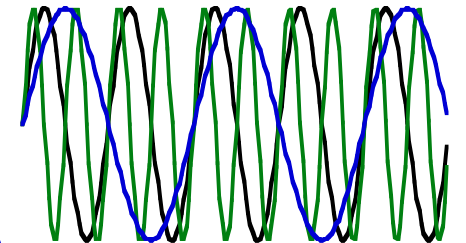
Event-related constant ISI (1s SD, 15s ISI)

Neuronal Activation Input Strategies

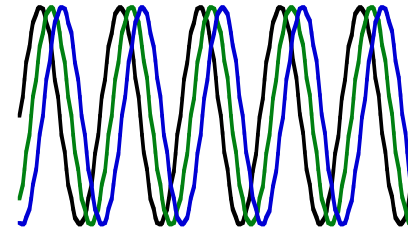
1. Block Design



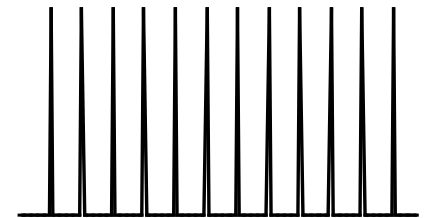
2. Frequency Encoding



3. Phase Encoding

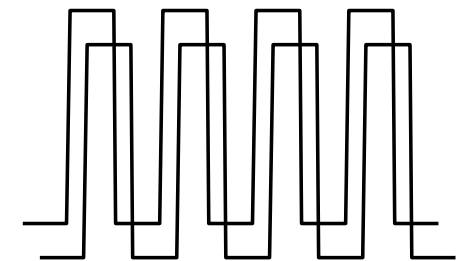


4. Event-Related



5. fMRI adaptation

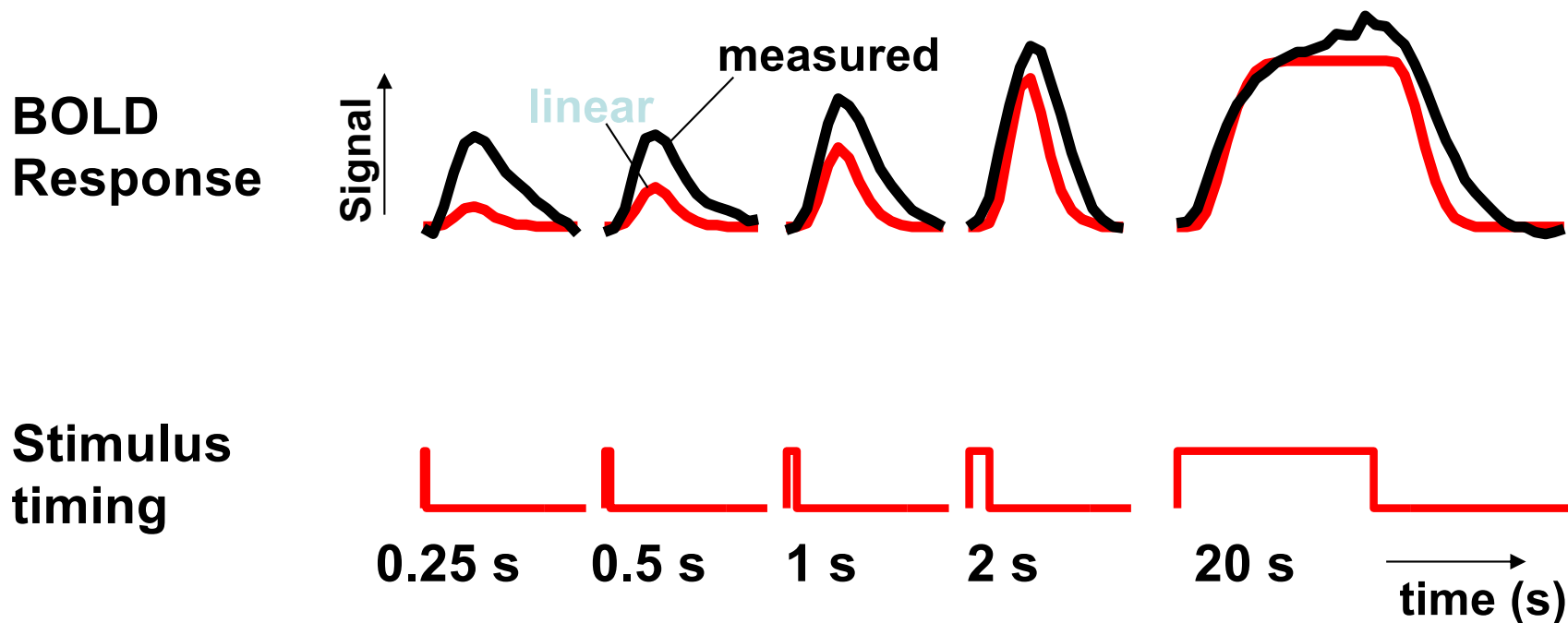
6. Orthogonal Block Design



7. Free Behavior Design.

Dynamic Nonlinearity Assessment

Different stimulus “ON” periods

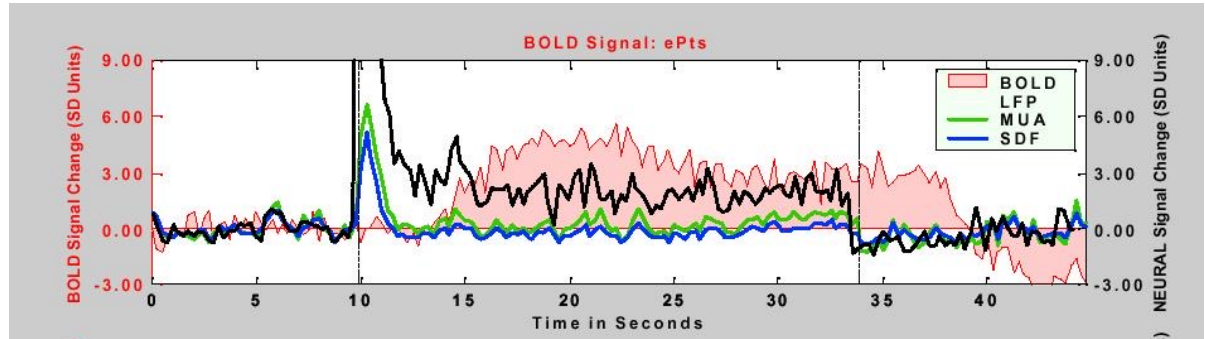


Brief stimuli produce larger responses than expected

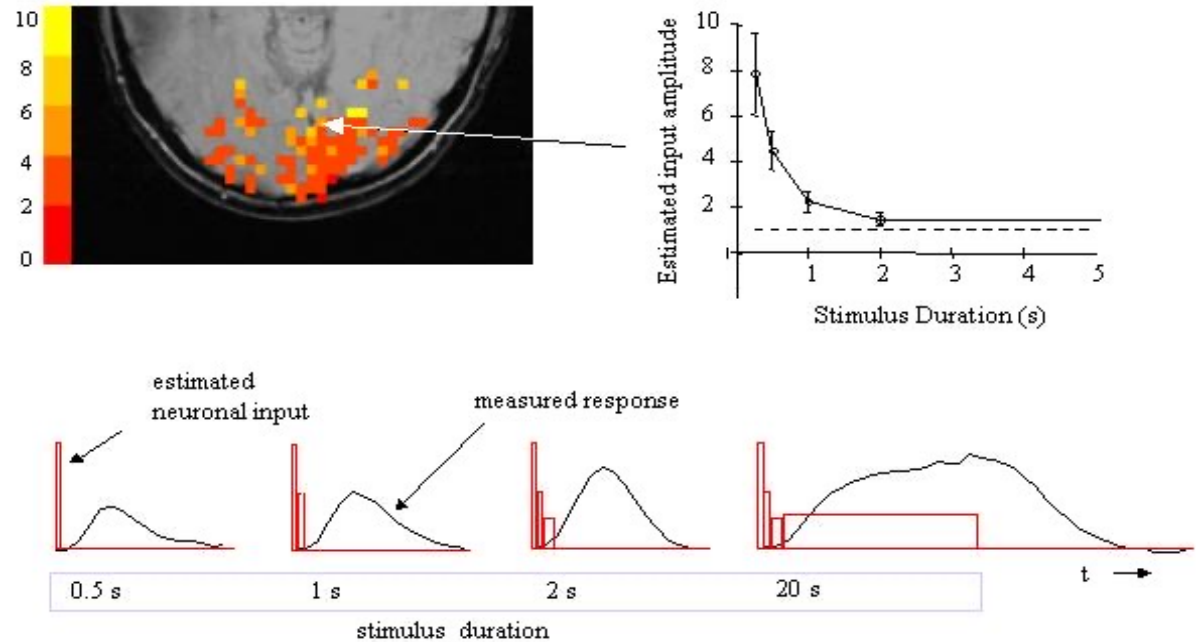
R. M. Birn, Z. Saad, P. A. Bandettini, (2001) “Spatial heterogeneity of the nonlinear dynamics in the fMRI BOLD response.” *NeuroImage*, 14: 817-826.

BOLD Correlation with Neuronal Activity

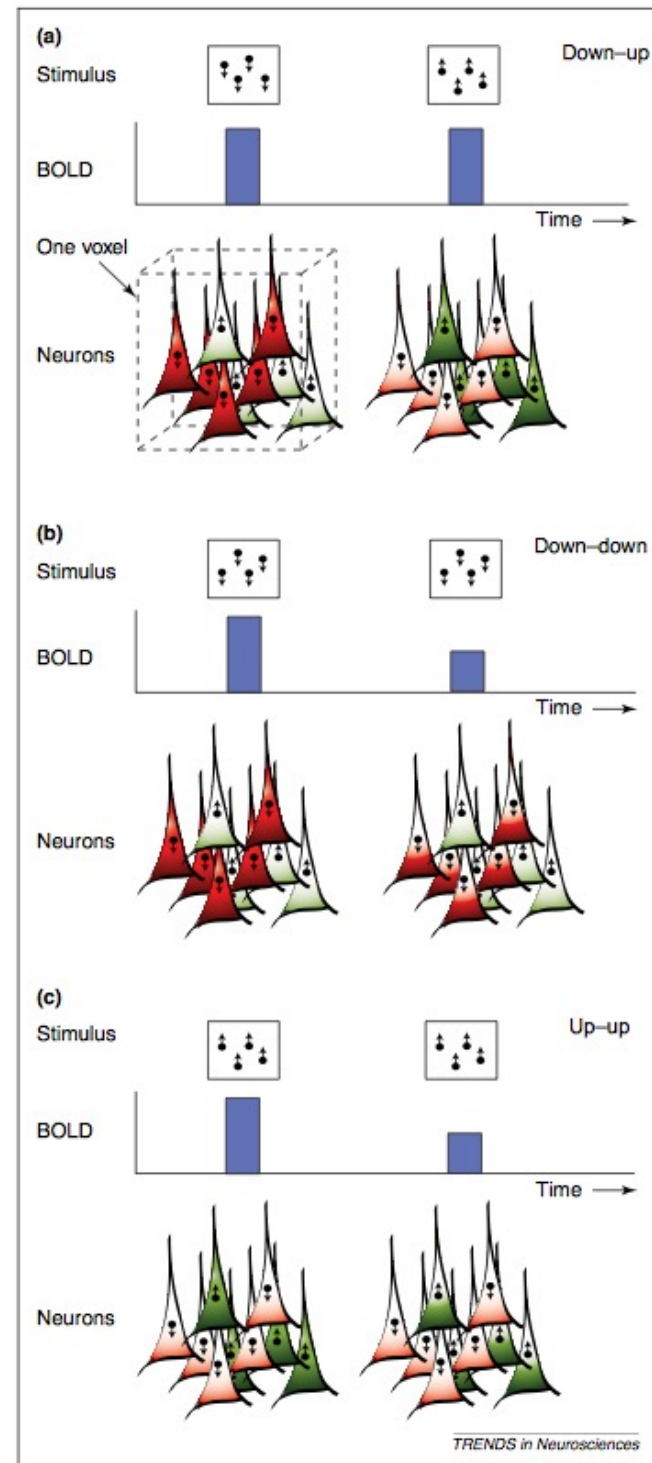
Logothetis et al. (2001)
“Neurophysiological investigation
of the basis of the fMRI signal”
Nature, 412, 150-157.

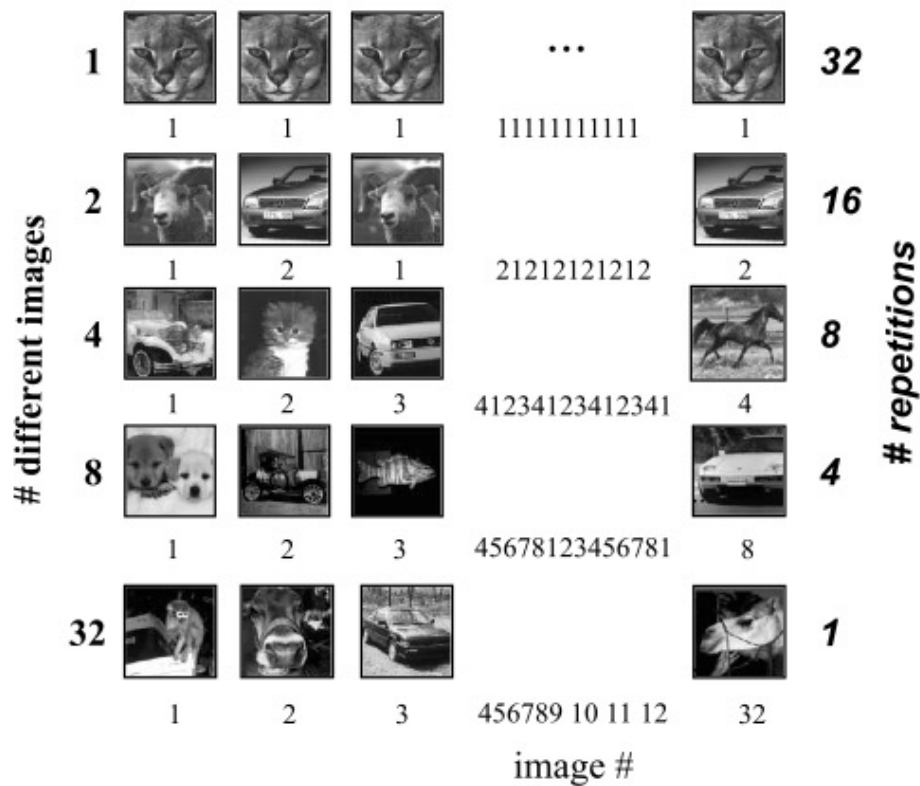


P. A. Bandettini and L. G. Ungerleider, (2001) “From neuron to BOLD: new connections.”
Nature Neuroscience, 4: 864-866.

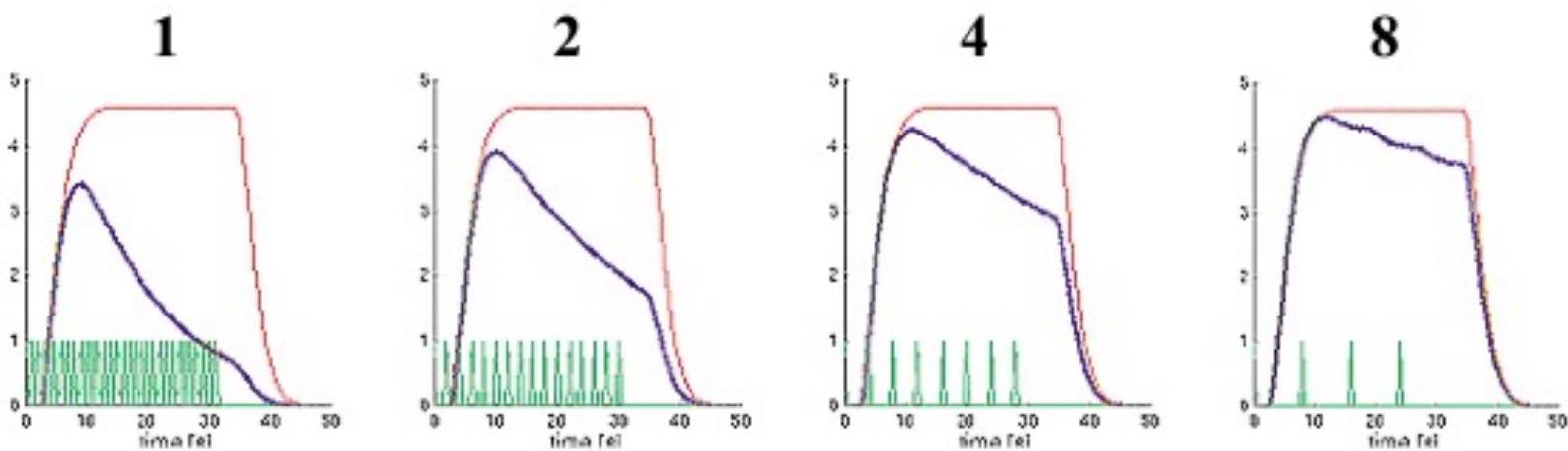


Adaptation: from single cells to BOLD signals, Bart Krekelberg, Geoffrey M. Boynton, and Richard J.A. van Wezel, Trends in Neurosciences, 29, 5, 2006



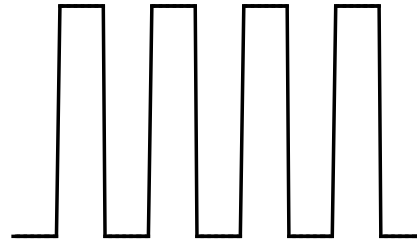


fMRI-adaptation: a tool for studying the functional properties of human cortical neurons Kalanit Grill-Spector, Rafael Malach, *Acta Psychologica*, 107 (2001), 293-321

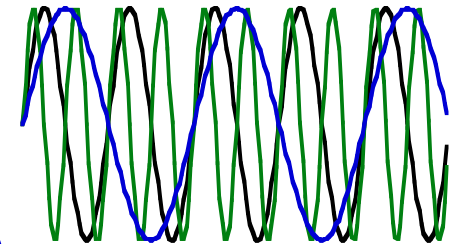


Neuronal Activation Input Strategies

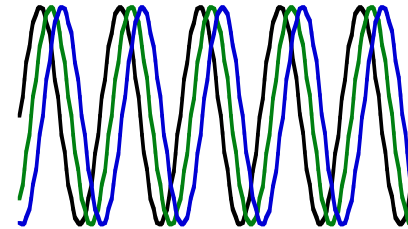
1. Block Design



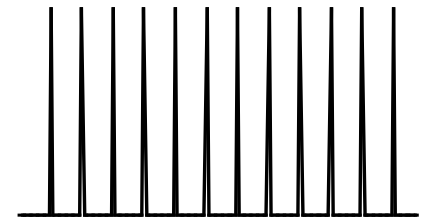
2. Frequency Encoding



3. Phase Encoding

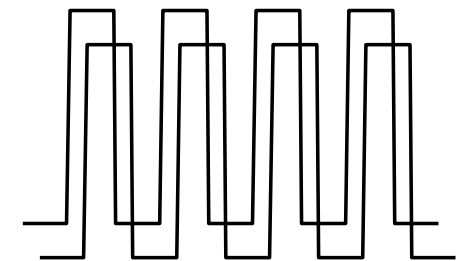


4. Event-Related



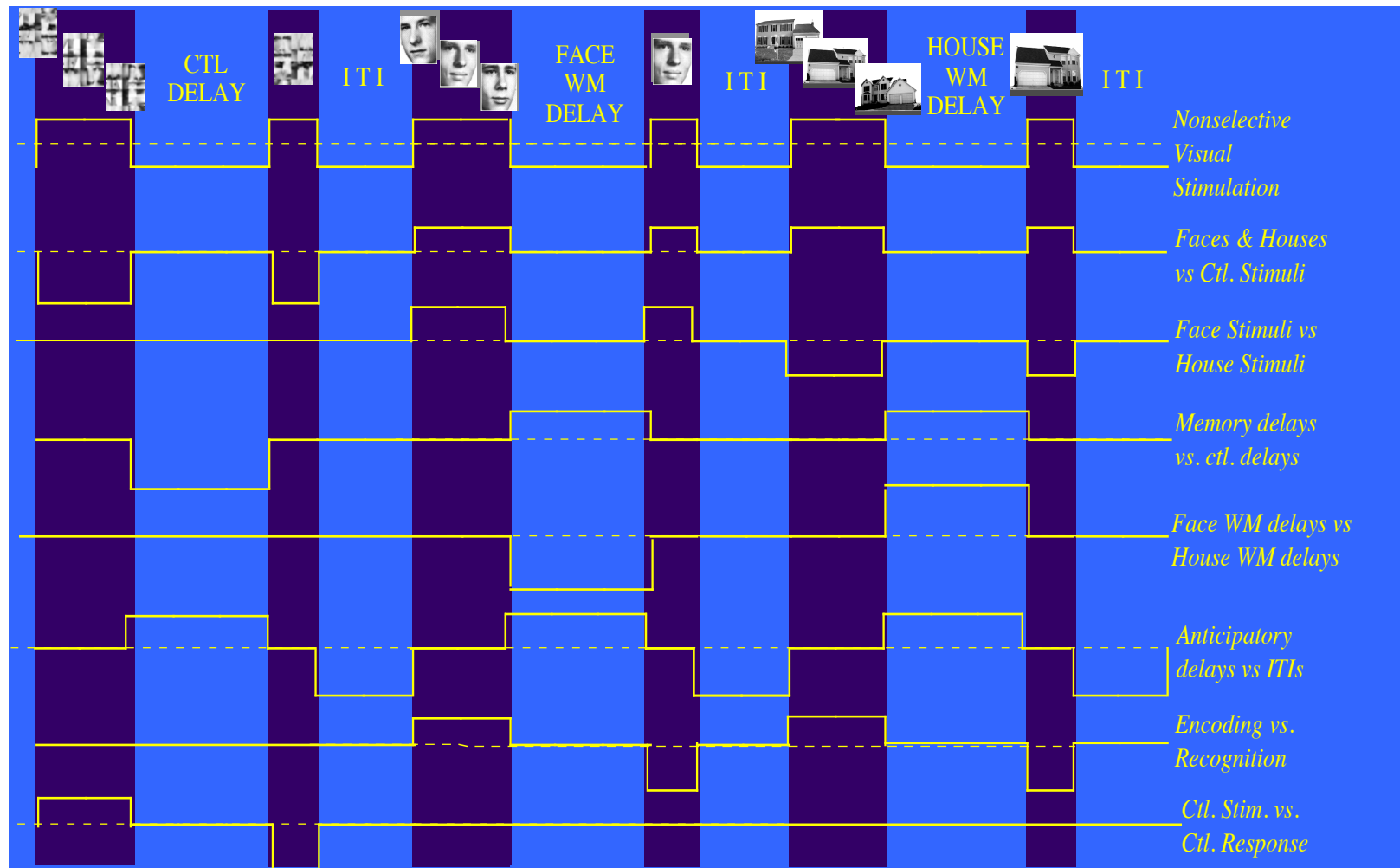
5. fMRI adaptation

6. Orthogonal Block Design



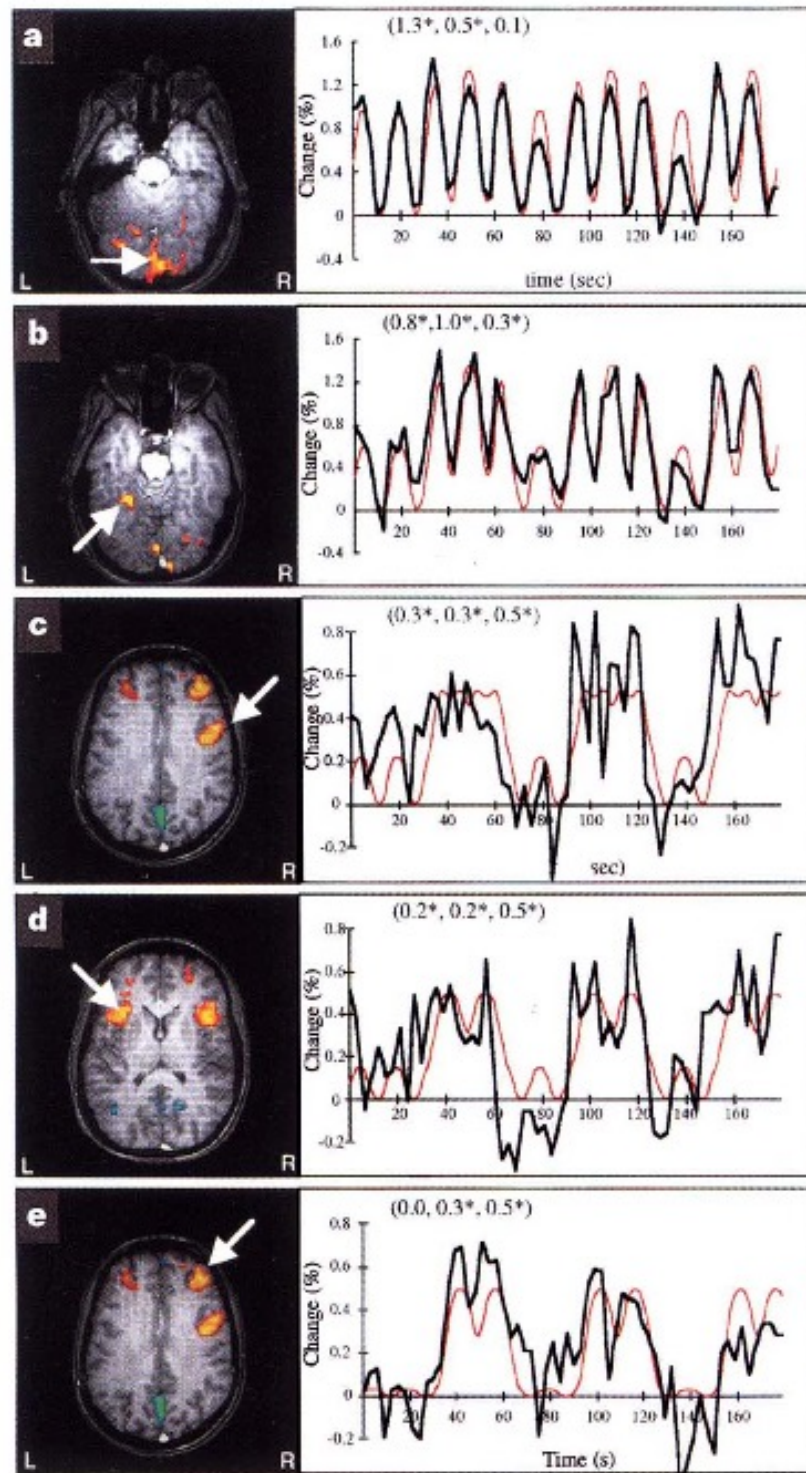
7. Free Behavior Design

Example of a Set of Orthogonal Contrasts for Multiple Regression



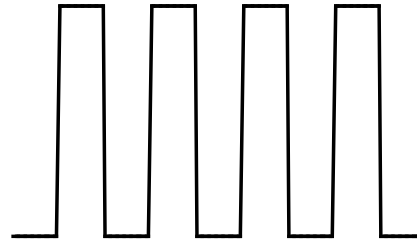
Transient and Sustained activity in a distributed neural system for human working memory, S. M. Courtney, L. G. Ungerleider, K. Keil, J. V. Haxby, Nature, 386, pp. 608-611

Transient and Sustained activity in a distributed neural system for human working memory, S. M. Courtney, L. G. Ungerleider, K. Keil, J. V. Haxby, Nature, 386, pp. 608-611

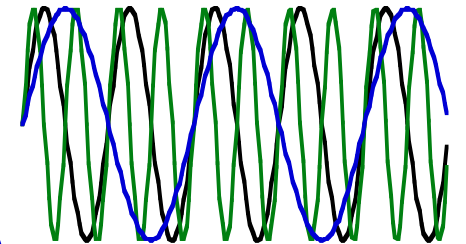


Neuronal Activation Input Strategies

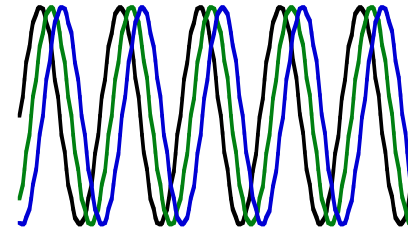
1. Block Design



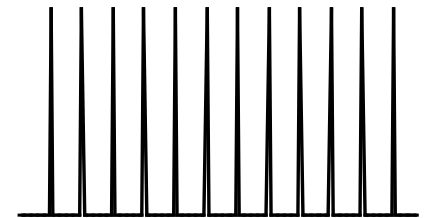
2. Frequency Encoding



3. Phase Encoding

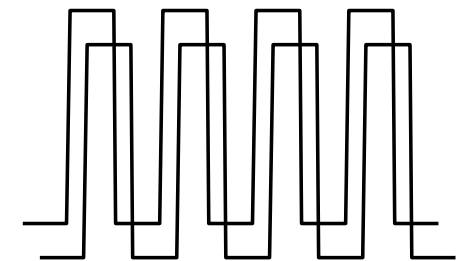


4. Event-Related



5. fMRI adaptation

6. Orthogonal Block Design



7. Free Behavior Design

Free behavior or naturalistic or continuous stimuli

Maguire – navigation

U. Hasson – time reversal, cross subject

Gallant – semantic space multiple regression

DARPA competition – guess what's happening

DeCharms, Goebel - Real time feedback

Category	Definition	Mean number of occurrences (SD)
Customer-driven Route Planning	Planning a route to a given destination	16.6 (1.8)
Subtypes: Initial plan	Planning from the initial request	6.8 (0.8)
Change in plan	Planning after an en route request from a customer to alter the destination	9.8 (1.0)
Spontaneous Route Planning	Further planning en route, independent of customers	34.3 (10.9)
Subtypes: Filling in	Planning the next stage of the journey	17.7 (6.6)
Re-planning	Altering the current plan to adapt to the environment	16.7 (5.7)
Action Planning	Planning future movements with the vehicle	45.8 (15.1)
Expectation Confirmation	Detecting the presence of an expected environmental feature	28.6 (9.9)
Expectation Violation	Detecting the absence of an expected environmental feature	31.6 (10.5)
Expectation	Looking out for the next expected environmental feature	24.5 (8.5)
Visual Inspection	Visual inspection of an environmental feature	36.0 (11.8)
Monitoring Traffic	Watching moving traffic in the environment	11.4 (5.9)
Coasting	Navigating automatically without any directed thoughts	25.8 (7.5)
Customers' Navigationally-Irrelevant Statements	Navigationally-irrelevant statements by customers, (a control for Customer-driven Route Planning)	6.6 (0.9)

A



B

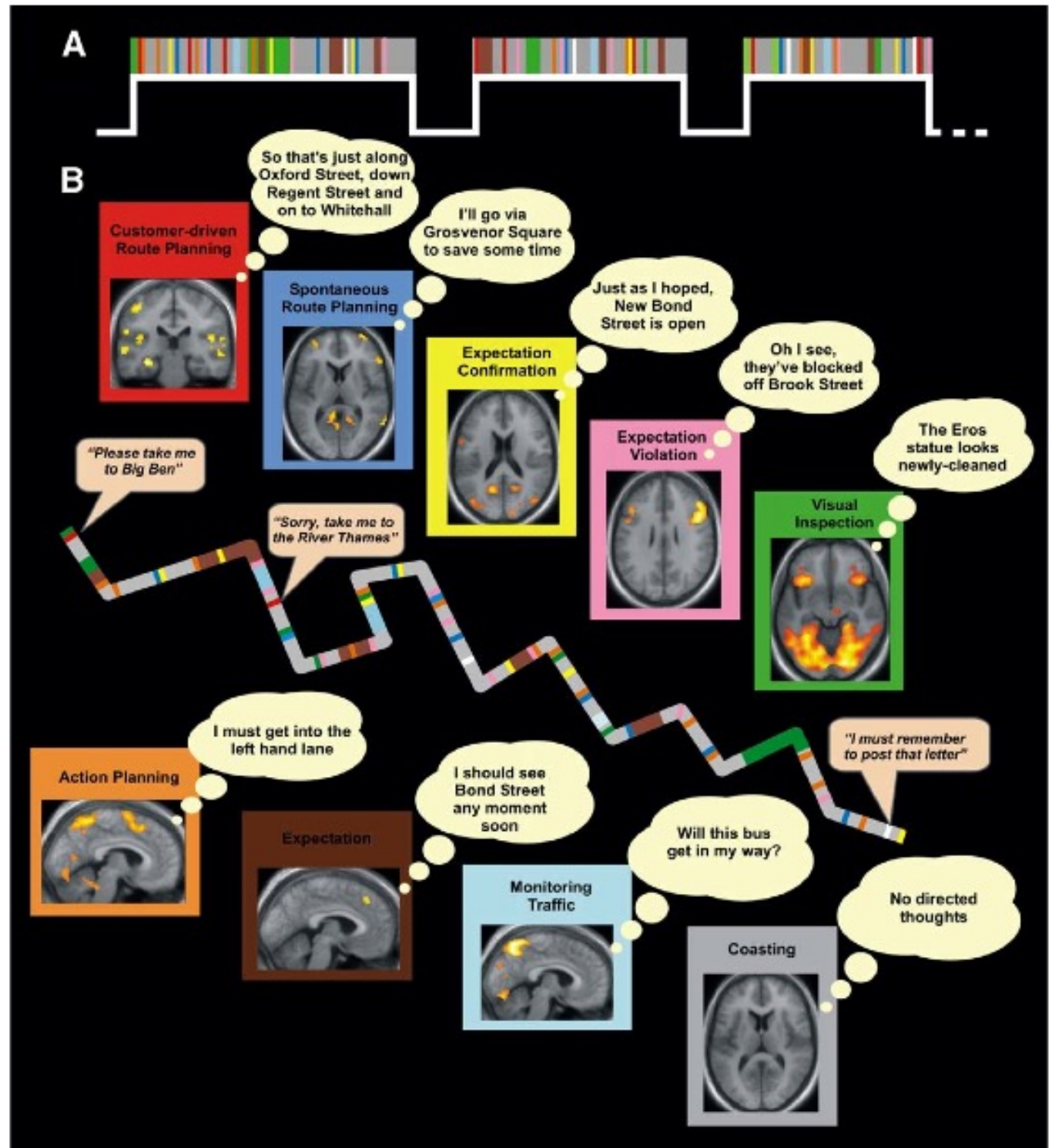


C



Thoughts, behaviour, and brain dynamics during navigation in the real world. Hugo J. Spiers and Eleanor A. Maguire, *NeuroImage*, 31 (2006), 1826-1840.

Thoughts, behaviour, and brain dynamics during navigation in the real world. Hugo J. Spiers and Eleanor A. Maguire, *NeuroImage*, 31 (2006), 1826-1840.



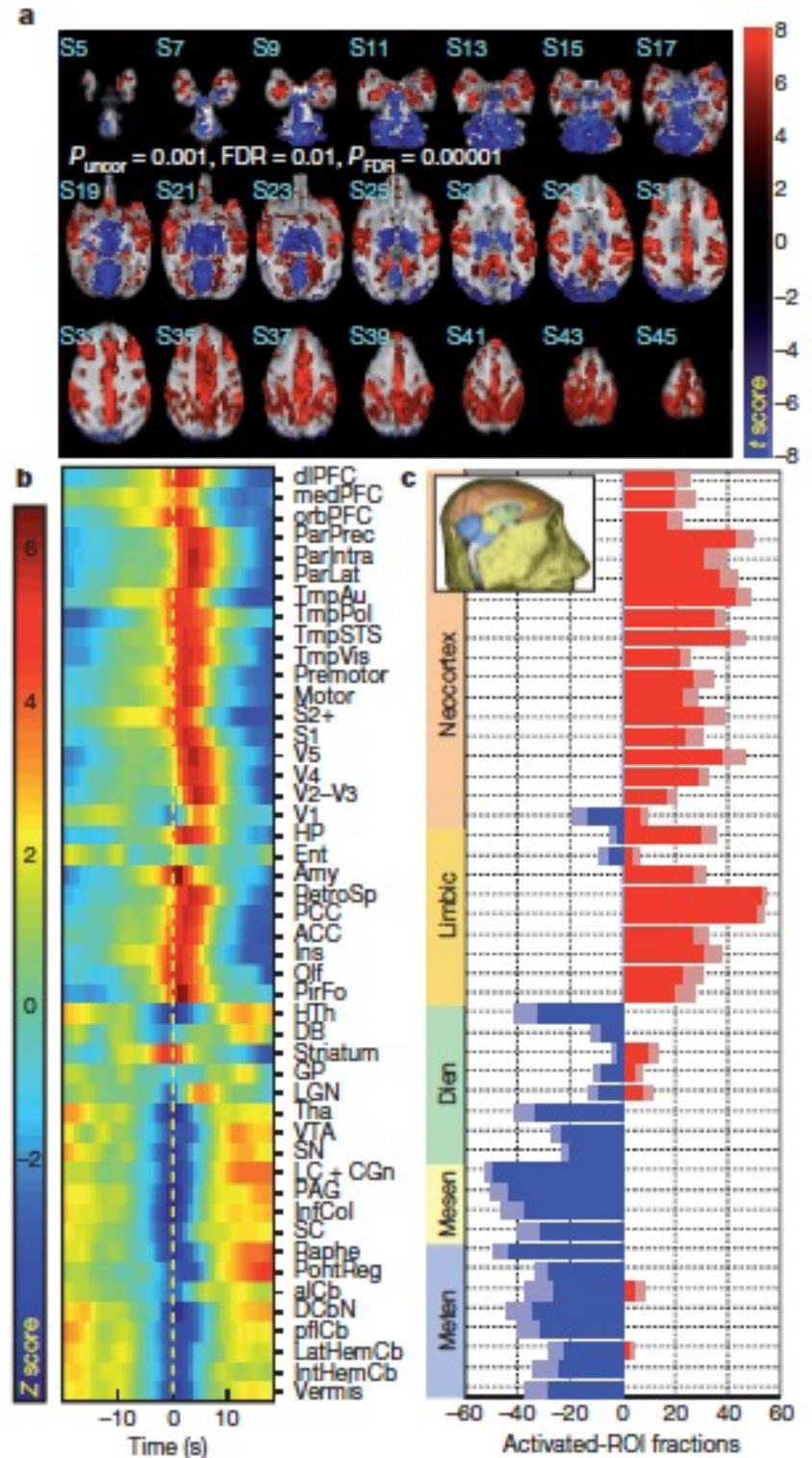
Multi-modal integration

Hippocampal–cortical interaction during periods of subcortical silence

N. K. Logothetis^{1,2}, O. Eschenko¹, Y. Murayama¹, M. Augath¹, T. Steudel¹, H. C. Evrard¹, M. Besserve^{1,3} & A. Oeltermann¹

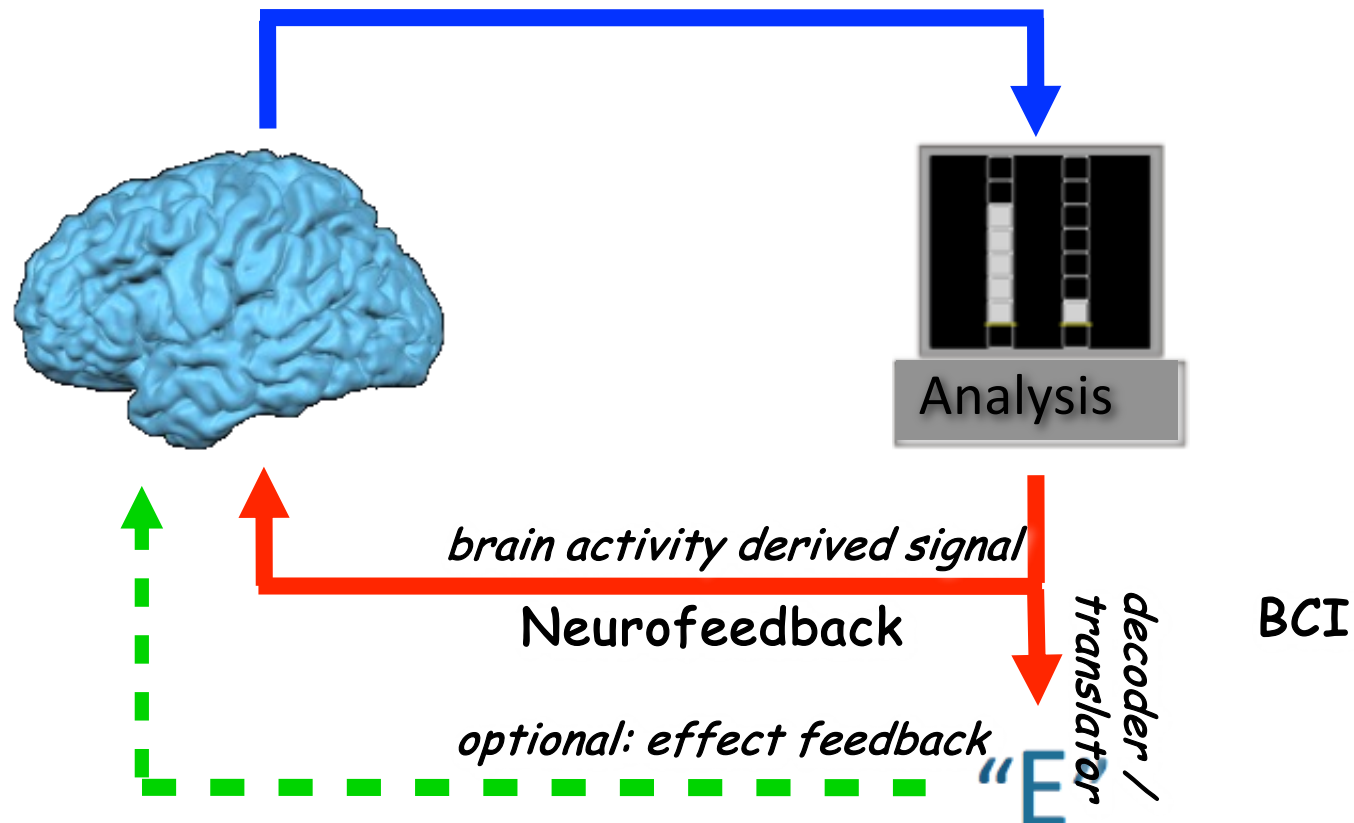
By combining electrophysiological recordings in hippocampus with ripple-triggered functional magnetic resonance imaging, here we show that most of the cerebral cortex is selectively activated during the ripples, whereas most diencephalic, midbrain and brainstem regions are strongly and consistently inhibited

22 NOVEMBER 2012 | VOL 491 | NATURE | 547

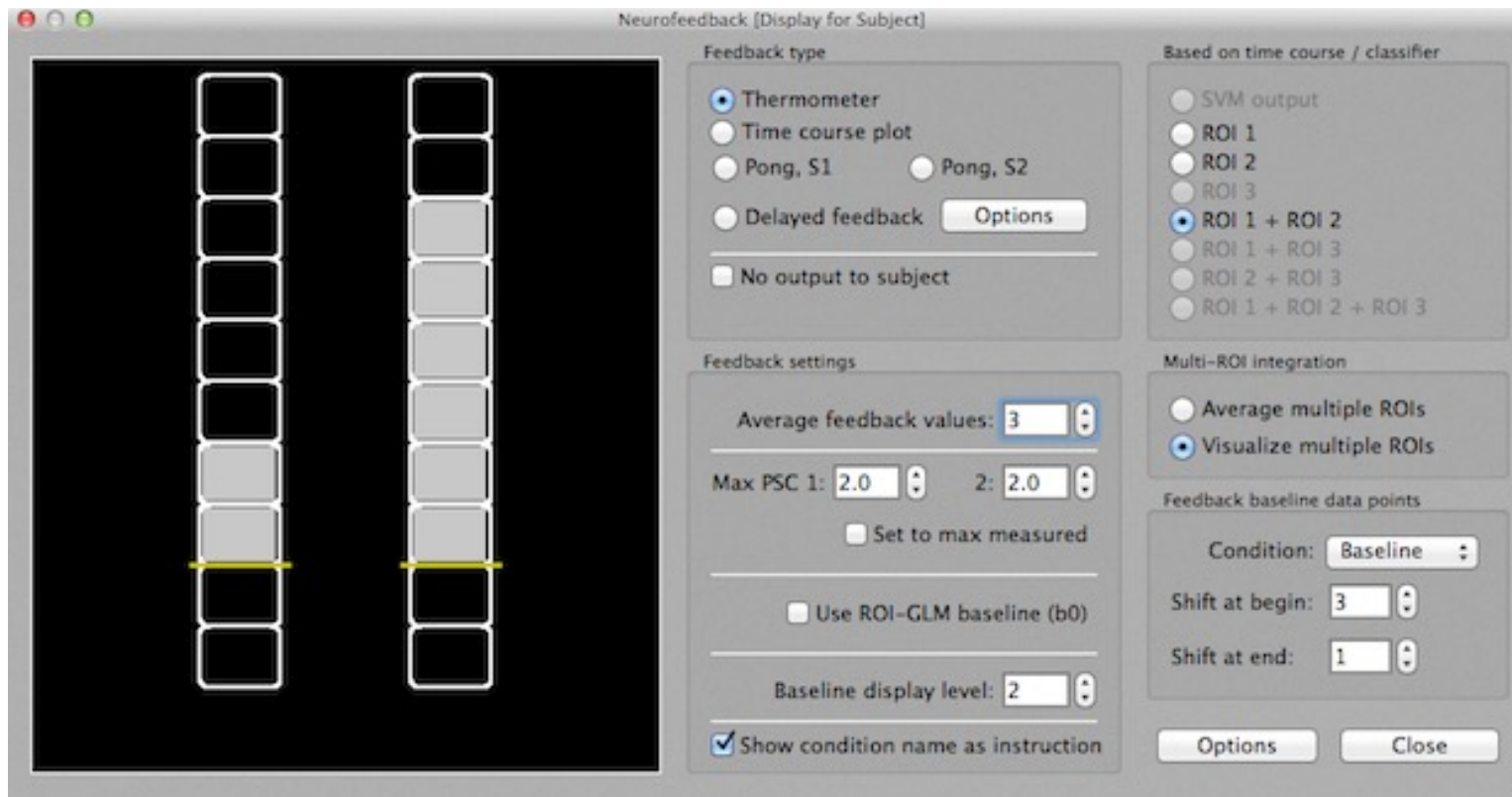


Applications of Real-Time fMRI Data Analysis

Online “brain reading” for neurofeedback and communication BCI



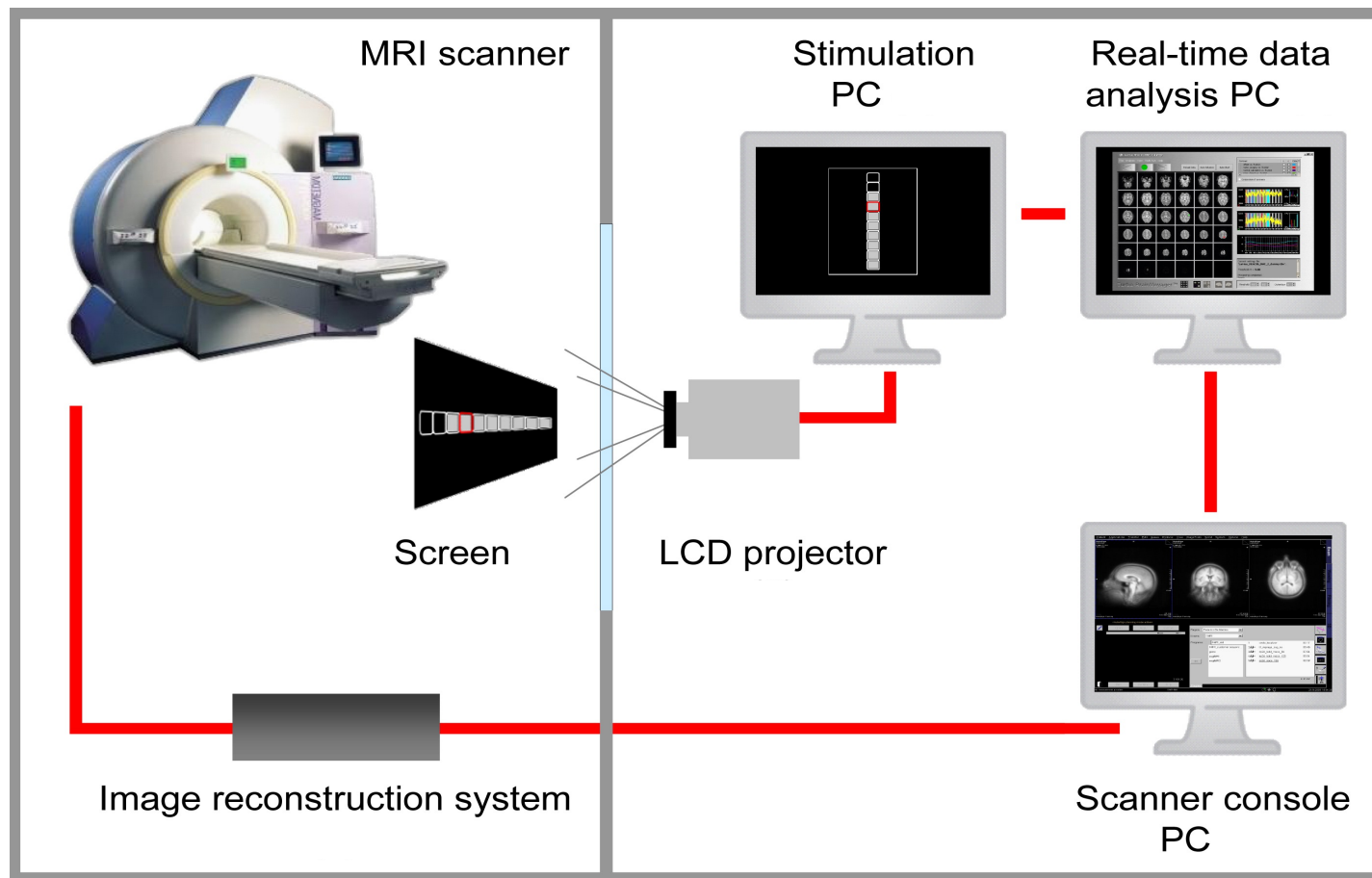
Real-Time fMRI Neurofeedback



- Real-time fMRI enables monitoring changes in the BOLD response *online*.
- The high spatial resolution of fMRI offers the possibility to investigate the control over *localized* brain regions -> *Feedback is content-specific*.
- Subjects can learn to influence own brain activity from *one* or *multiple* circumscribed brain regions.

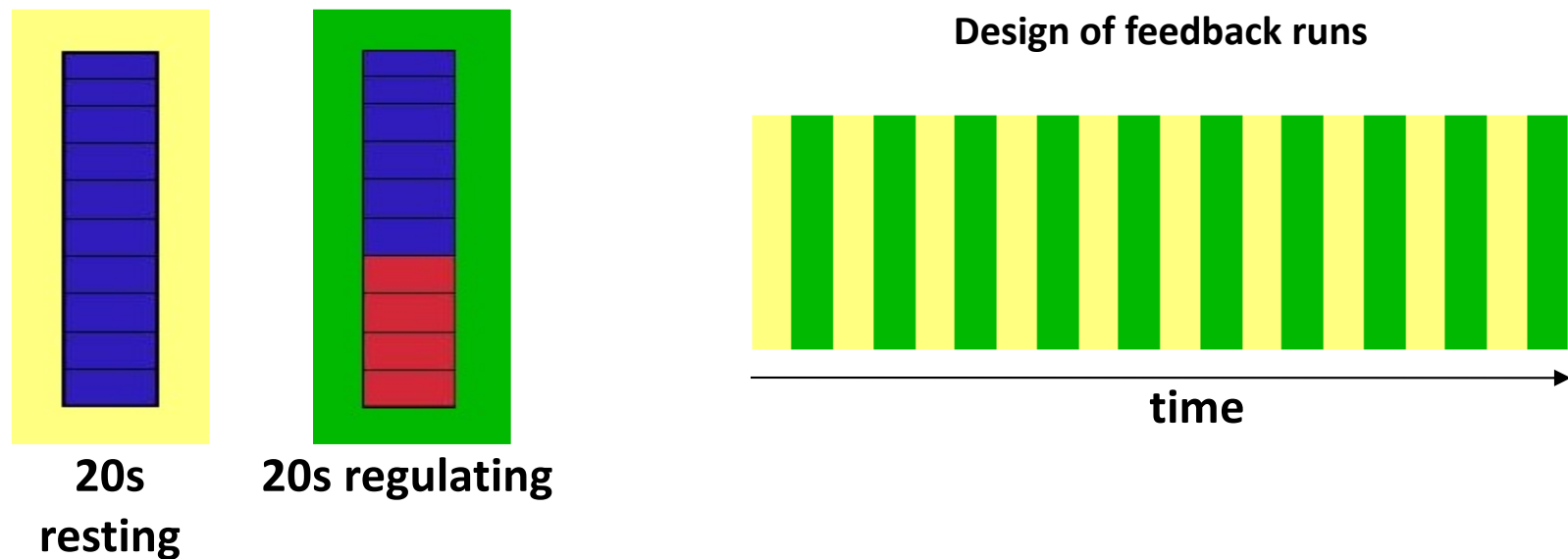
fMRI Neurofeedback as a Therapeutic Tool

Technical setup and data flow of fMRI-based neurofeedback training study



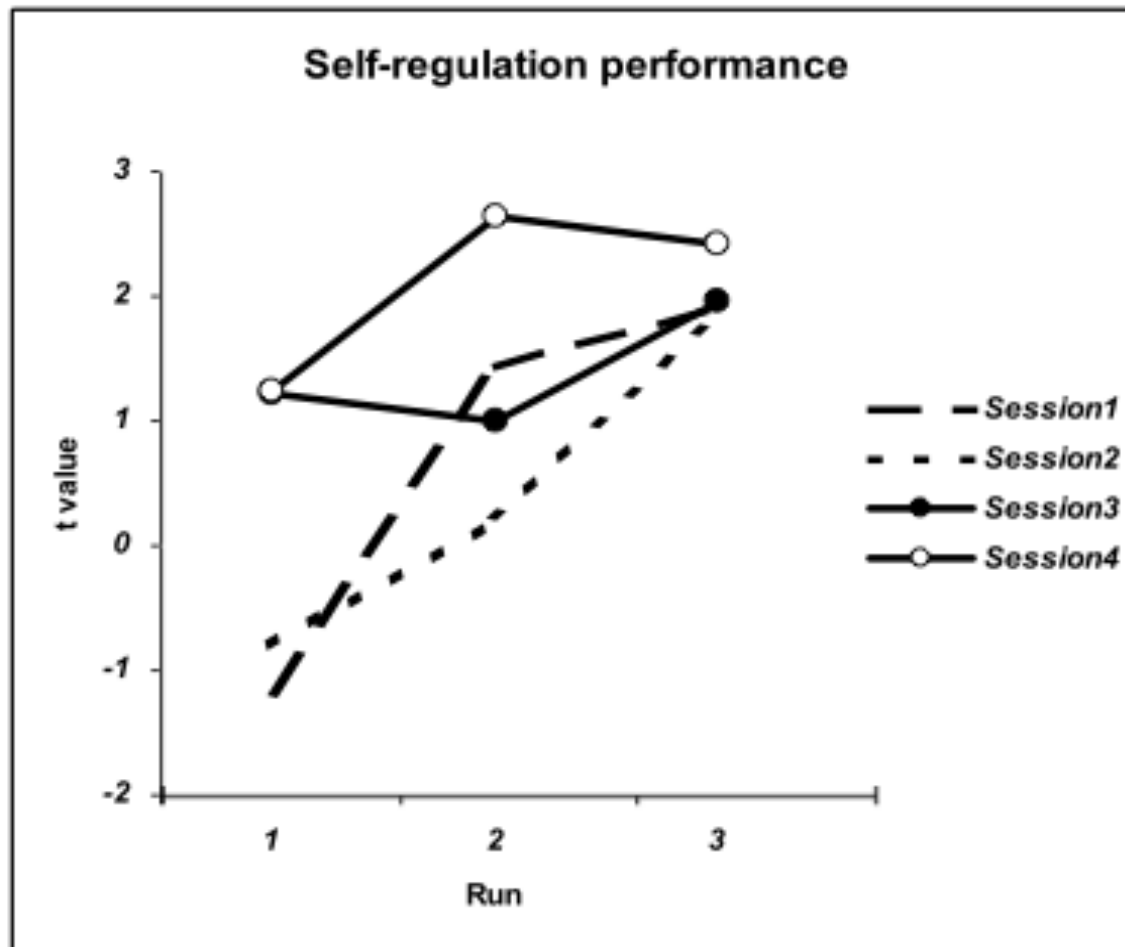
Neurofeedback Therapy for Patients with Depression

- Patients with recurrent depressive episodes after unsuccessful conventional therapy
- Neurofeedback design
 - learning to up-regulate brain activation within the emotion network (amygdala, prefrontal cortex *etc.*)
 - 4 sessions (within 4 weeks)
 - one session = 3 runs (1h)



Neurofeedback Therapy for Patients with Depression

Effect of the rt-fMRI neurofeedback training on the reached brain activation level within the emotion network (group results)

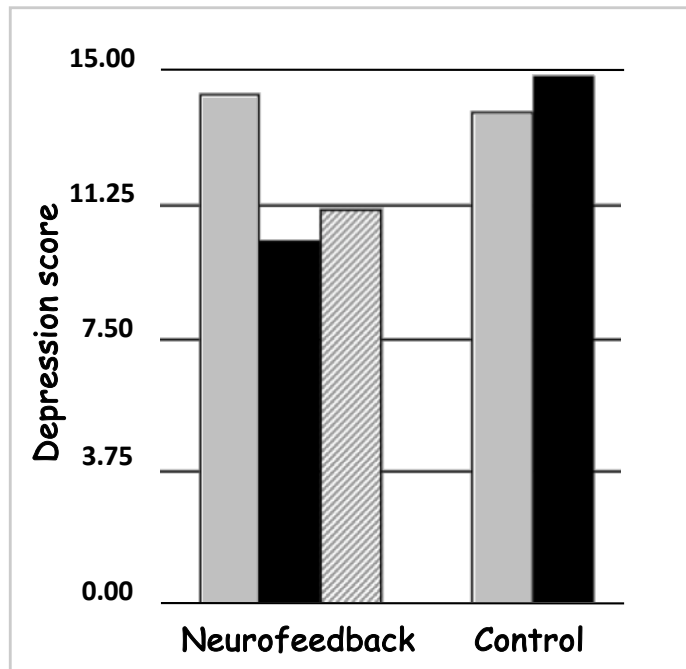


Linden, D.E.J., Habes, I., Johnston, S.J., Linden, S., Tatineni, R., Subramanian L., Sorger, B., Healy, D., Goebel, R. (2012) Real-time Self-regulation of Emotion Networks in Patients with Depression. *PLOS One*, 7, e38115.

Neurofeedback Therapy for Patients with Depression

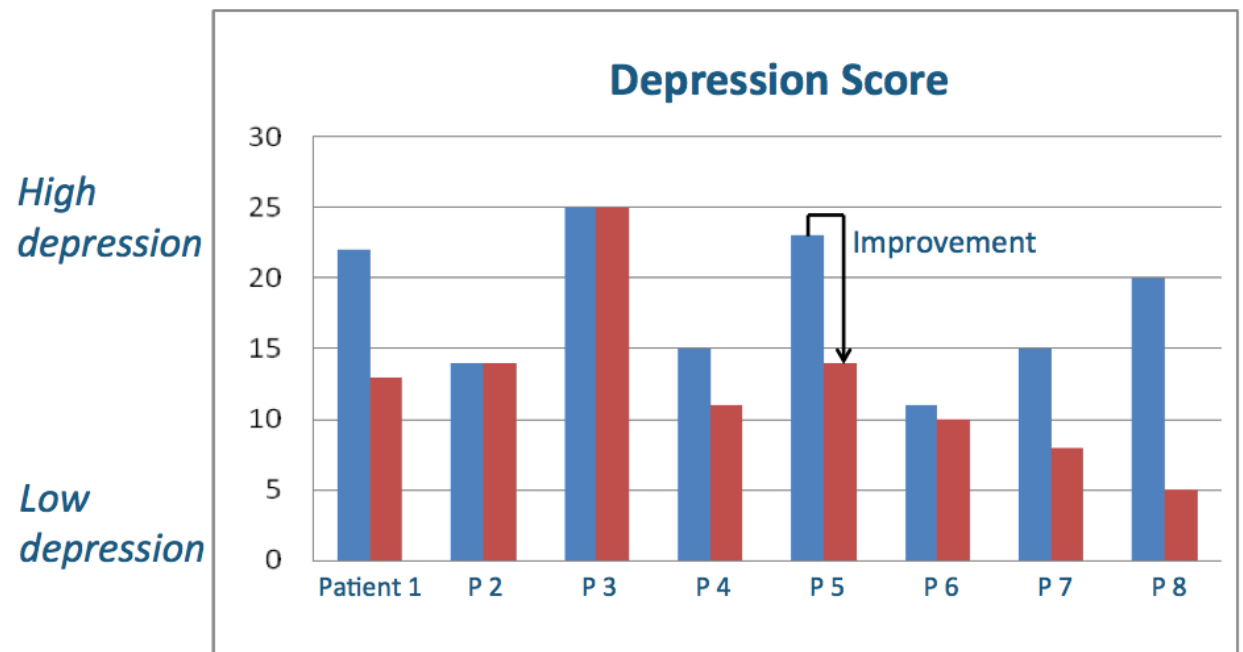
Behavioral effects of neurofeedback training after 4 sessions (HRSD score)

group results



- pre
- post
- ▨ follow-up

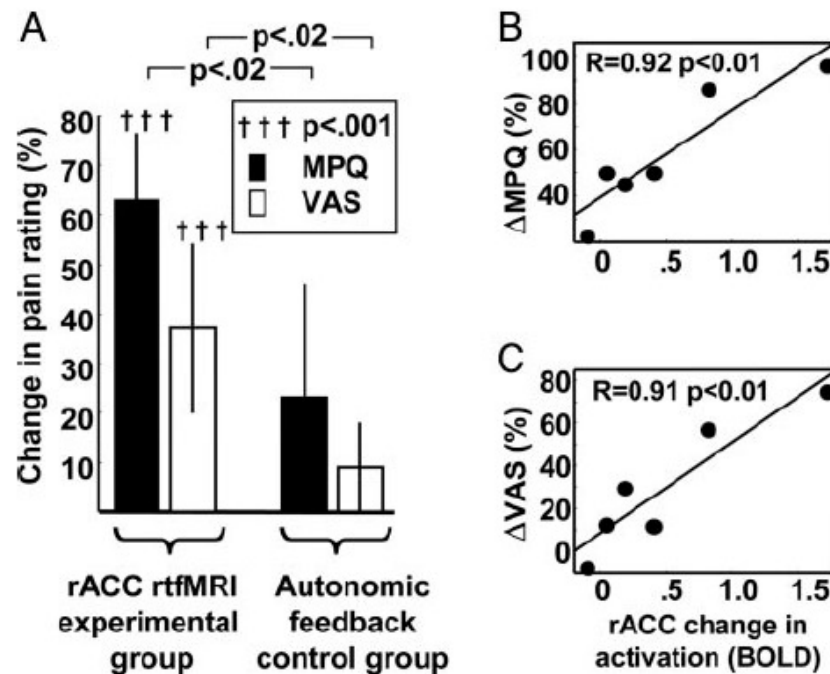
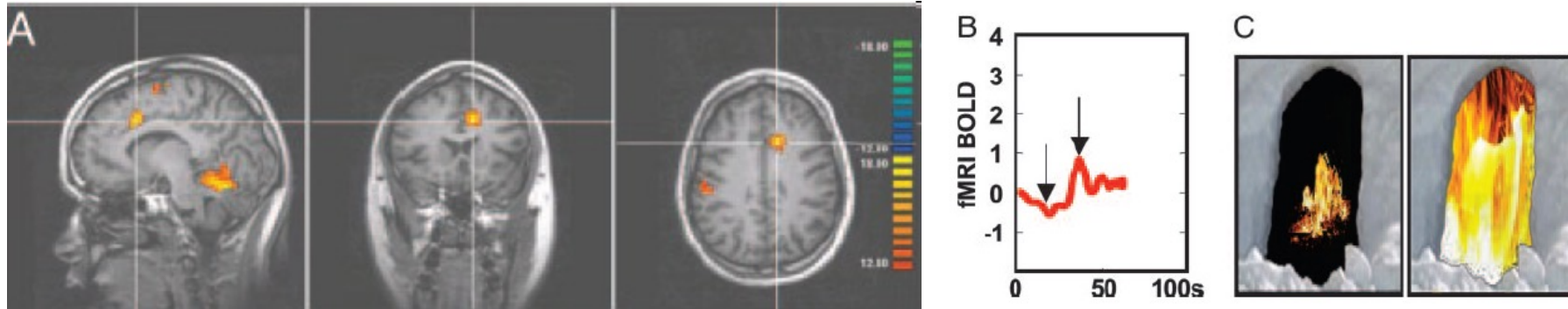
single-subject results



- pre
- post

-> First clinical trial study in UK

Real time fMRI feedback to reduce chronic pain

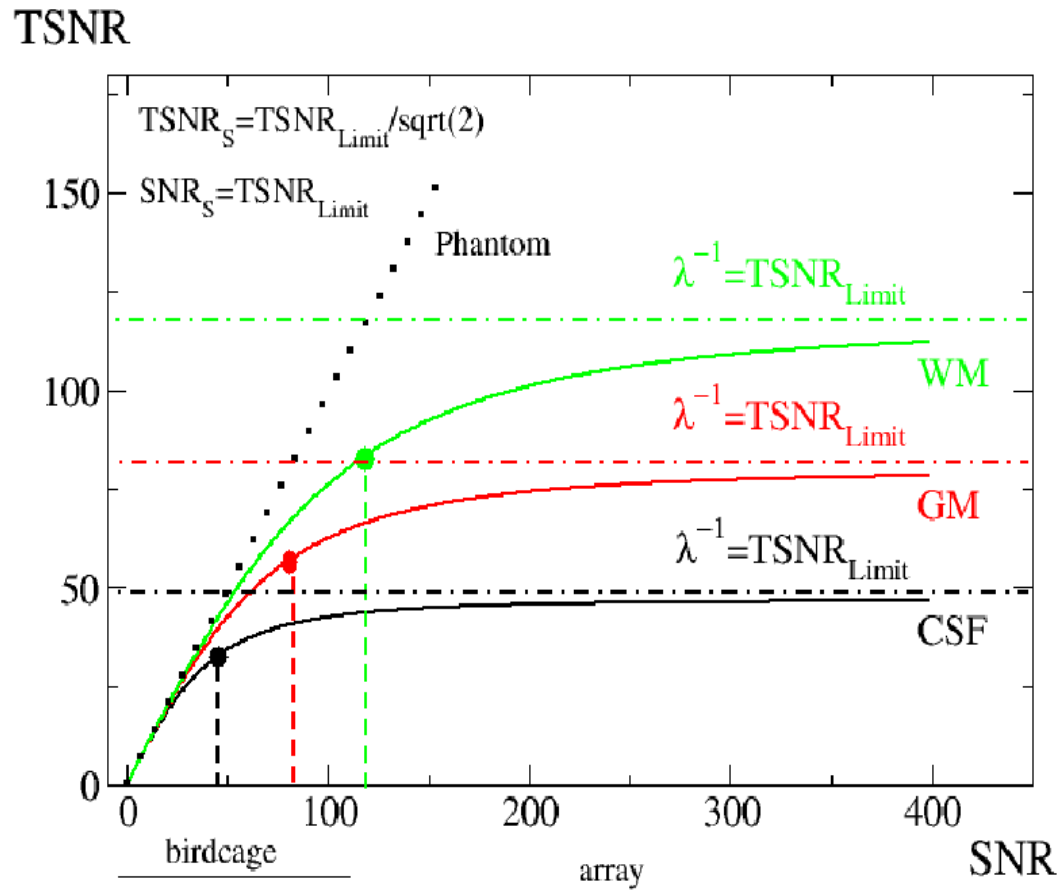


Control over brain activation and pain learned by using real-time functional MRI,
 R. C. deCharms, et al. PNAS, 102; 18626-18631 (2005)

fMRI Paradigm Designs and Processing Strategies

- 1. Neuronal Activation Input Strategies**
- 2. Resting State fMRI**
- 3. fMRI Decoding**

Temporal Signal to Noise Ratio (TSNR) vs. Signal to Noise Ratio (SNR)

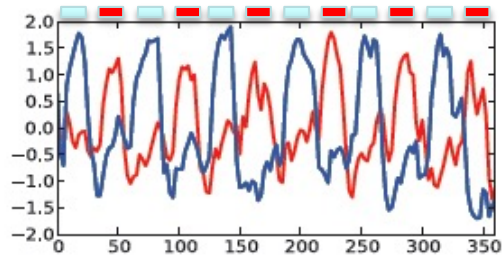
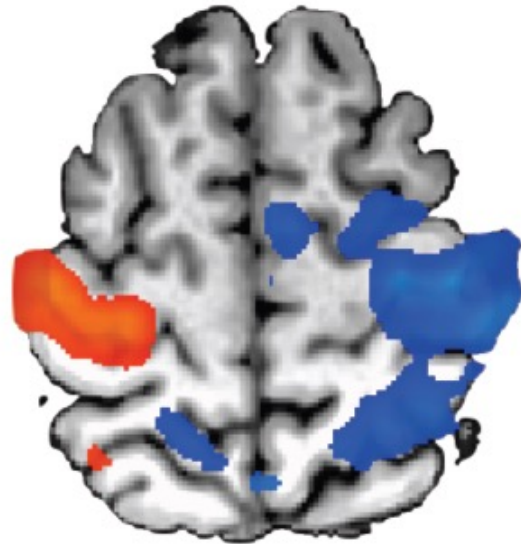


Sources of time series fluctuations:

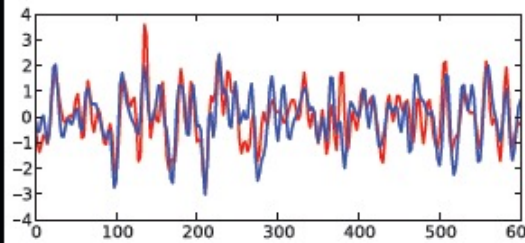
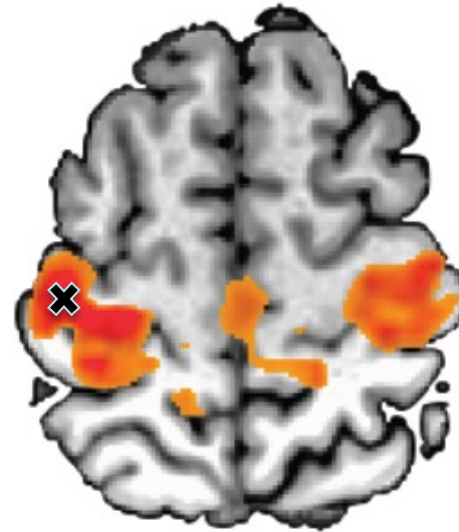
- Blood, brain and CSF pulsation
- Vasomotion
- Breathing cycle (B_0 shifts with lung expansion)
- Bulk motion
- Scanner instabilities
- Changes in blood CO_2 (changes in breathing)
- Spontaneous neuronal activity

Activation-based fMRI and “resting state” fMRI

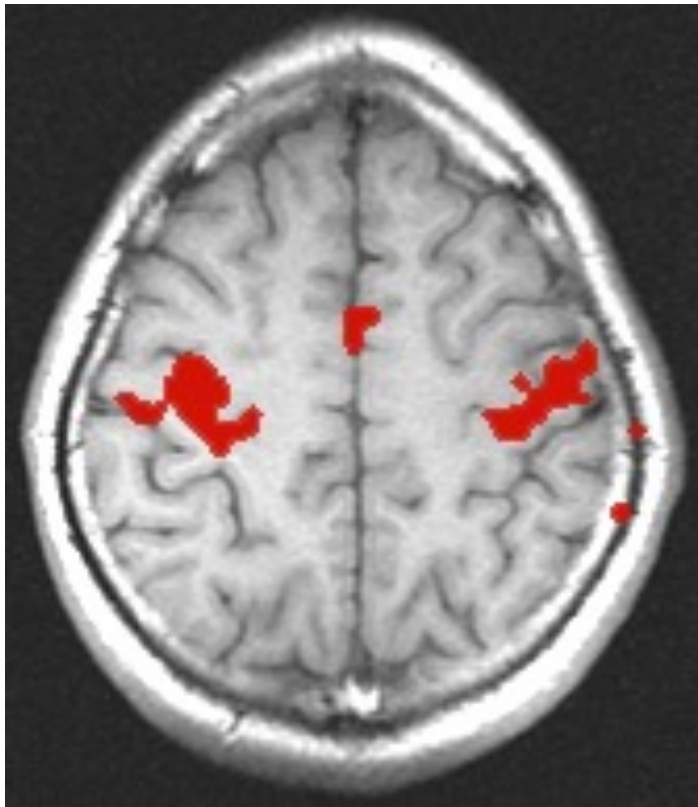
Task Activation
(Right vs. Left Hand Tapping)



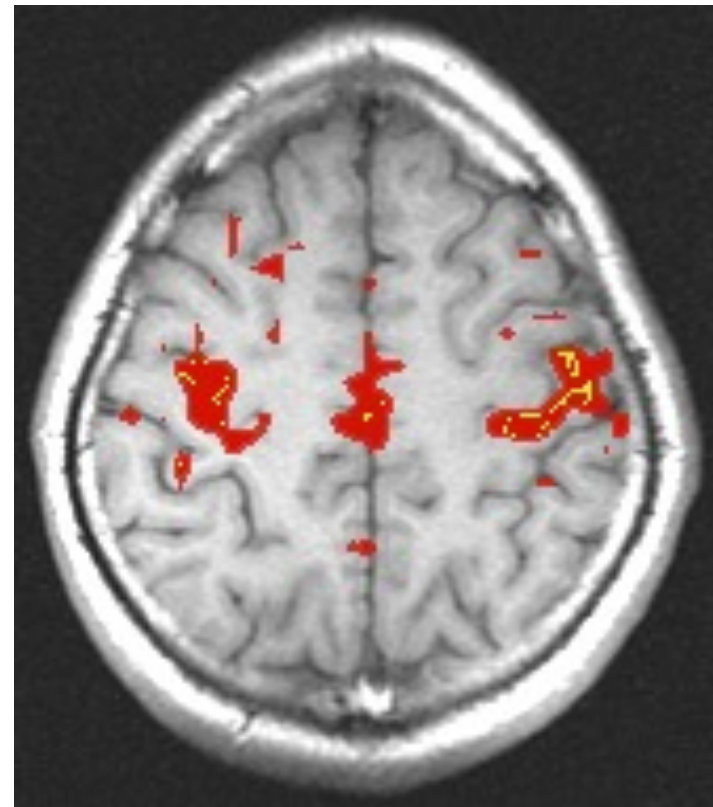
Resting Correlation
(Right Hand Seed)



Resting State Correlations



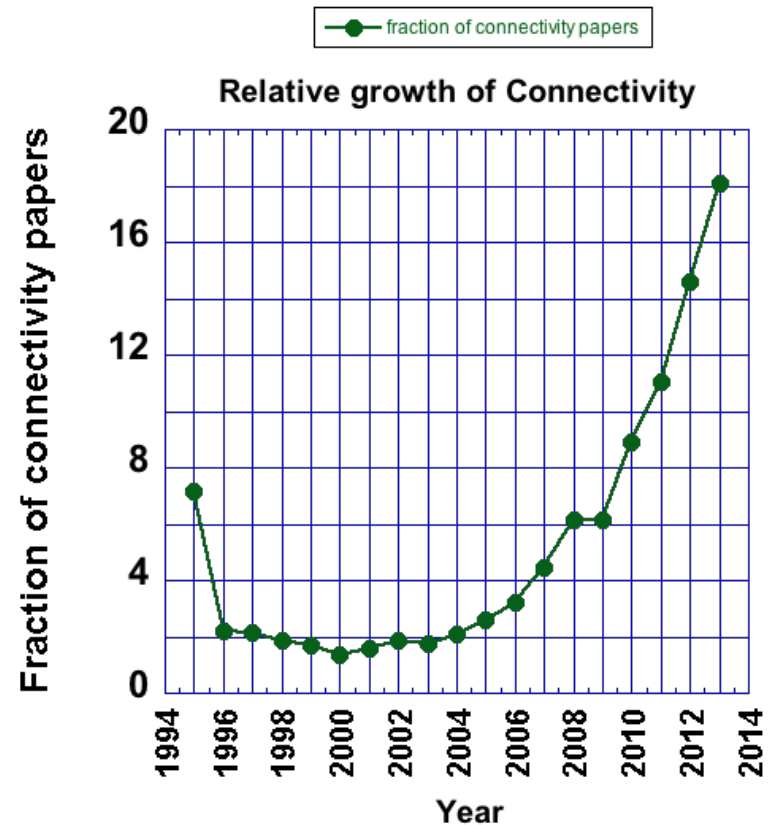
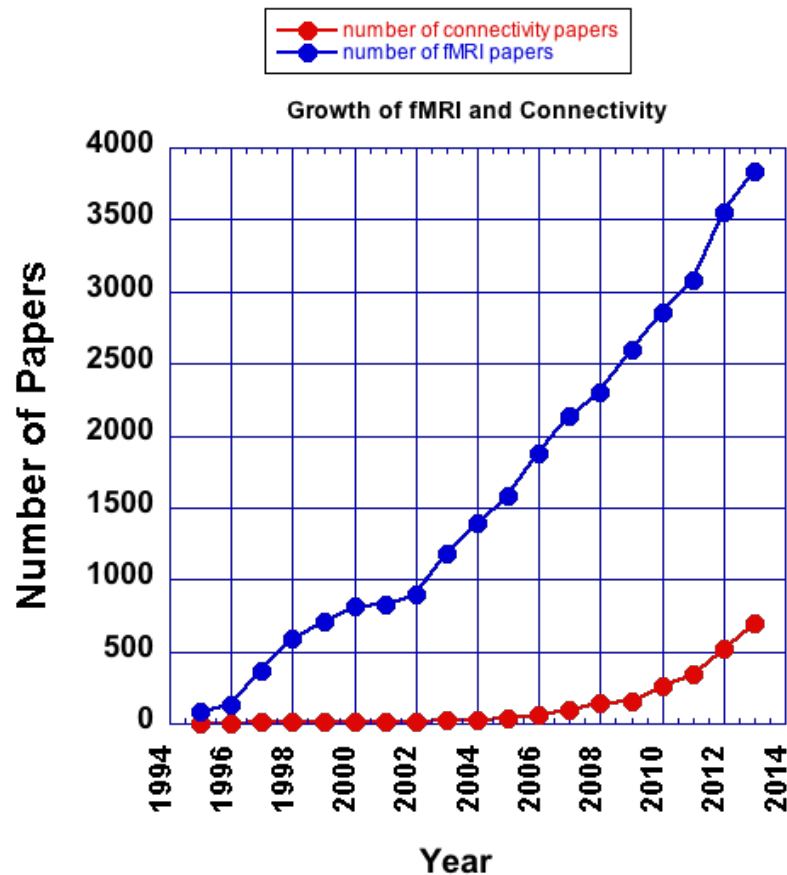
Activation:
correlation with reference function



Rest:
seed voxel in motor cortex

Resting state fMRI: Why is this area important?

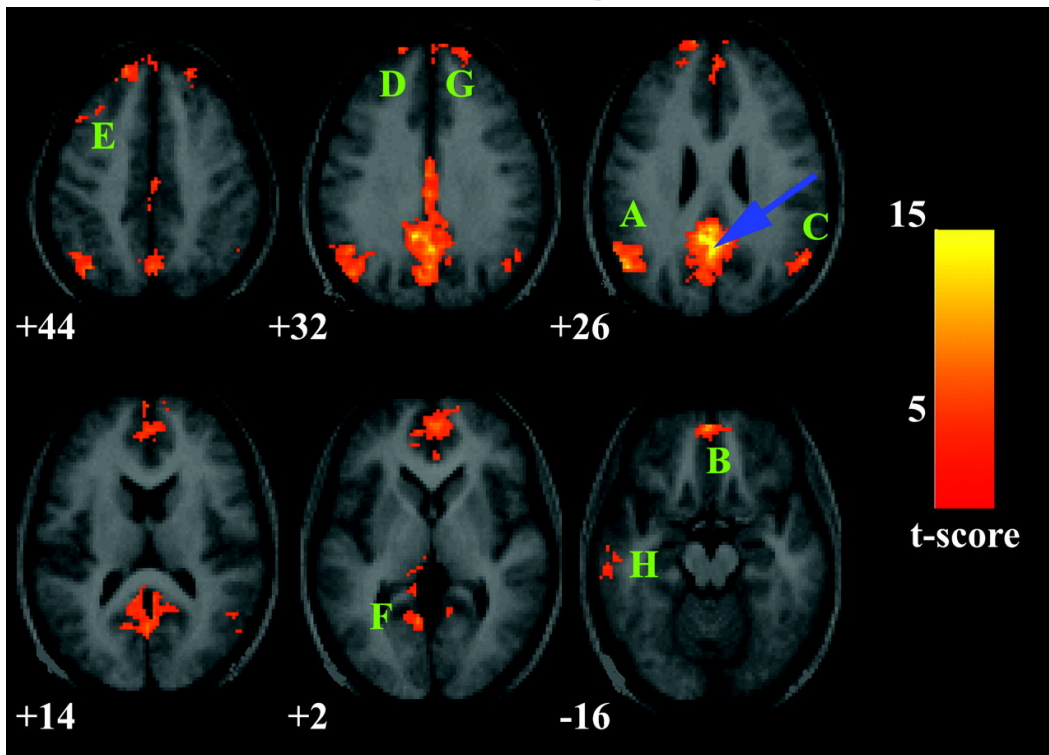
- The number of papers and applications has exploded.
- Neuronal, psychiatric, and developmental disorders may relate to altered connectivity.
- Methods are in their infancy, and rapidly evolving.
- Neuronal correlates of spontaneous fluctuations are not fully understood.



ICA

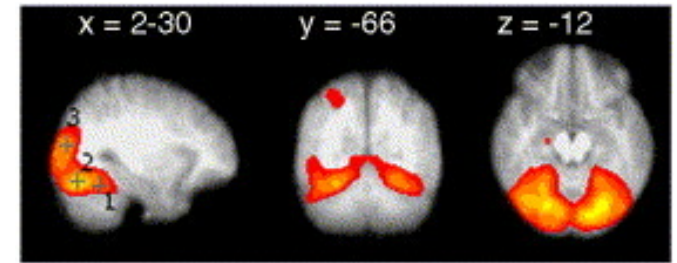
Seed Voxel

Seed Based Correlation from the Posterior Cingulate Cortex

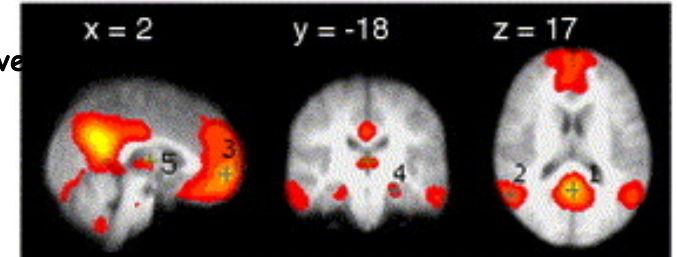


Greicius M D et al. PNAS 2003;100:253-258

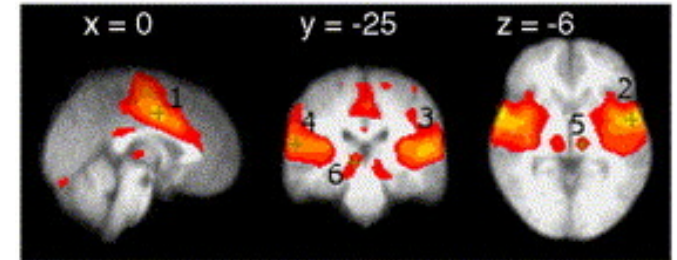
Visual



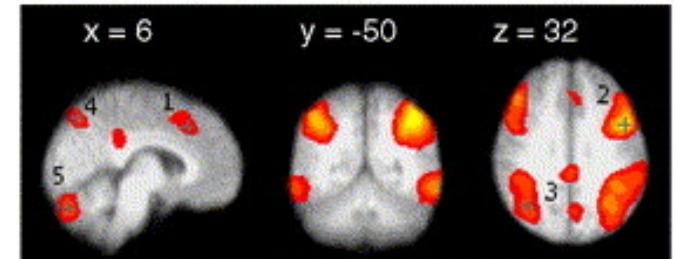
Visuospatial Executive



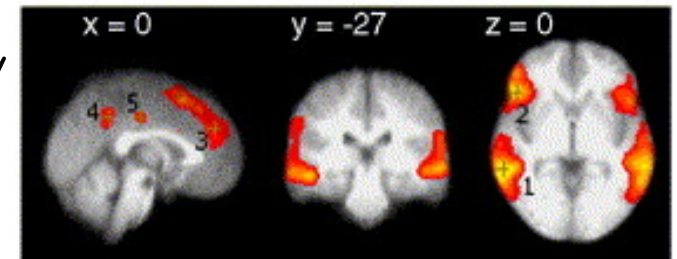
Sensory Auditory



Dorsal Pathway



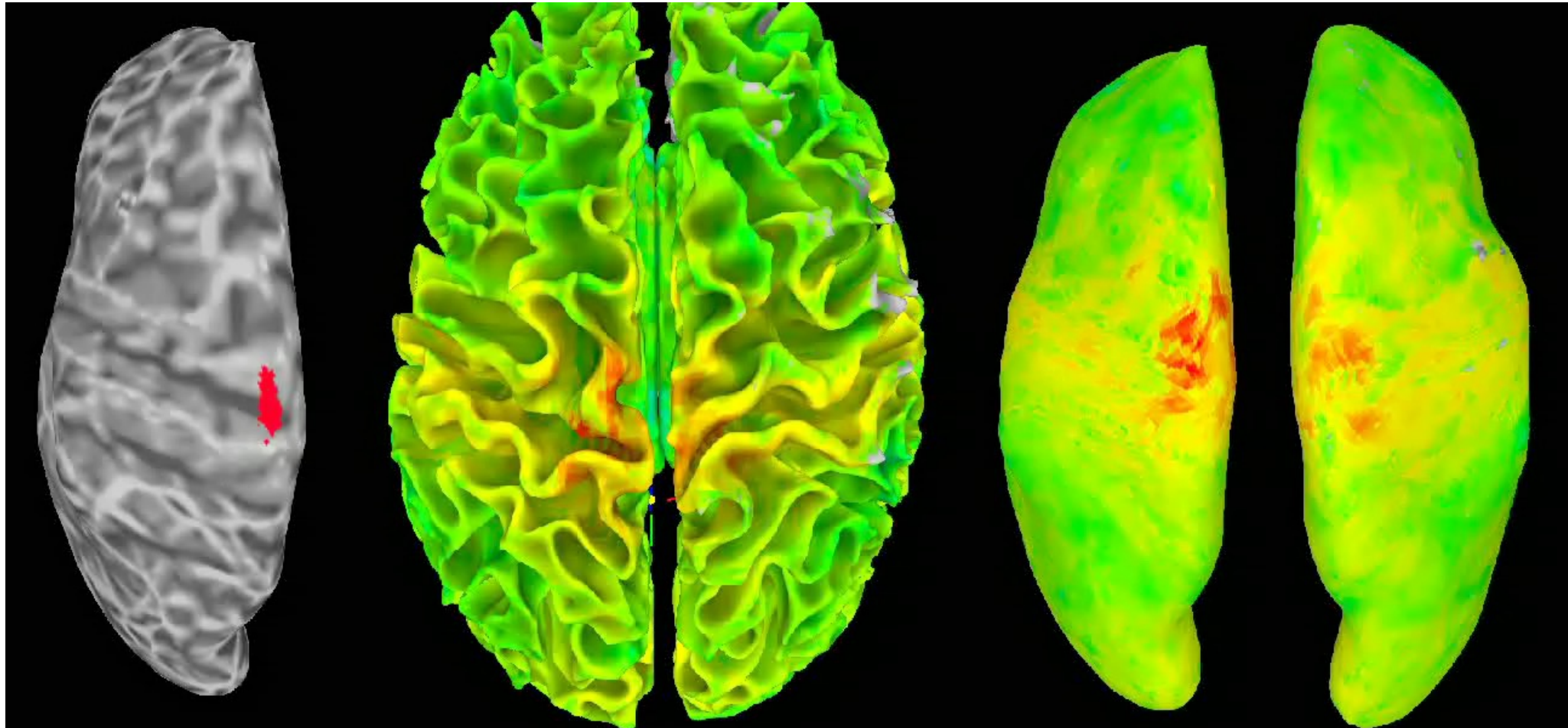
Ventral Pathway



De Luca, Neuroimage 27(4) 2000

Sliding Seed Movies

Relative correlation strength pattern obtained with a systematically shifted seed region

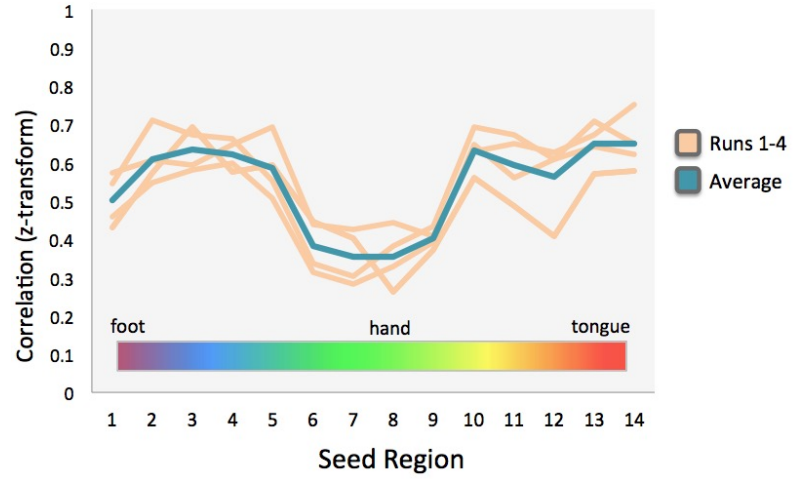
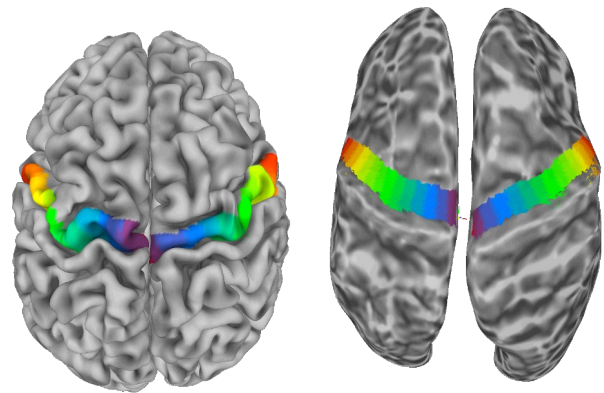
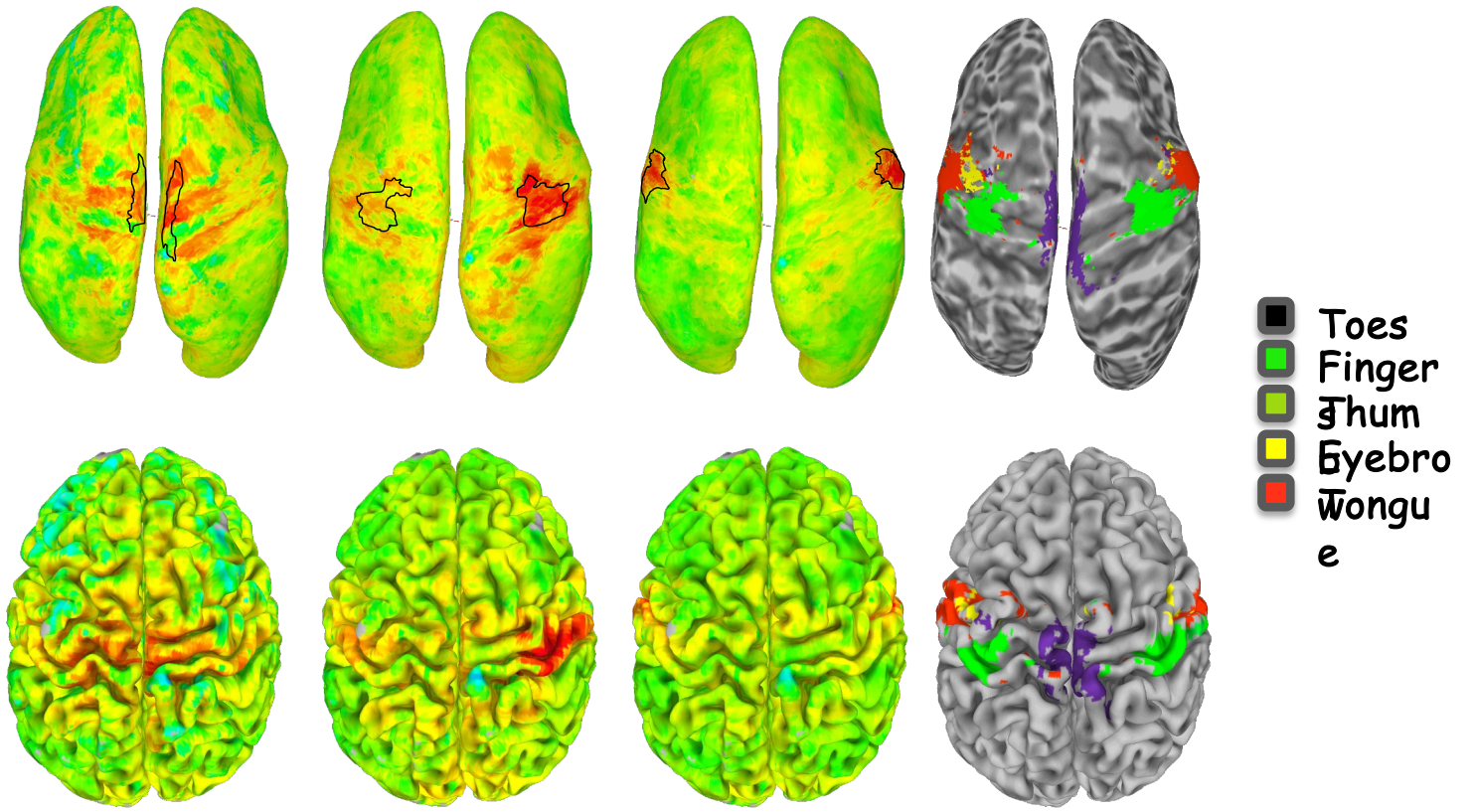


Seed 1

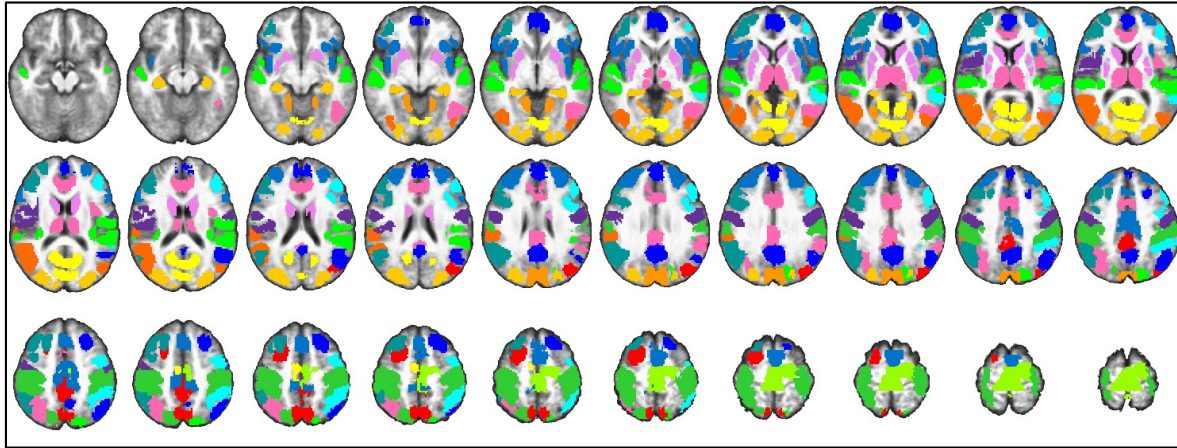
GM/WM Boundary

LH (seed hemi)

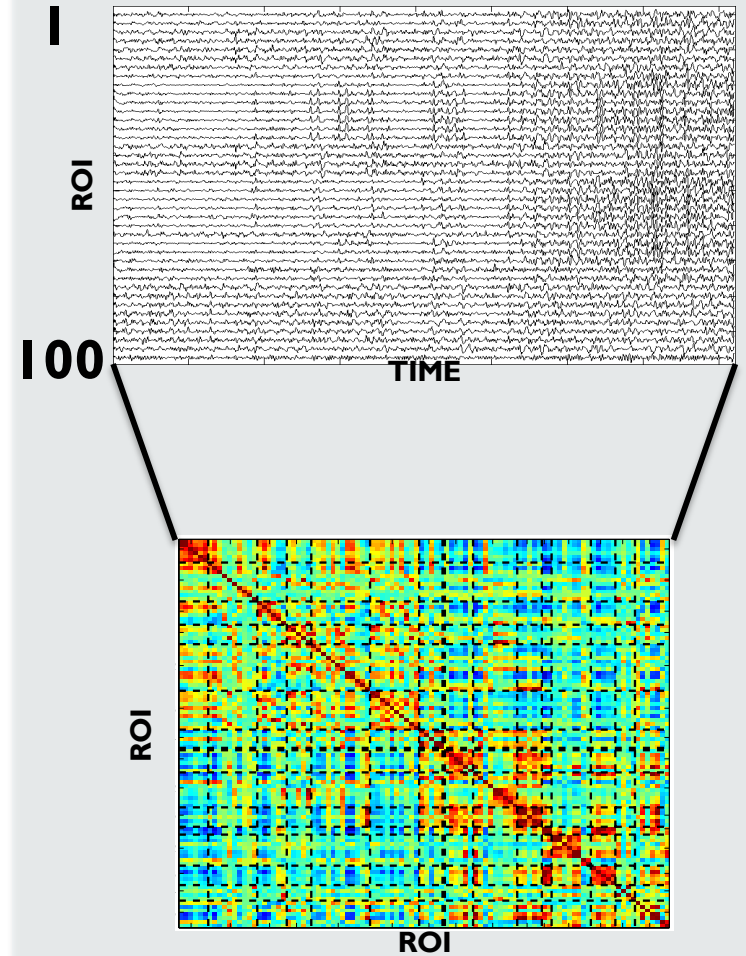
RH (contra hemi)

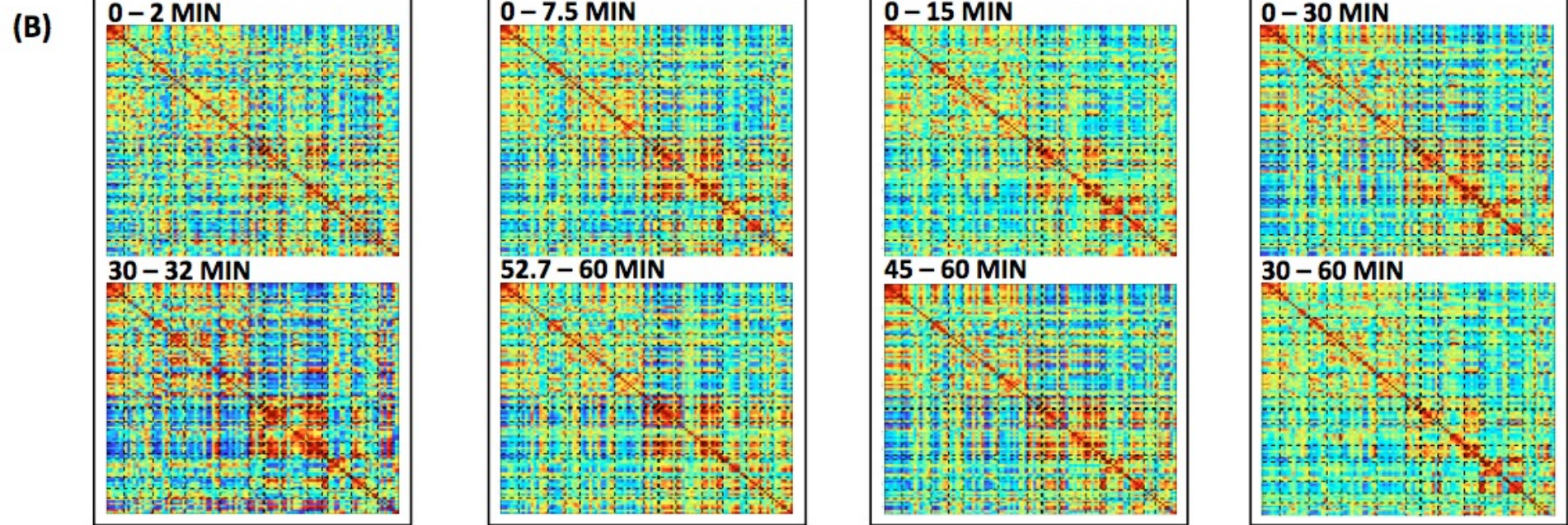
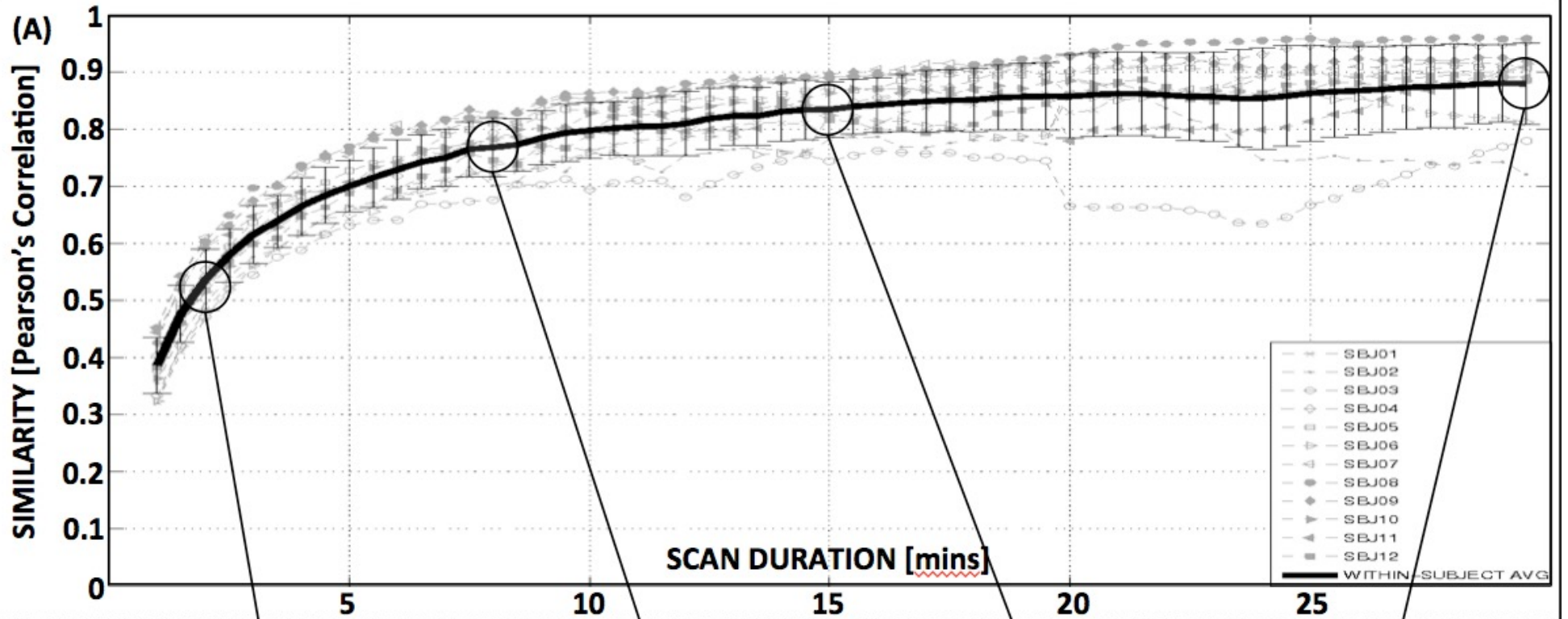


Time Course Correlation Matrix



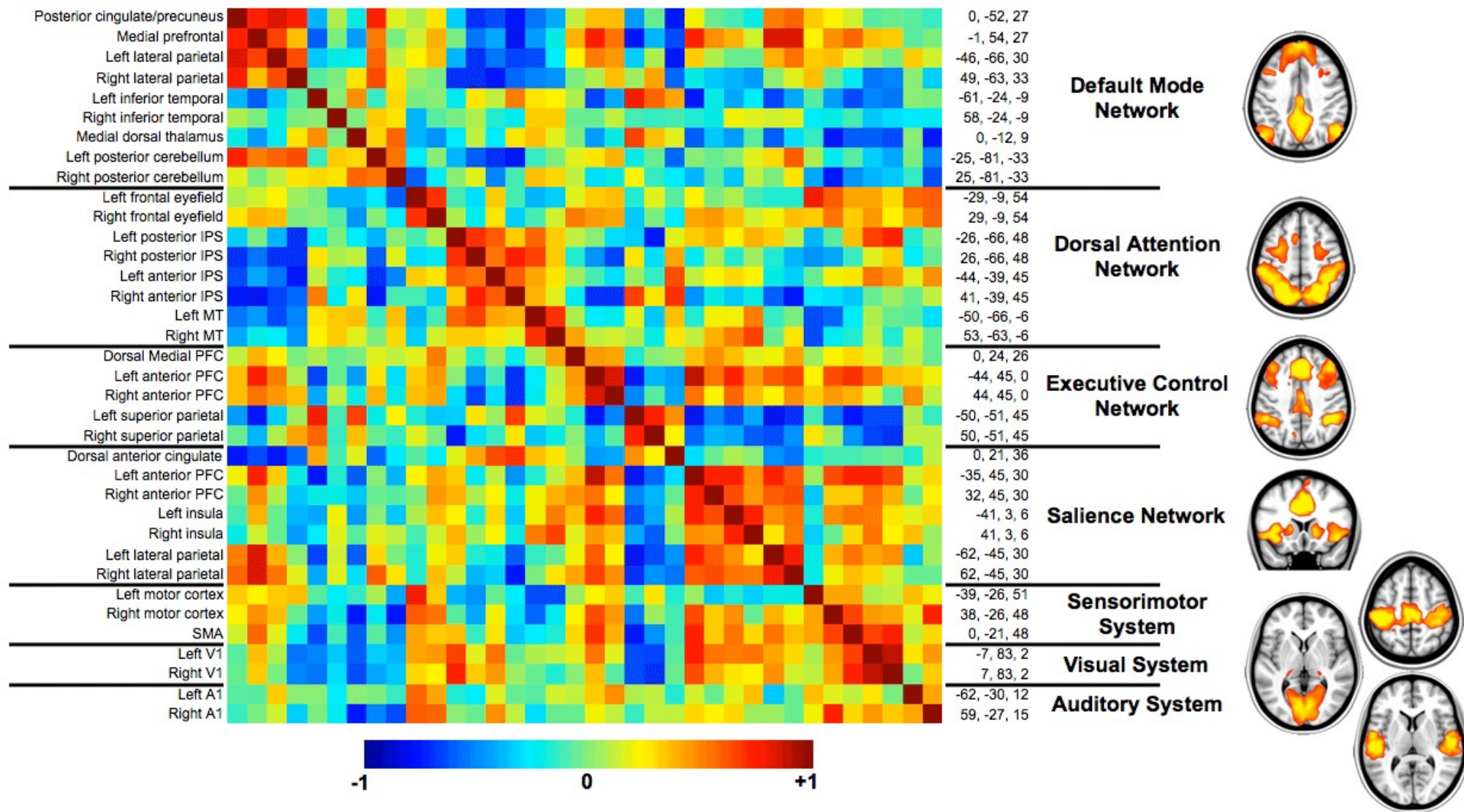
PAIR-WISE TIME COURSE CORRELATION MATRIX







<http://www.nil.wustl.edu>



http://www.nil.wustl.edu/labs/raichle/images/Restless_Brain/correlation_matrix.html

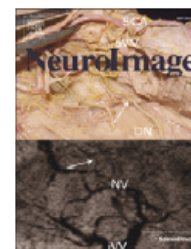


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Differentiating BOLD and non-BOLD signals in fMRI time series using multi-echo EPI

Prantik Kundu^{a,c,*}, Souheil J. Inati^b, Jennifer W. Evans^{a,d}, Wen-Ming Luh^b, Peter A. Bandettini^{a,b}

^a Section on Functional Imaging Methods, Laboratory of Brain and Cognition, National Institutes of Health, Bethesda, MD, 20892 USA

^b Functional MRI Facility, National Institute of Mental Health, National Institutes of Health, Bethesda, MD, 20892 USA

^c Department of Psychiatry, University of Cambridge, Addenbrooke's Hospital, Hills Road, Cambridge, CB2 2QQ UK

^d Center for Neuroscience and Regenerative Medicine, Henry M. Jackson Foundation, Rockville, Maryland, 20852 USA

Integrated strategy for improving functional connectivity mapping using multiecho fMRI

Prantik Kundu^{a,b,1}, Noah D. Brenowitz^a, Valerie Voon^b, Yulia Worbe^b, Petra E. Vértes^b, Souheil J. Inati^c, Ziad S. Saad^d, Peter A. Bandettini^{a,c,2}, and Edward T. Bullmore^{b,e,f,2}

PNAS Vol 110, No 40, 16187-

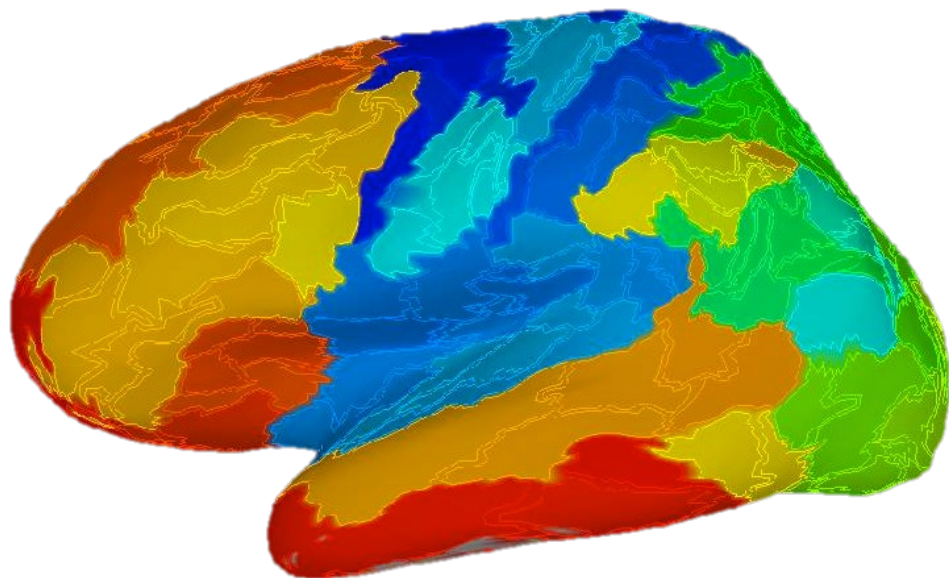
16192

^aSection on Functional Imaging Methods, ^bFunctional MRI Core Facility, and ^cStatistical and Scientific Computing Core, National Institute of Mental Health, Bethesda, MD 20814; ^dBehavioural and Clinical Neuroscience Institute, University of Cambridge, Cambridge CB2 1QP, United Kingdom; ^eNational Institute of Health Research Cambridge Biomedical Research Centre, Cambridgeshire Peterborough National Health System Foundation Trust, Cambridge SW1A 2NS, United Kingdom; and ^fClinical Unit Cambridge, GlaxoSmithKline, Cambridge CB2 0QQ, United Kingdom

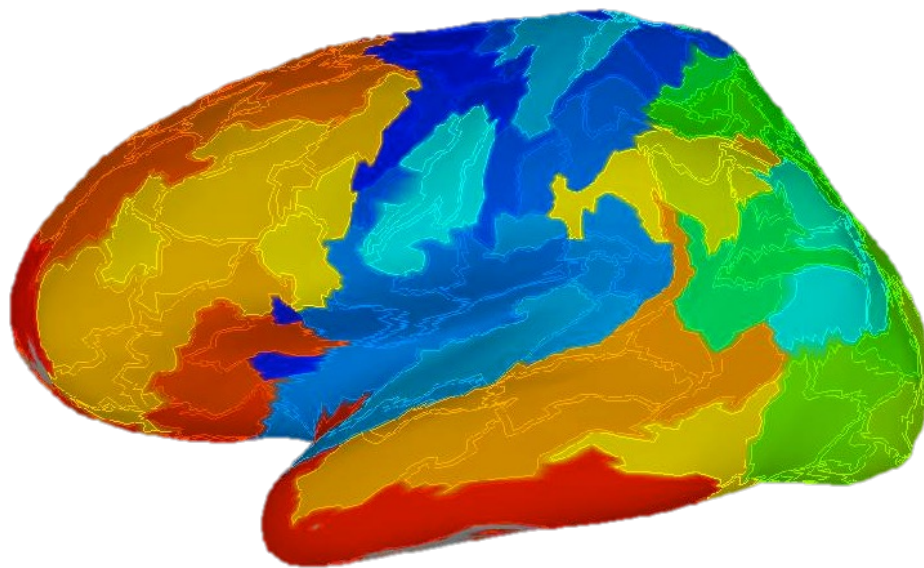
Edited by Marcus E. Raichle, Washington University in St. Louis, St. Louis, MO, and approved July 31, 2013 (received for review January 29, 2013)

Test-retest of **group** clustering at 350 clusters

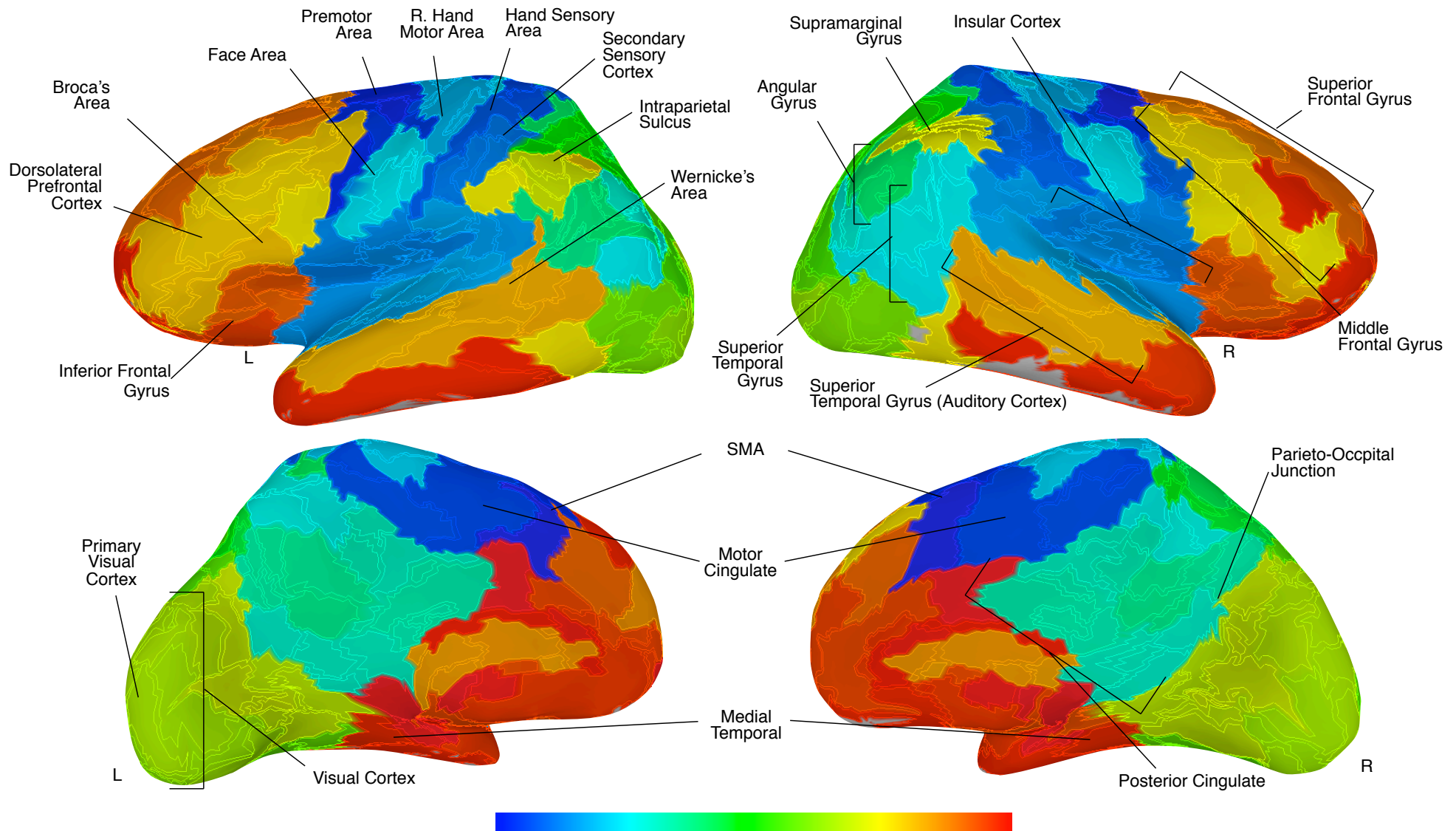
Rest 1

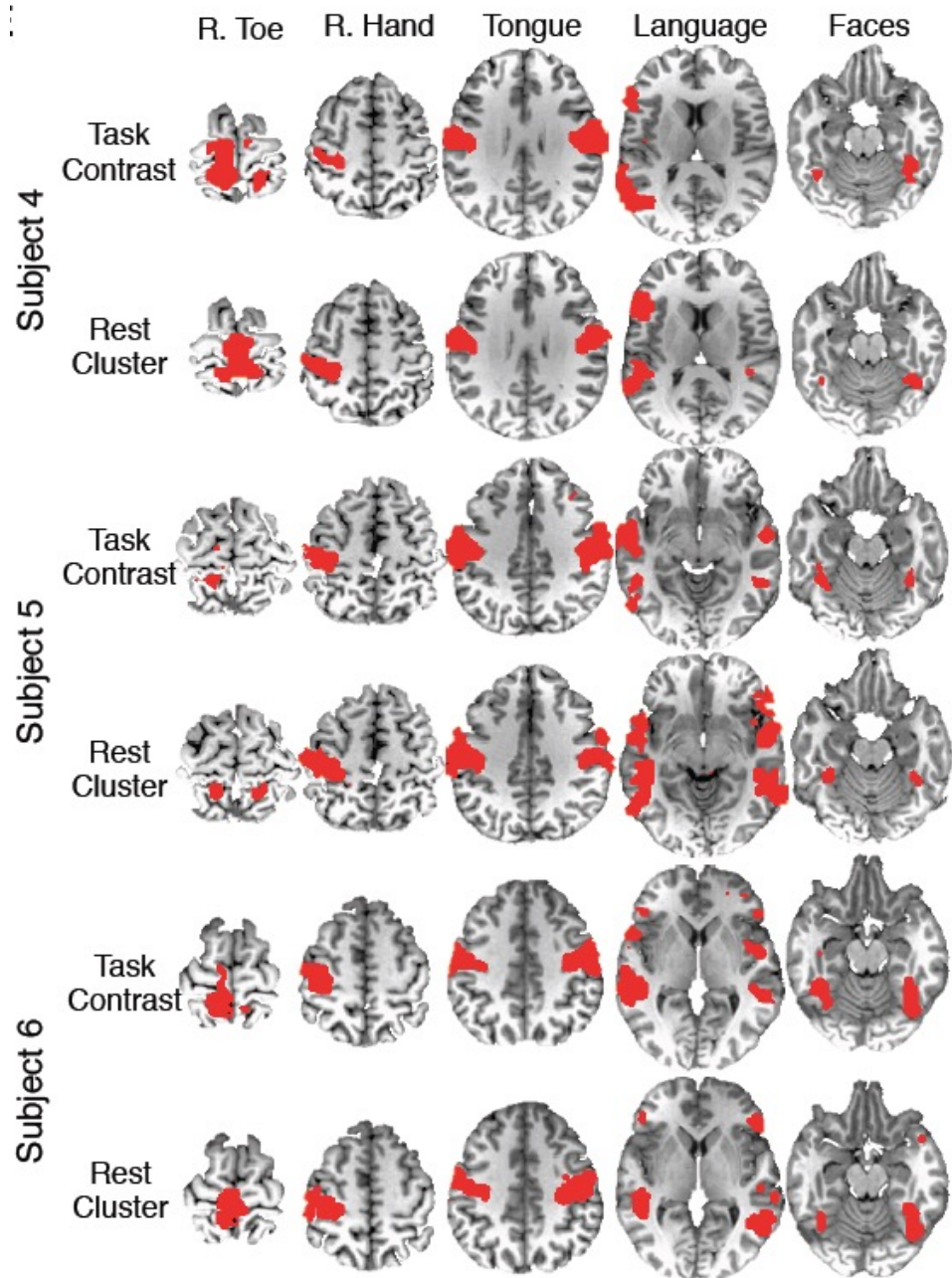
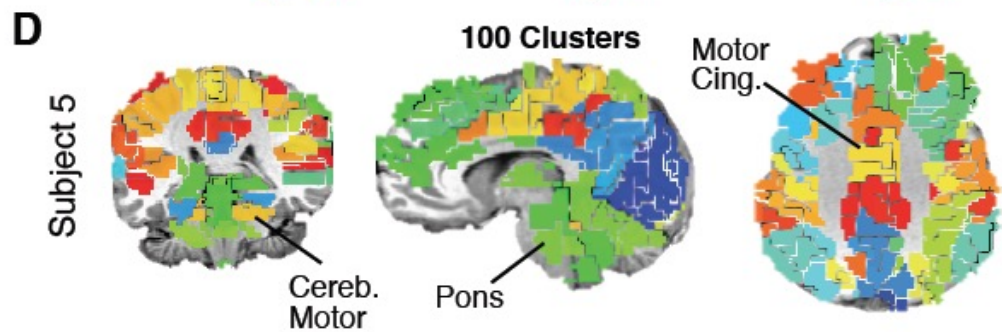
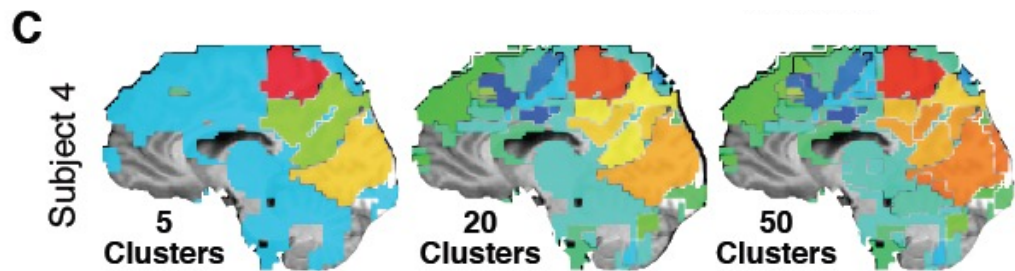


Rest 2
(color matched to Rest 1)



Clustering based on Resting State

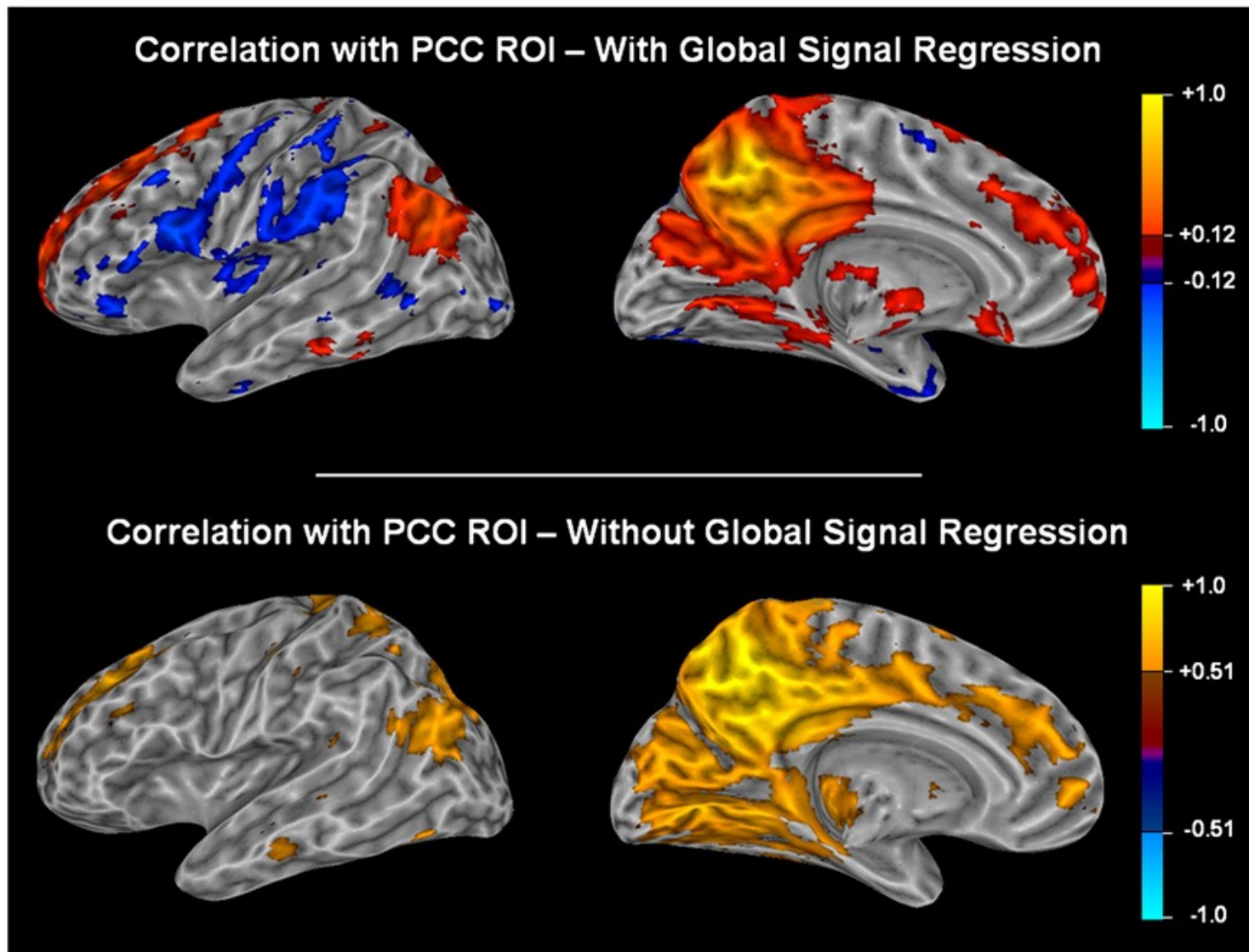




Two other issues with imaging resting state fluctuations:

1. Global signal correction or not?
2. Short range correlations may be scanner-related.

The issue of global signal regression

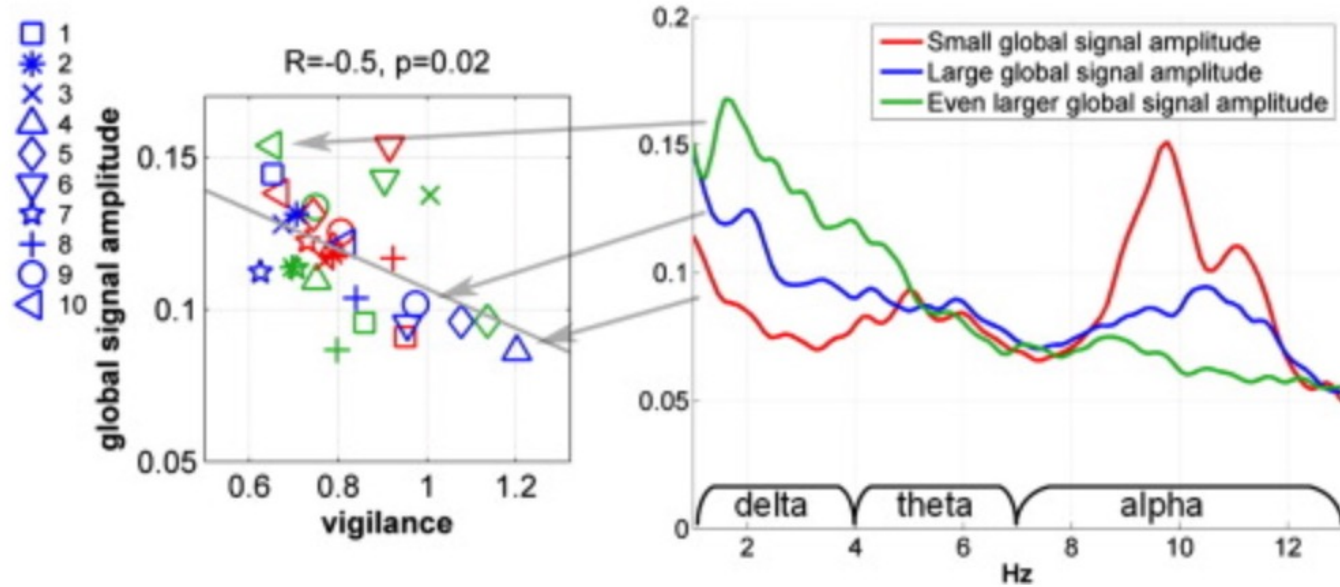


K. Murphy, R. M. Birn, D. A. Handwerker, T. B. Jones, P. A. Bandettini, *NeuroImage*, 44, 893-905 (2009)

Global Signal Contains Information on Vigilance

Higher vigilance -> lower global signal

Vigilance = alpha / delta

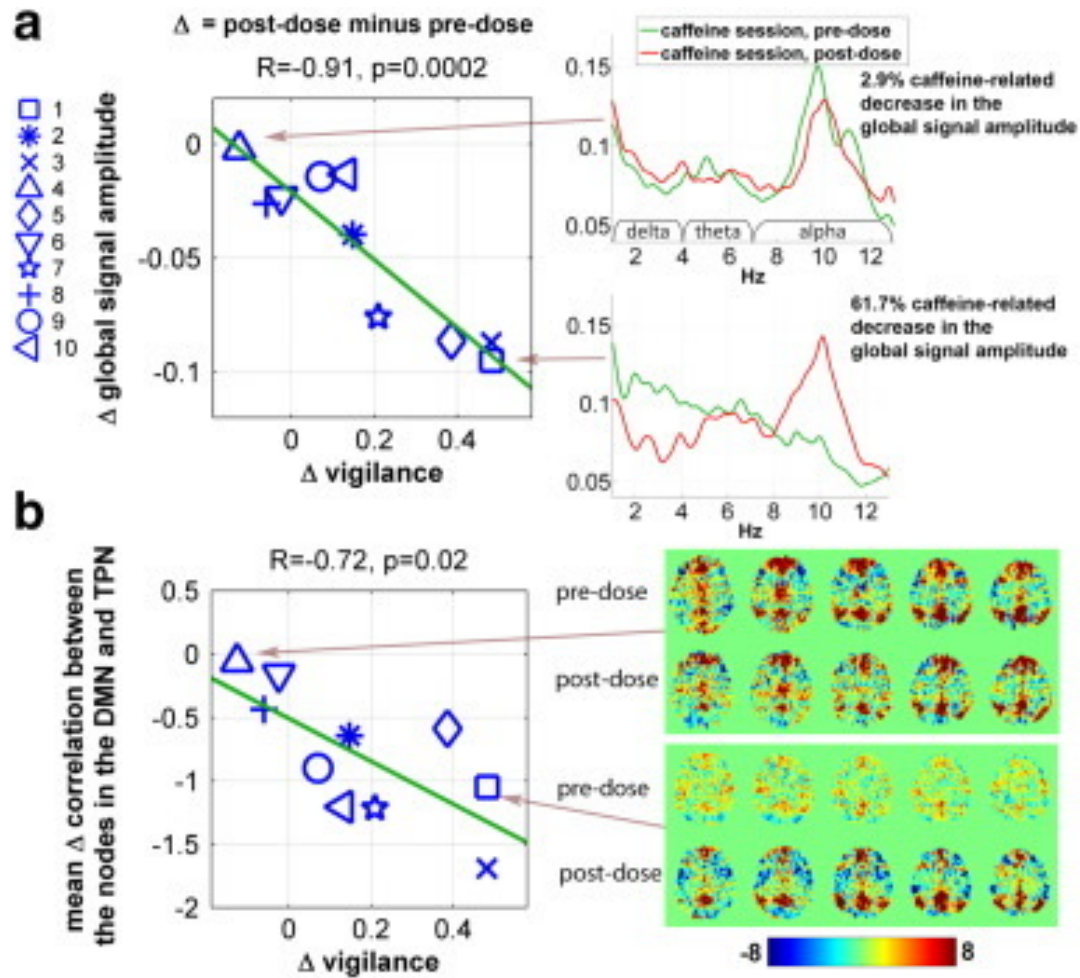


Chi Wah Wong, Valur Olafsson, Omer Tal, Thomas T. Liu

The amplitude of the resting-state fMRI global signal is related to EEG vigilance measures

NeuroImage, Volume 83, 2013, 983–990

<http://dx.doi.org/10.1016/j.neuroimage.2013.07.057>



Vigilance = alpha / delta

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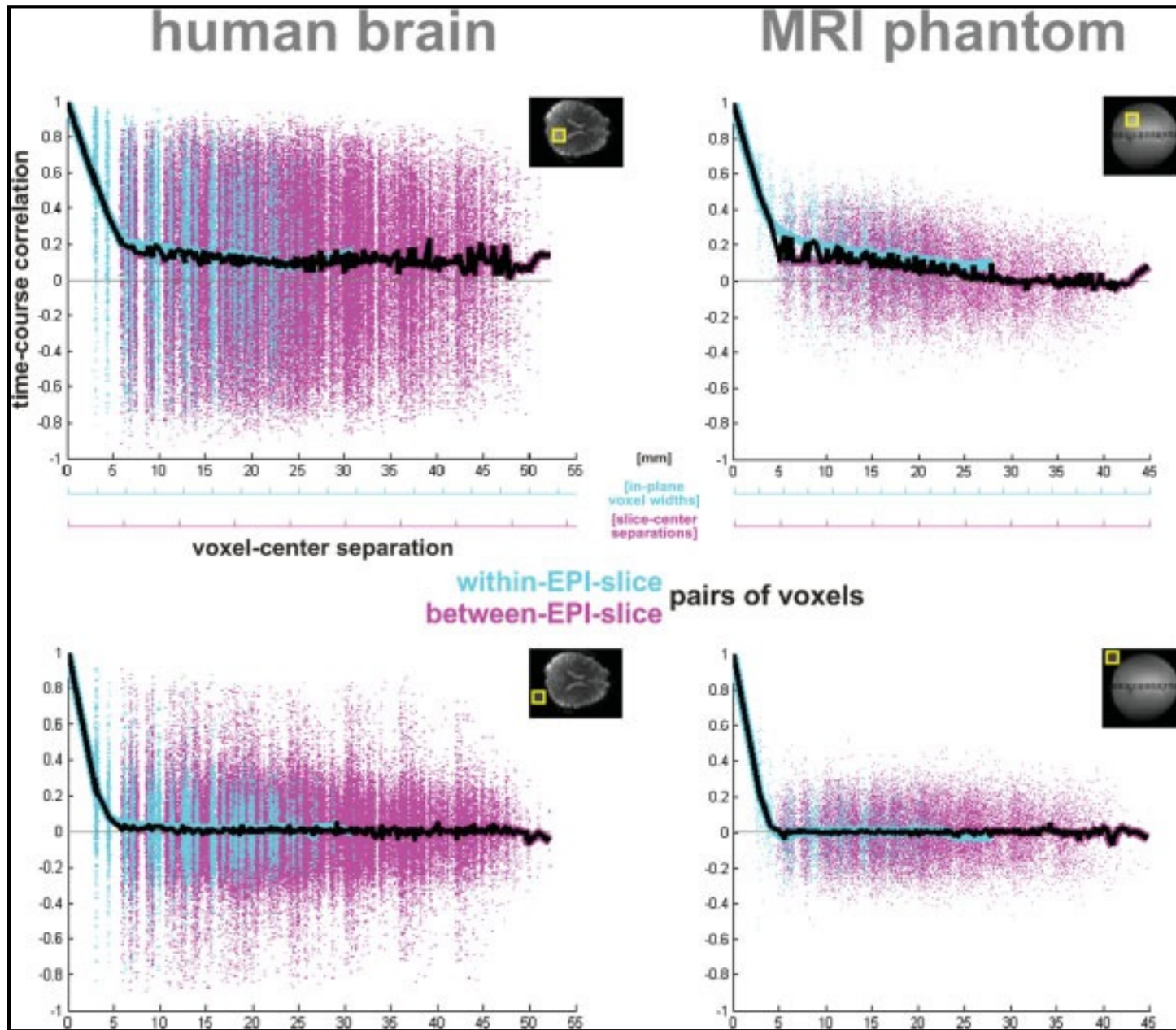
Chi Wah Wong, Valur Olafsson, Omer Tal, Thomas T. Liu

The amplitude of the resting-state fMRI global signal is related to EEG vigilance measures

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<http://dx.doi.org/10.1016/j.neuroimage.2013.07.057>

The issue of correlation across voxels due scanner instabilities

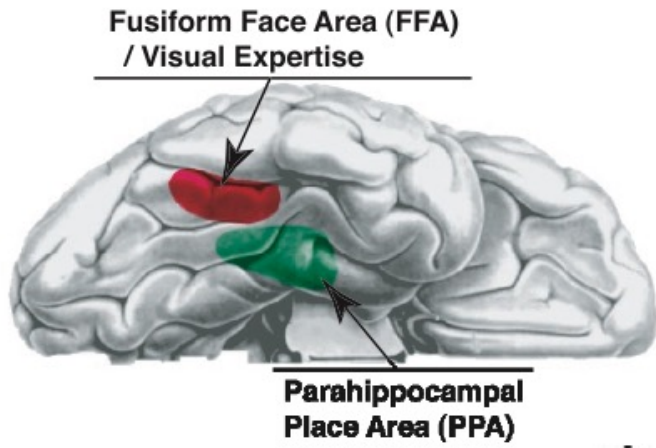


N. Kriegeskorte, J. Bodurka, P. Bandettini, *International Journal of Imaging Systems and Technology*, 18 (5-6), 345-349 (2008)

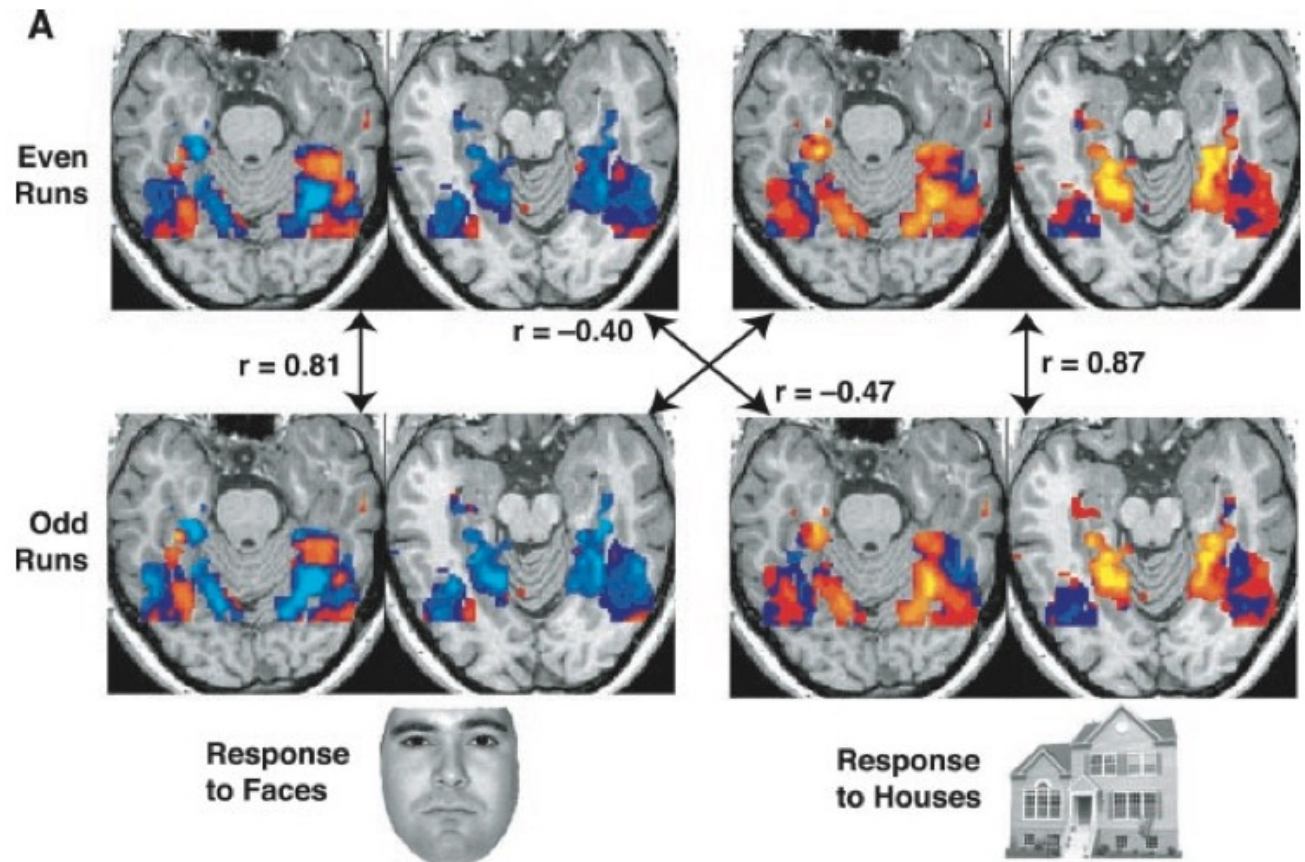
fMRI Paradigm Designs and Processing Strategies

- 1. Neuronal Activation Input Strategies**
- 2. Resting State fMRI**
- 3. fMRI Decoding**

Brain Reading

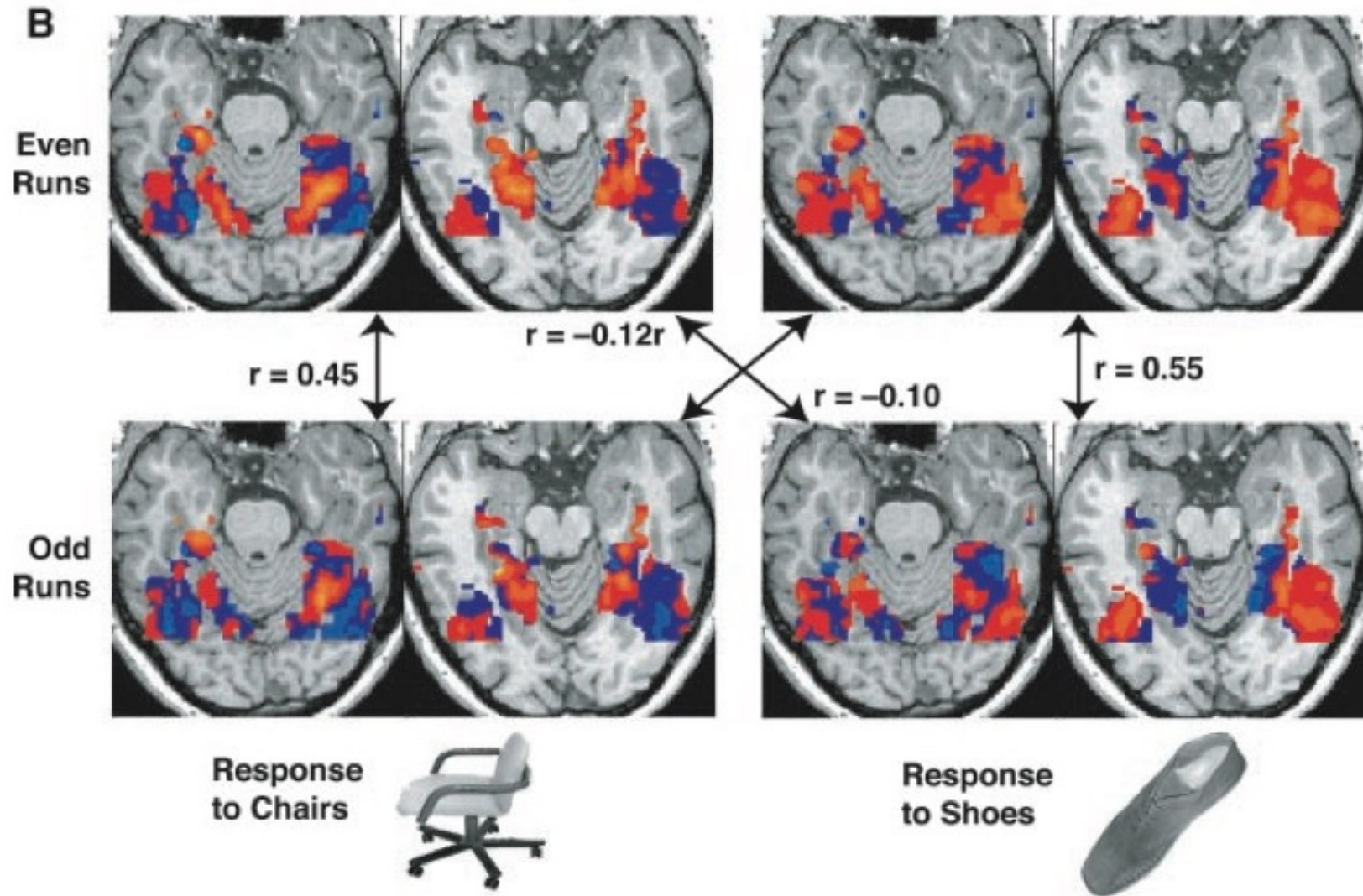


Face Area vs House Area

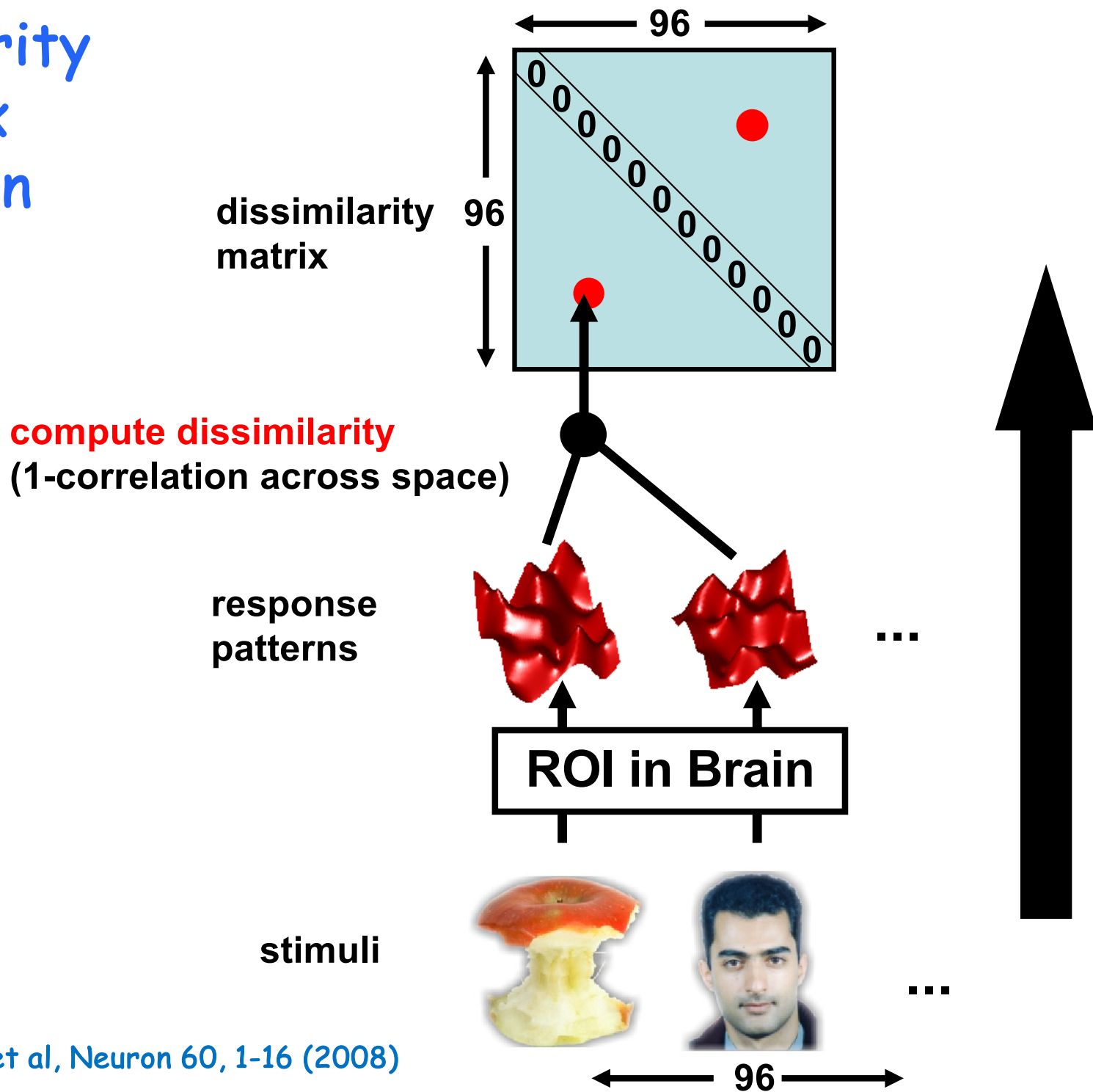


Brain Reading

Decoding more complex activity where obvious blobs don't appear



Dissimilarity Matrix Creation

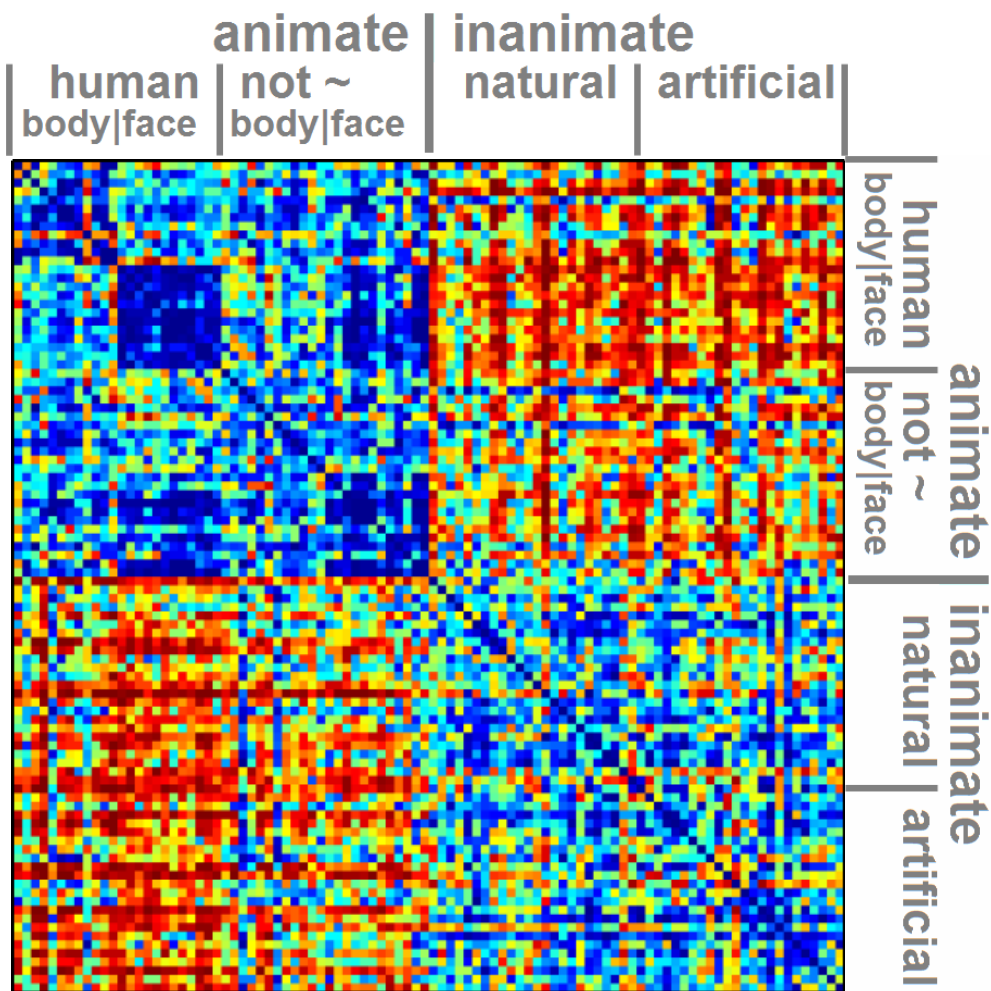


Visual Stimuli



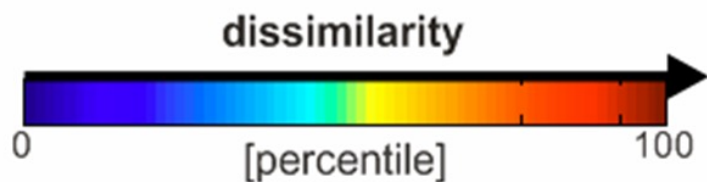
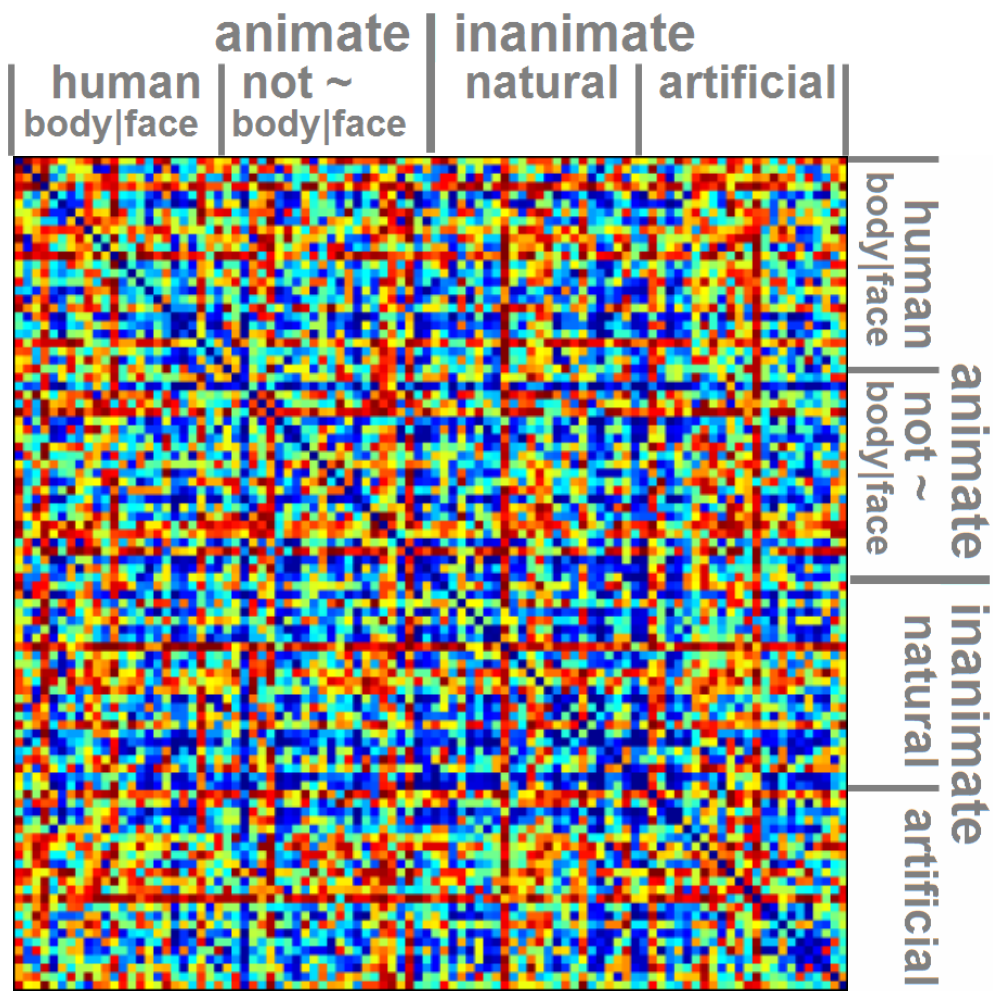
Human IT

(1000 visually most responsive voxels)



Human Early Visual Cortex

(1057 visually most responsive voxels)



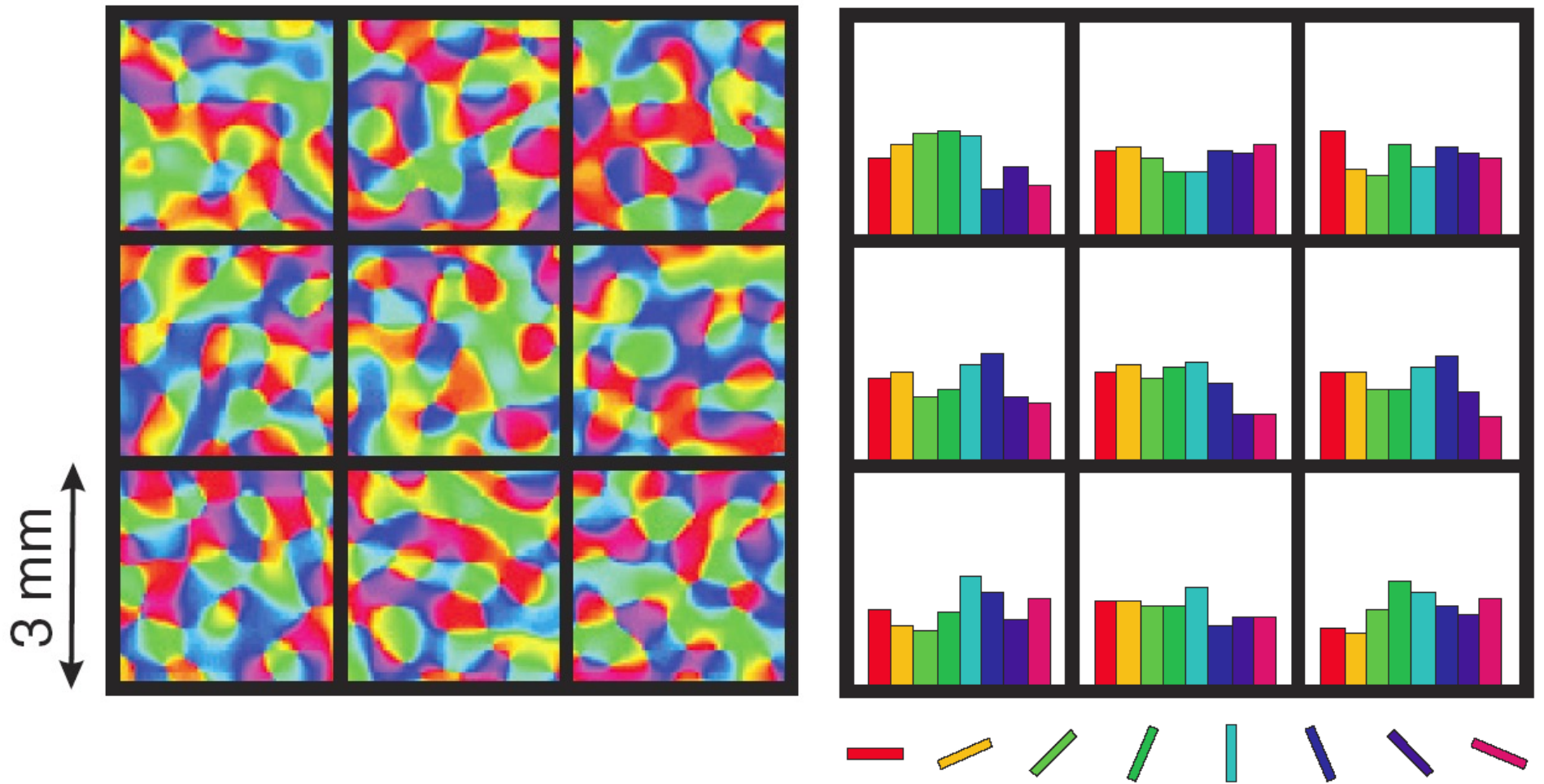
Monkey-Human Comparison Procedure

Human

- fMRI in four subjects
(repeated sessions,
>12 runs per subject)
- "quick" event-related design
(stimulus duration: 300ms,
stimulus onset asynchrony: 4s)
- fixation task
(with discrimination of fixation-point
color changes)
- occipitotemporal
measurement slab
(5-cm thick)
- small voxels ($1.95 \times 1.95 \times 2 \text{mm}^3$)
- 3T magnet, 16-channel coil
(SENSE, acc. fac. 2)

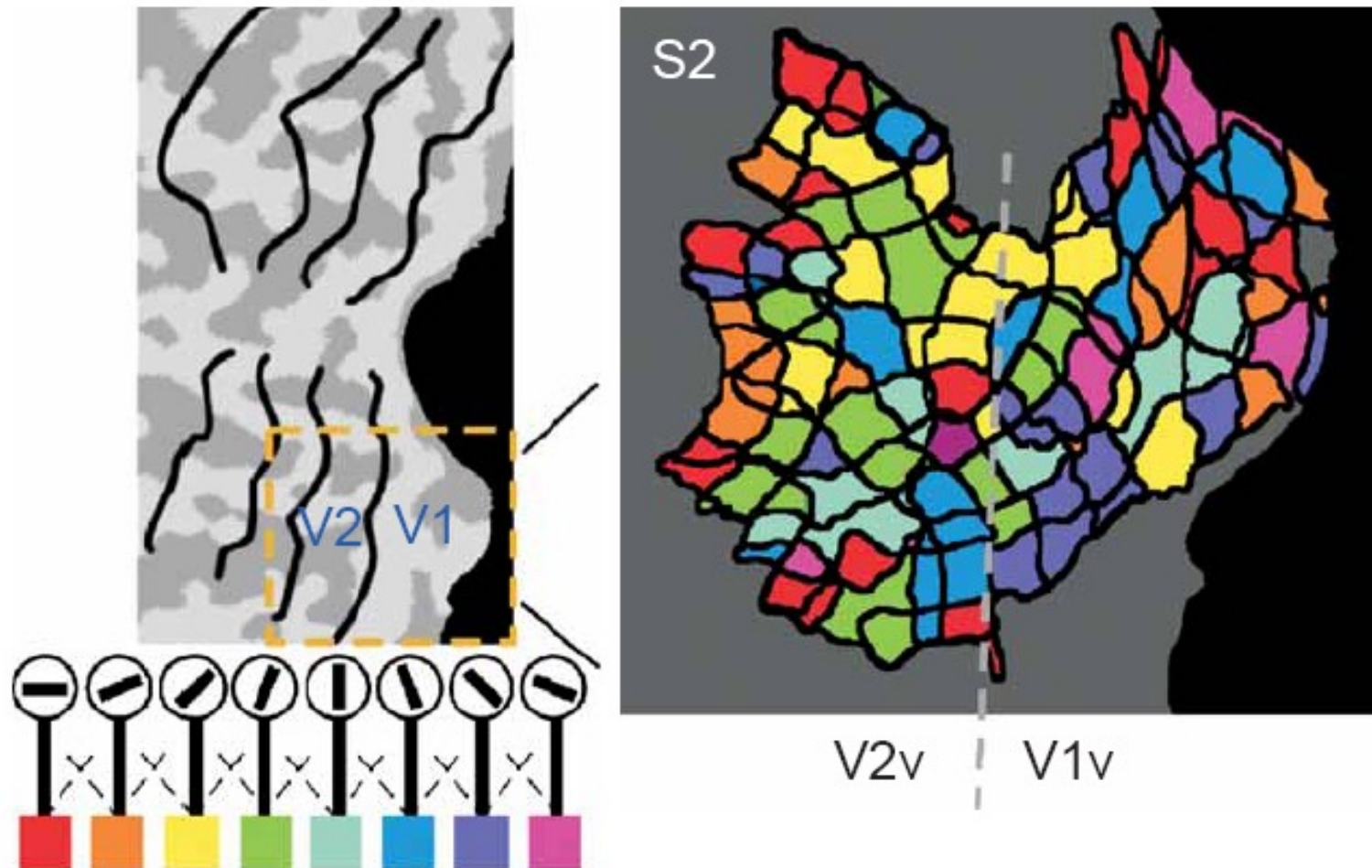
Monkey (Kiani et al. 2007)

- single-cell recordings
in two monkeys
- rapid serial presentation
(stimulus duration: 105ms)
- fixation task
- electrodes in anterior IT
(left in monkey 1, right in monkey 2)
- 674 cells total
- windowed spike count
(140-ms window starting 71ms after
stimulus onset)



Boynton (2005), News & Views on Kamitani & Tong (2005) and Haynes & Rees (2005)

Lower spatial frequency clumping



Kamitani & Tong (2005)

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