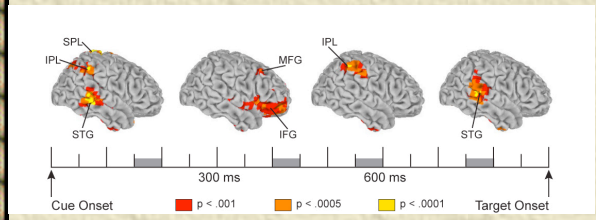
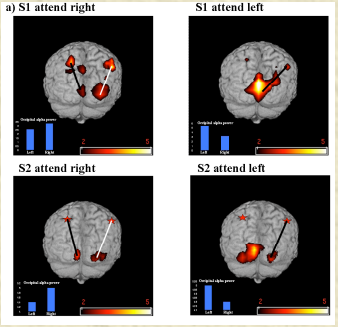
Neural Synchronization and Attention





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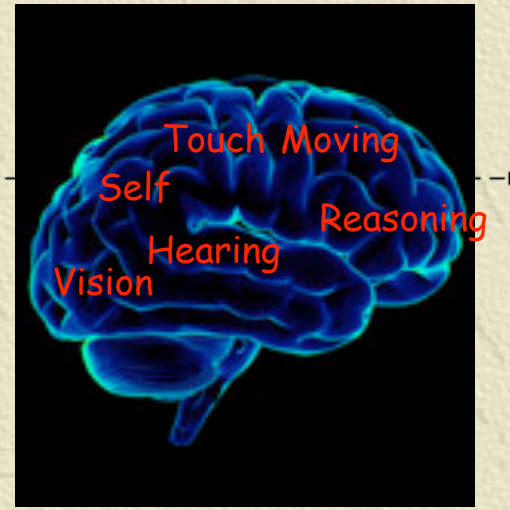
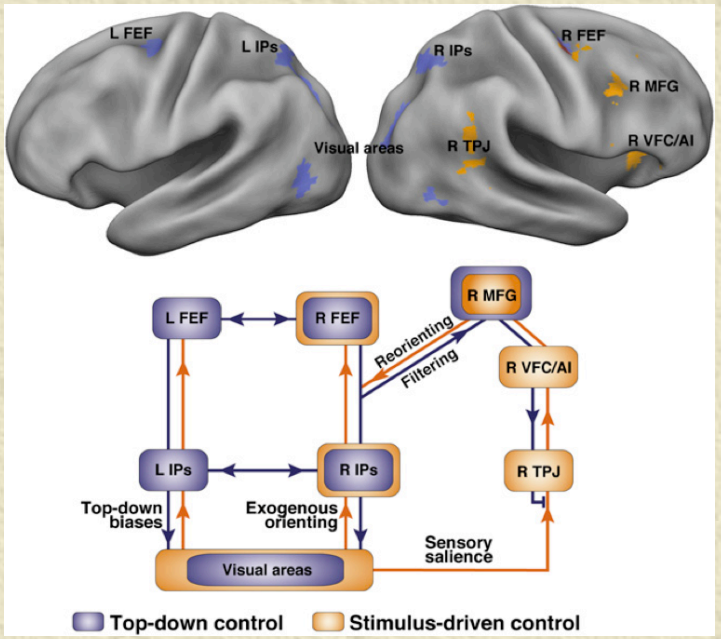
Themes

- Neural synchronization and its measurement
- Neural synchronization in endogenous attention orienting: EEG/MEG sensors and sources
  - Gamma-band synchronization establishes network
  - Alpha-band synchronization maintains network
  - Theta-band synchronization mediates "baton-passing" in the cerebral cortex via gamma band?

How is cognition implemented in the brain?



- Functionally specialized brain regions (grey matter)
  - E.g. visual cortex, auditory cortex, dorso-lateral prefrontal cortex
- Regions arranged in networks via neural pathways (white matter)
  - E.g., dorsal and ventral attention networks
- Each region participates in many different networks
- Regional function depends on active network: e.g. R MFG
- Functional networks are transient: e.g., attention shifts every 0.5 to 2 sec.

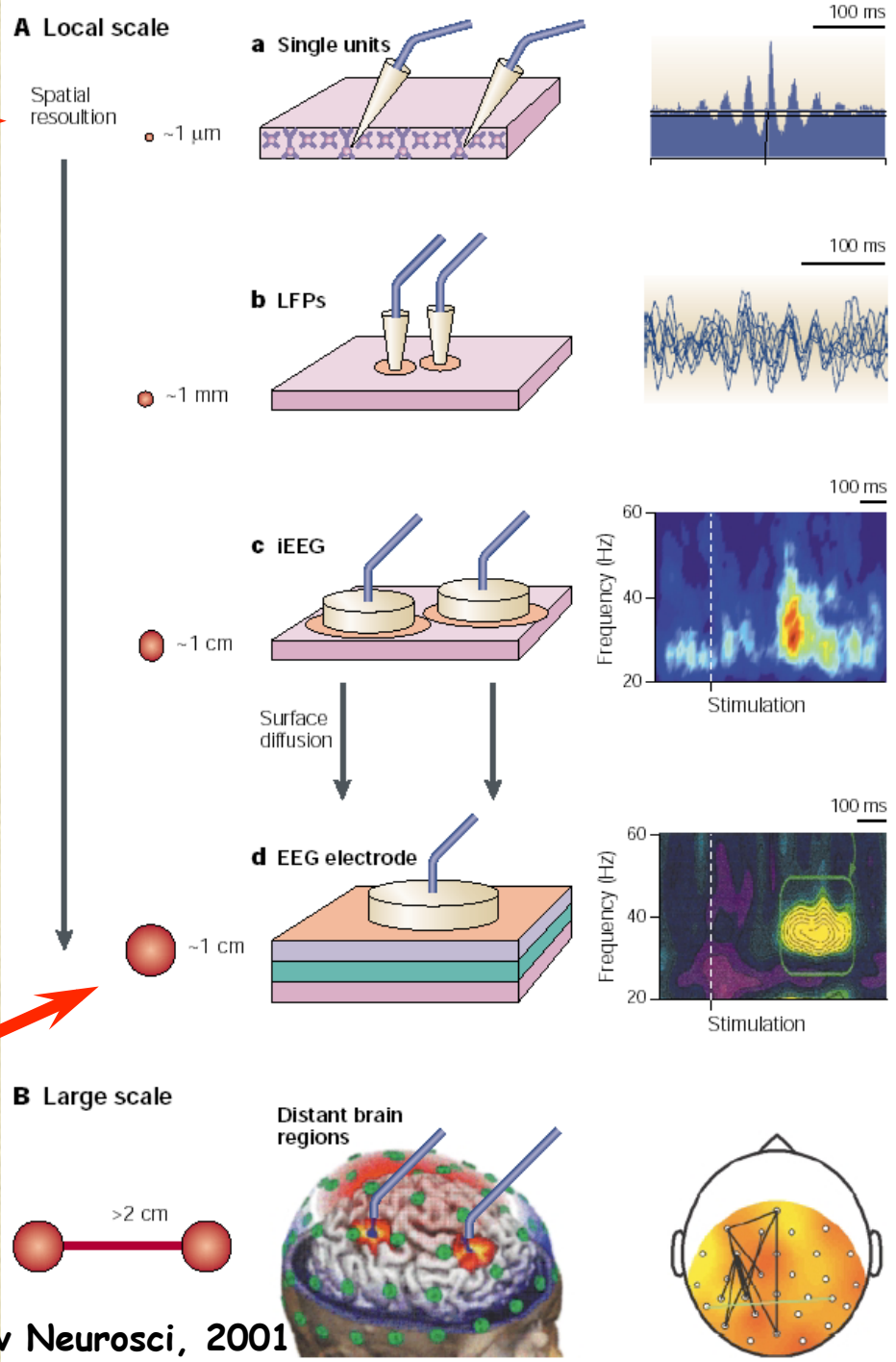


Corbetta, Patel, Shulman, 2008, *Neuron*

Gray & Singer's cats

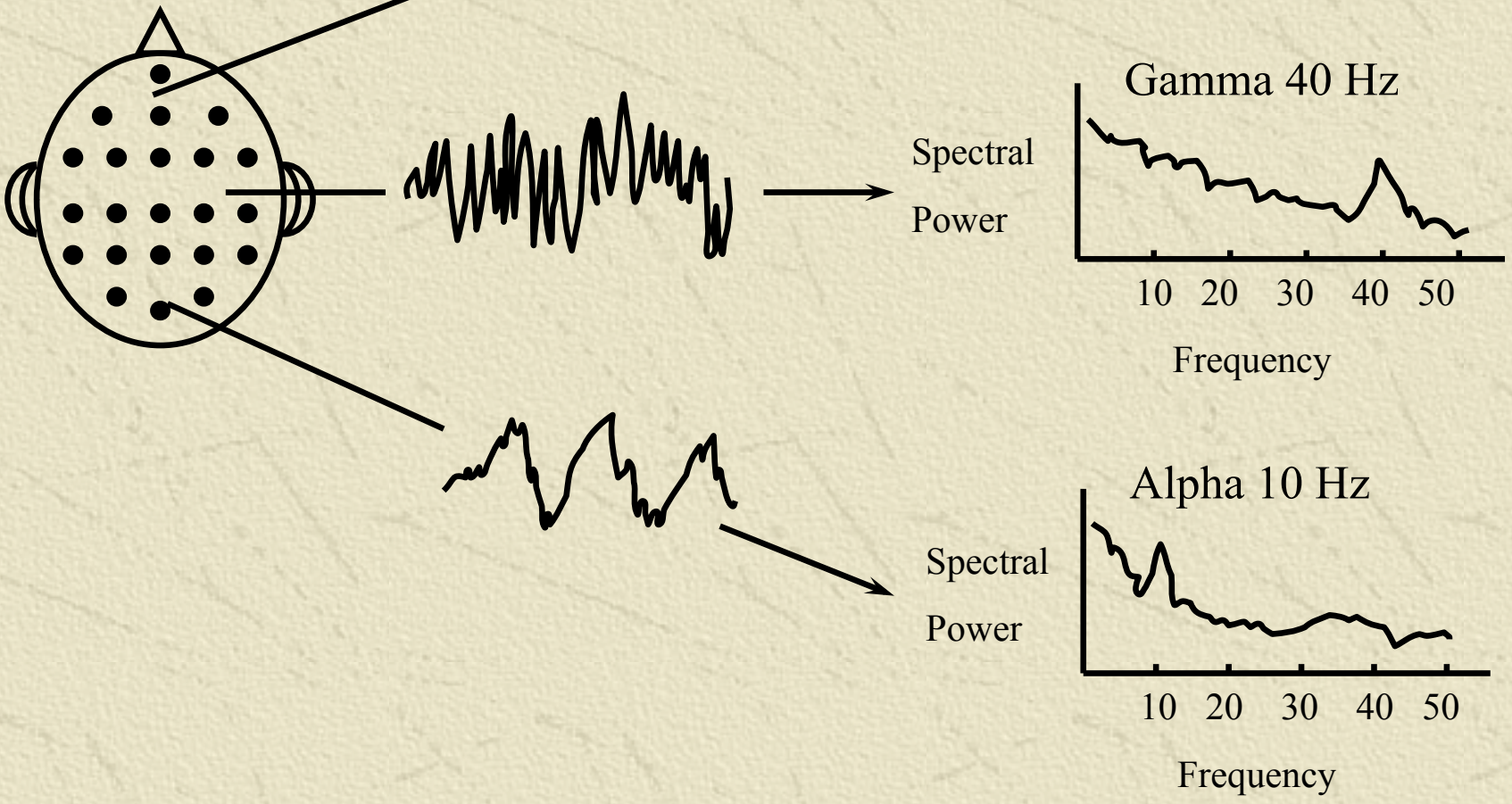
Neural synchrony occurs when neural activity, spiking or dendritic currents, in disparate locations rises and falls in a fixed relationship

Ward et al's humans



Varela et al, Nat Rev Neurosci, 2001

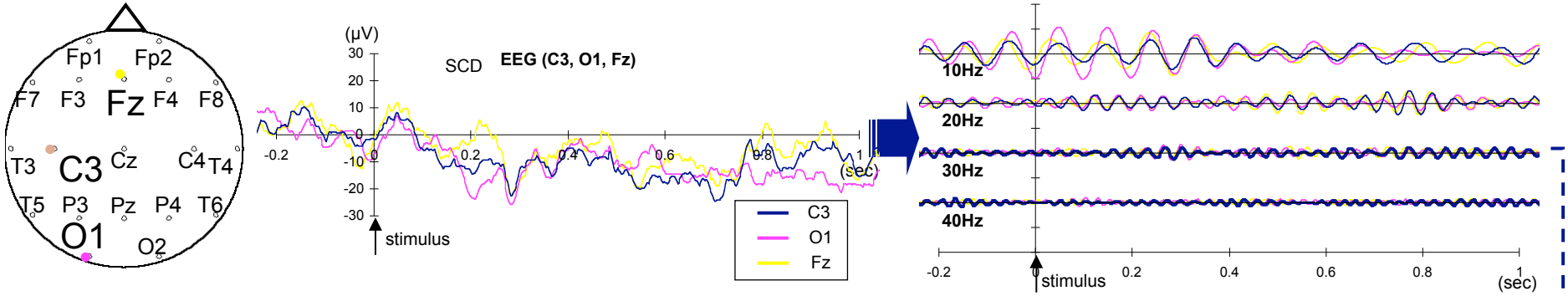
Spectral power in a given frequency range reflects local synchrony



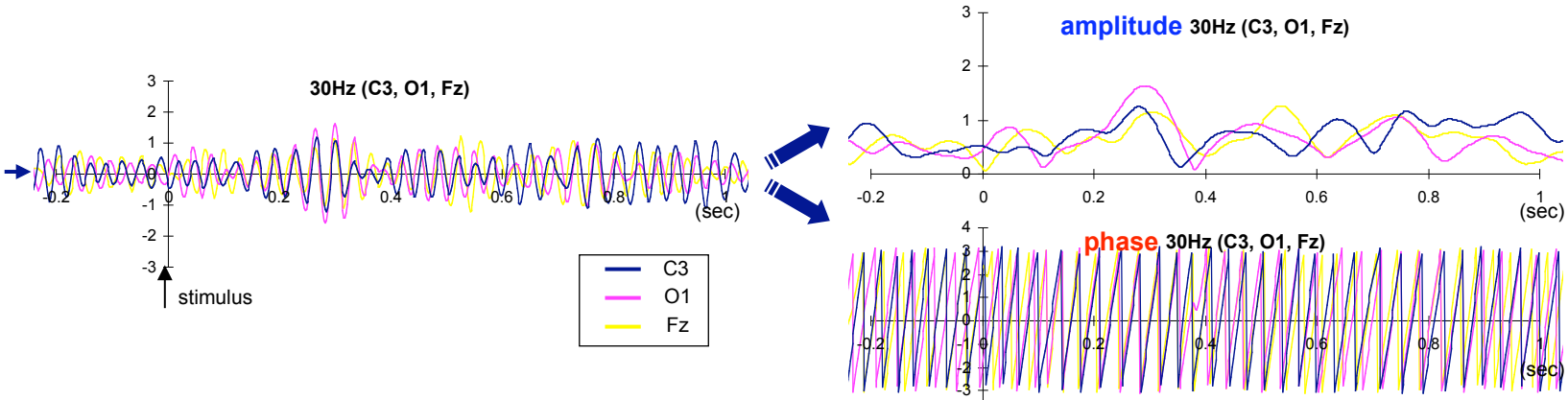
EEG/MEG synchronization analysis: calculation of phase locking value (PLV)

i.e. $-\sigma \cdot \Delta\Phi$, or MEG field strength, or neural source activity

Step.1 Obtain SCD of filtered signals *f(t)* via bandpass filtering at chosen frequencies



Step.2 instantaneous phase and amplitude

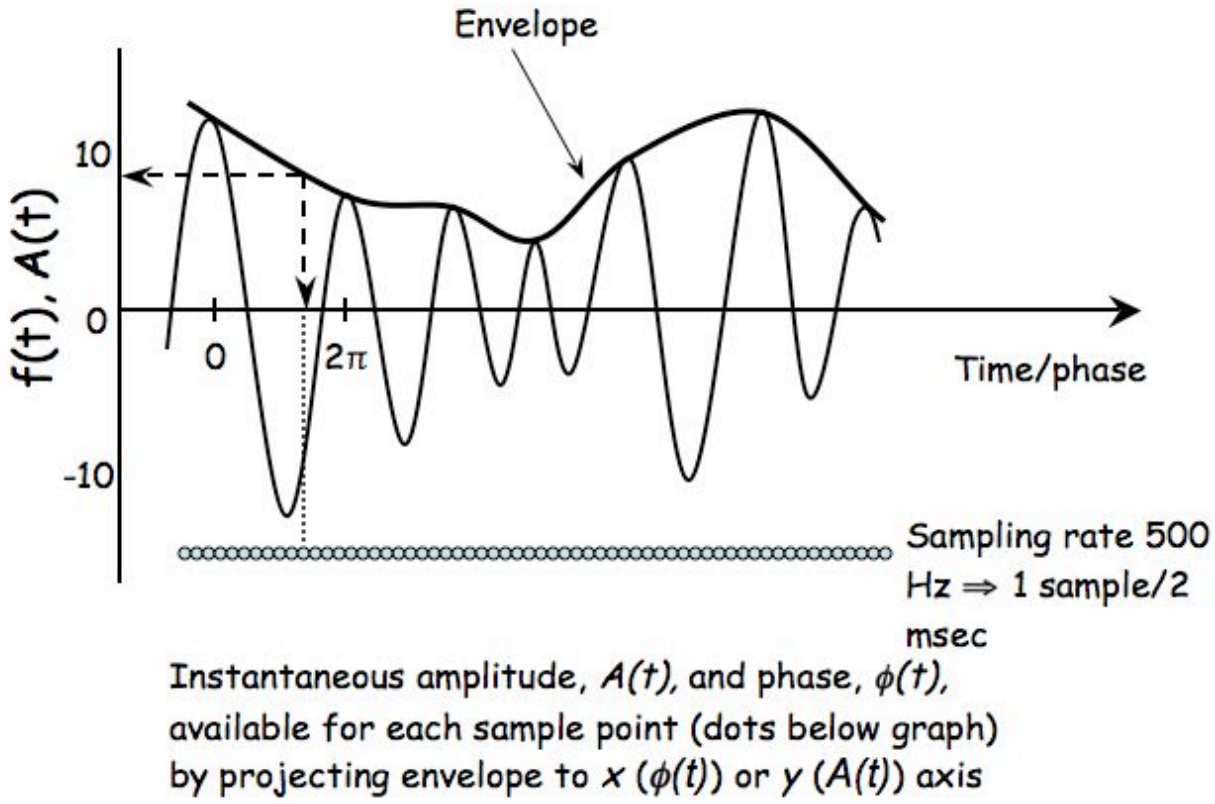


$$\zeta(t) = f(t) + i\tilde{f}(t) = \underline{A(t)}\exp\left(i\underline{\phi(t)}\right)$$

amplitude phase

where $\tilde{f}(t)$ *is Hilbert transform of* $f(t)$, $\quad \tilde{f}(t) = \pi^{-1} P.V. \int_{-\infty}^{\infty} \frac{f(\tau)}{t-\tau} d\tau$

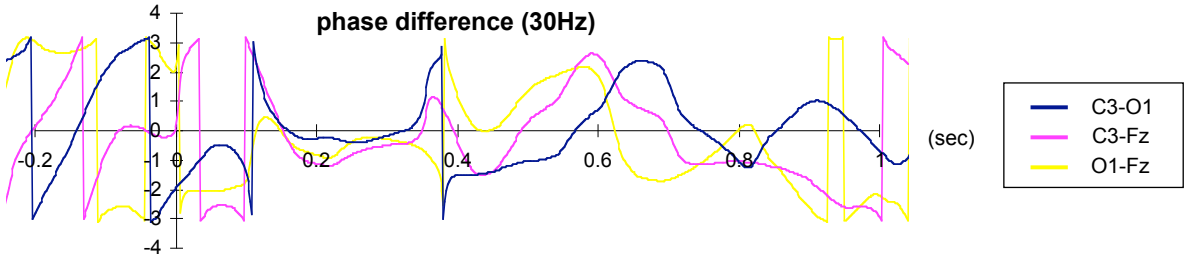
Analytic signal via Hilbert transform



Instantaneous amplitude, *A(t)*, and phase, $\phi(t)$, available for each sample point (dots below graph) by projecting envelope to *x* ($\phi(t)$) or *y* (*A(t)*) axis

Ward & Doesburg, 2009, in Handy (Ed) *Brain Signal Analysis*

Step.3 Calculation of phase locking value (PLV) for each time point



$$PLV(t)_{1,2} = \frac{1}{N}\left|\sum_{n=1}^{N} e^{i\theta(t,n)}\right| \quad \Rightarrow \begin{cases} \text{complete synchronization:1} \\ \text{random phase difference:0} \end{cases}$$

where

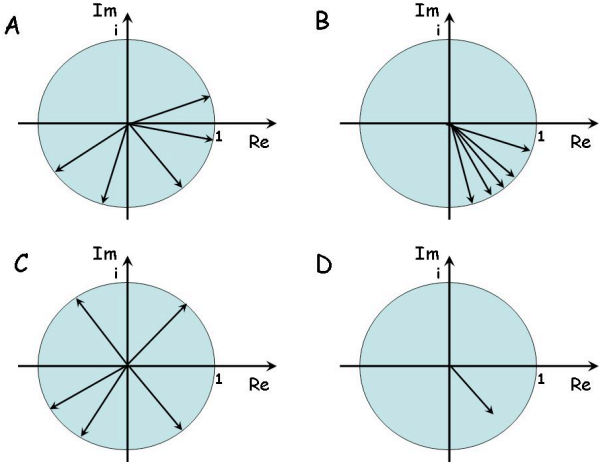
$\theta(t,n) = \phi_1(t,n) - \phi_2(t,n)$ (phase difference)

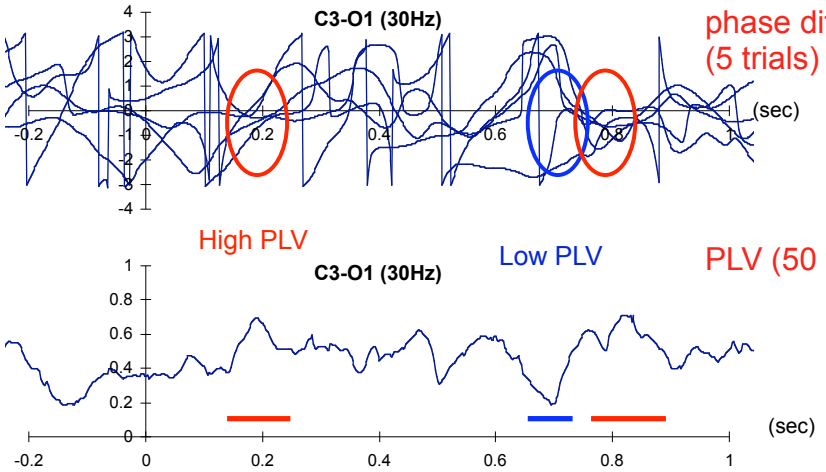
N : the number of trials

t : time points

ϕ_1 : the phase of the signal from electrode 1

ϕ_2 : the phase of the signal from electrode 2





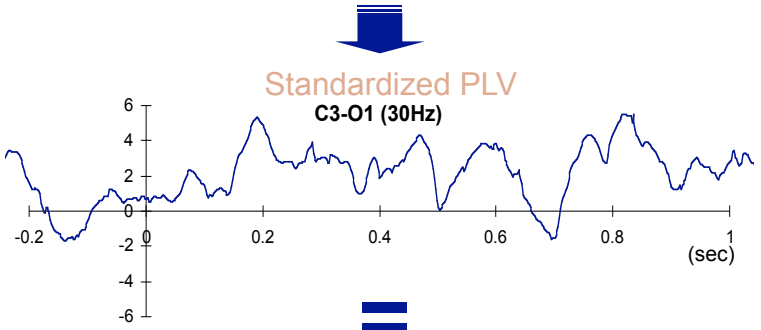
Step.4 standardization of PLV

To reduce the effect of volume conduction of stable sources and compare between electrode pairs at different distances

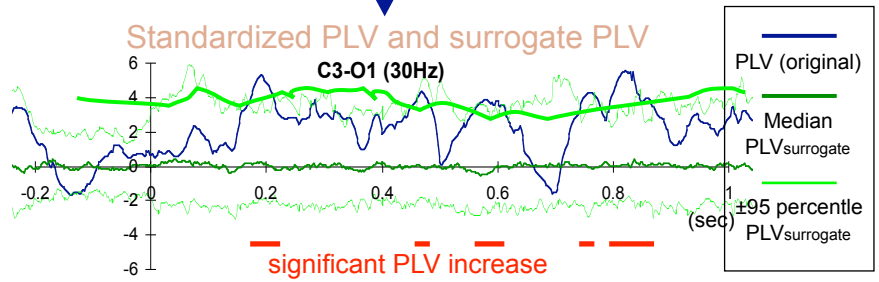
$$PLVz(t) = \frac{\left(PLV - PLV_{Bmean}\right)}{PLV_{Bsd}}$$

PLV_{Bmean} : the mean of PLV in the baseline period (400ms)

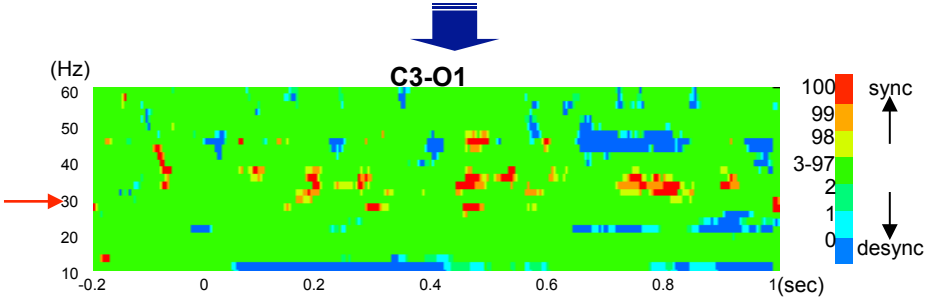
PLV_{Bsd} : the standard deviation of PLV in the baseline period (400ms)



Step.5 statistical test using surrogate data



Note: Amplitude and long-range PLV_z must change together for spurious synchronization to be indicated (Doesburg, Roggeveen, Kitajo, Ward, *Cerebral Cortex*, 2007)



Alpha, gamma and attention

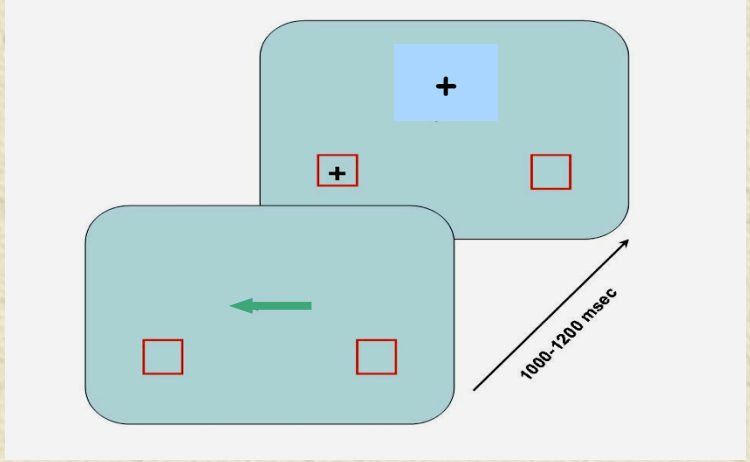
- Increased intra-regional alpha power associated with active suppression of processing
- Increased intra-regional gamma power associated with active processing
- Decreased alpha power necessary for gamma binding?
- Roles of inter-regional alpha and gamma synchrony?
- Coordination of intra- and inter-regional synchronization?
- Cross-frequency coupling? Theta-modulated gamma synchrony?

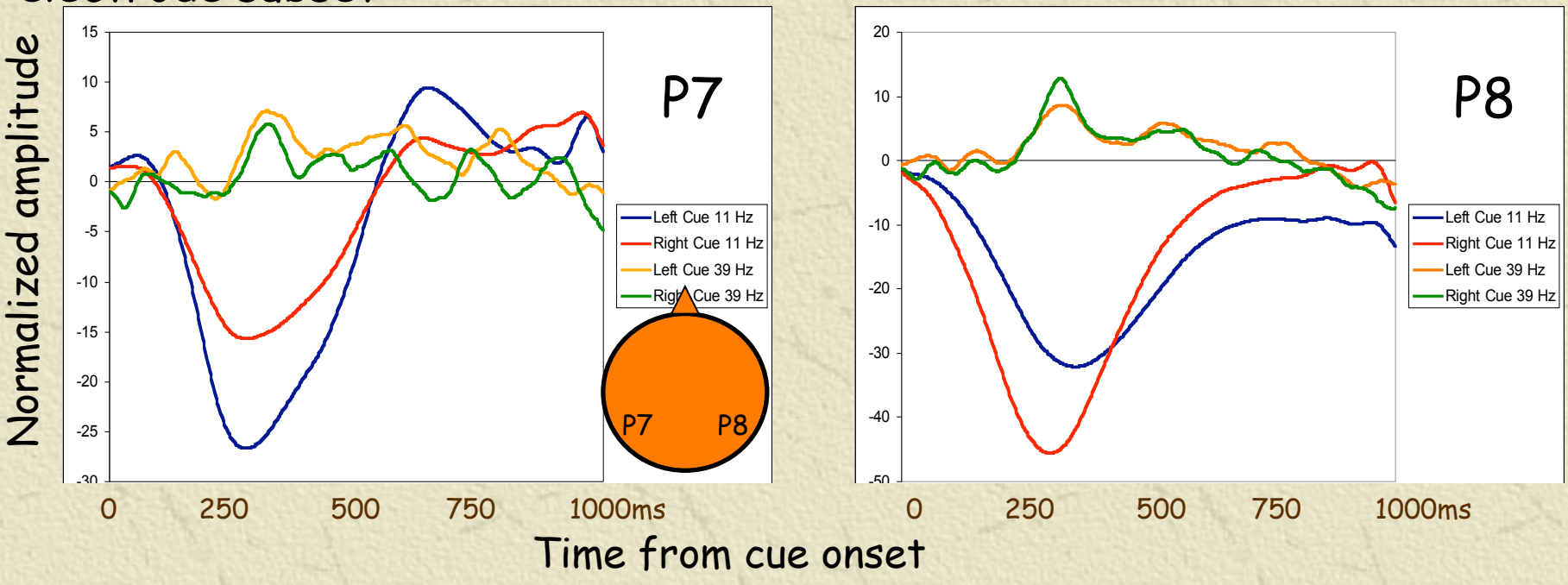
e.g., Klimesch, Jensen & Colgin, Palva & Palva, Ward

Alpha/gamma local synchrony (amplitude) indexes spatial attention orienting

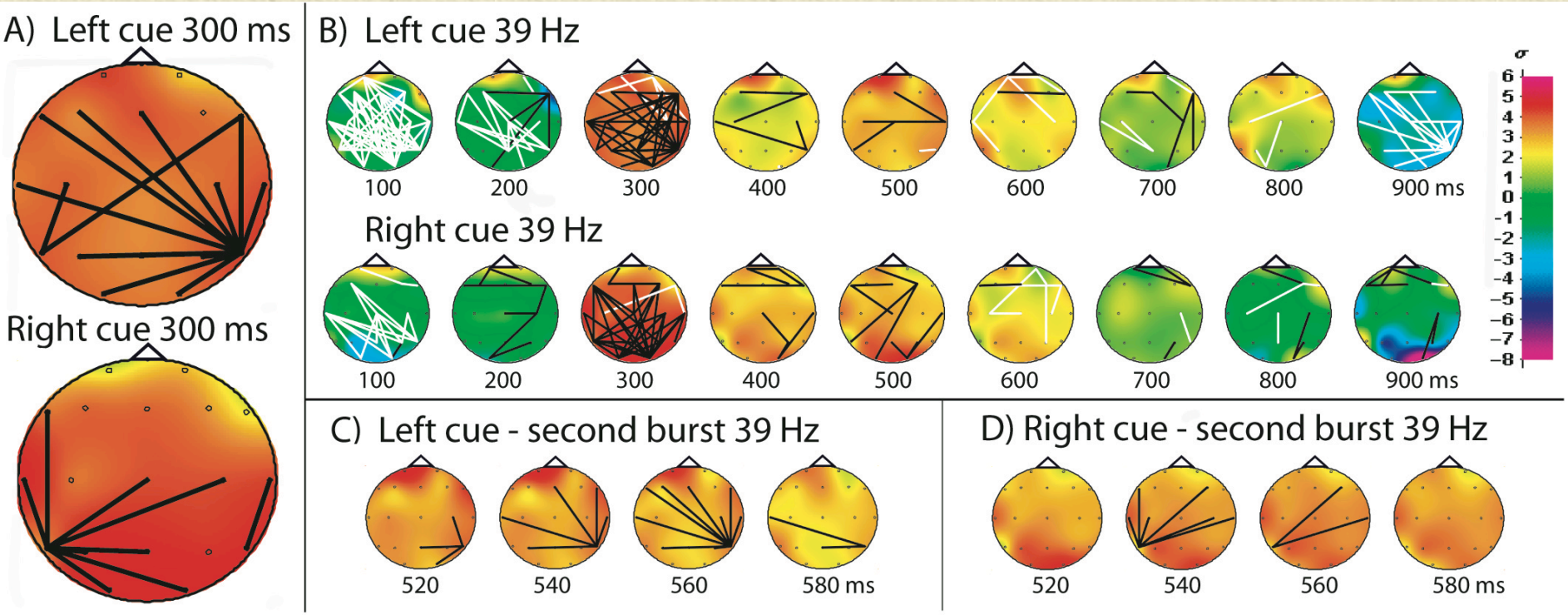
Doesburg, Roggeveen, Kitajo & Ward, 2008, *Cerebral Cortex*

- Attend to arrow-cued box
- Press button only if + in attended box, not if x nor if either in unattended box
- Cue-target SOA 1000-1200 ms
- Cue onset at 0 ms in figures
- EEG 64-channel SA system; 19-electrode subset



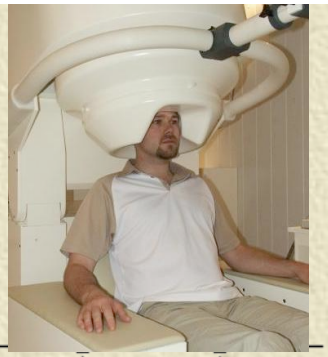


Long-distance gamma synchrony establishes focused attention network

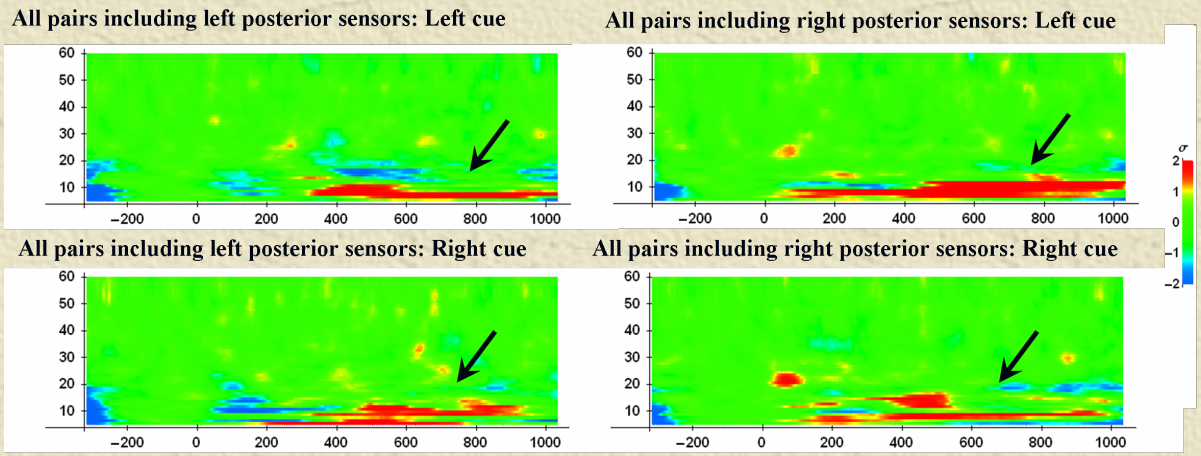


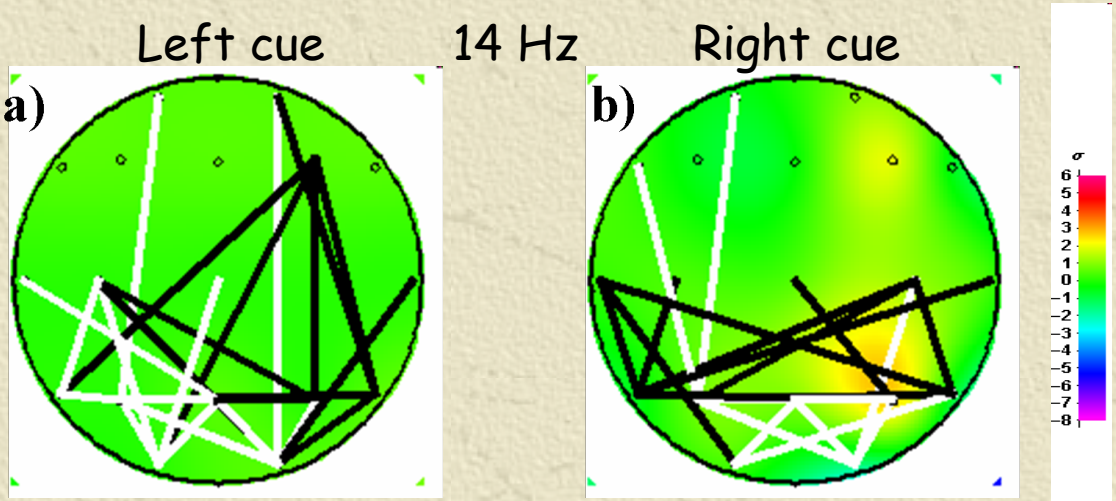
- At 250 ms (same as local power max gamma/min alpha) increase in global phase locking at diverse frequencies
- Lateralized in gamma band: P7 (left) for right target, P8 (right) for left target (orienting?)
- Increased synch in beta band also but not lateralized (readying?)
- Desynch at 100 ms in gamma: erasing old network?

MEG replication: 151 sensor CTF system, 3rd order synthetic gradiometers



- Increased lateralized synchronization in high alpha band from ~400 ms post cue onset until end of epoch
- Decreased synchronization side ipsilateral to cue
- Synchronization in alpha band associated with maintenance of attentional focus at cued location





Doesburg, Ward, 2007, *Proceedings BIOMAG2006*

What is SAM beamformer?

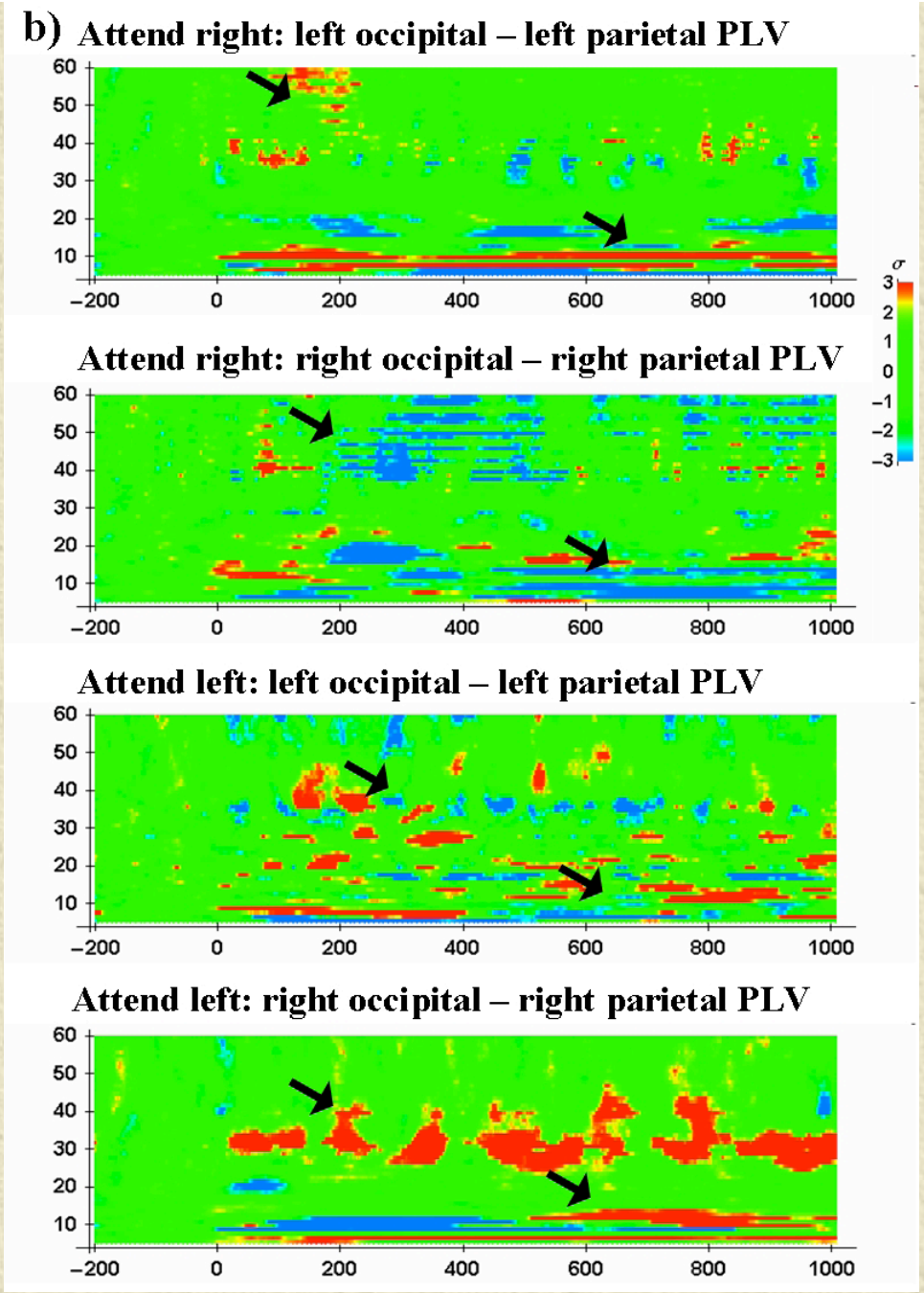
- Synthetic Aperture Magnetometry (Vrba & Robinson 2001, *Methods*)
- Based on time/space covariance matrix of sensor records
- Achieves estimate of source power for each voxel in brain region from weighted linear combination of all measurements (where weights are selected to attenuate signals from all other voxels):

$$\hat{S}_\theta(t) = \mathbf{W}_\theta^t \mathbf{m}(t)$$

- Optimal coefficients found by minimizing total power over time (computational tricks used in practice).
- Spatial filtering technique utilizing forward solutions from brain model

MEG Replication

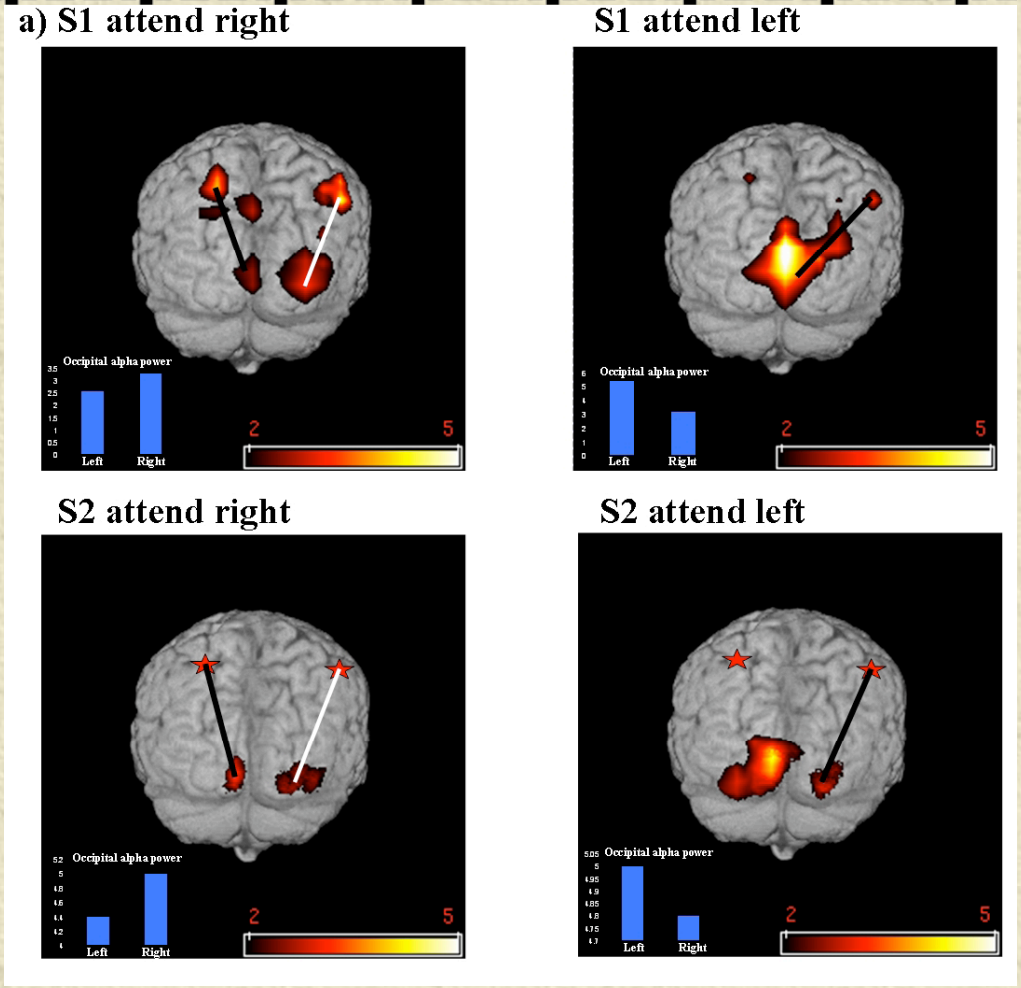
- MEG filtered at 14 Hz
- SAM beamformer sources in parietal (SPL?) and visual cortices (n=5)
- PLV analysis applied to broadband source activity filtered from 6 Hz to 60 Hz
- 14 Hz PLV shows lateralized increased synchrony similar to sensor analysis from 400-1000 ms post cue onset (right; n=2)
- 40 Hz (gamma-band) PLV shows burst of lateralized increased synchrony at ~200-250 ms post cue onset
- Theta rate gamma synch bursts at least for right parietal-occipital when attending left



Doesburg, Herdman, Ward, 2007, *Cognitive Neuroscience Society*

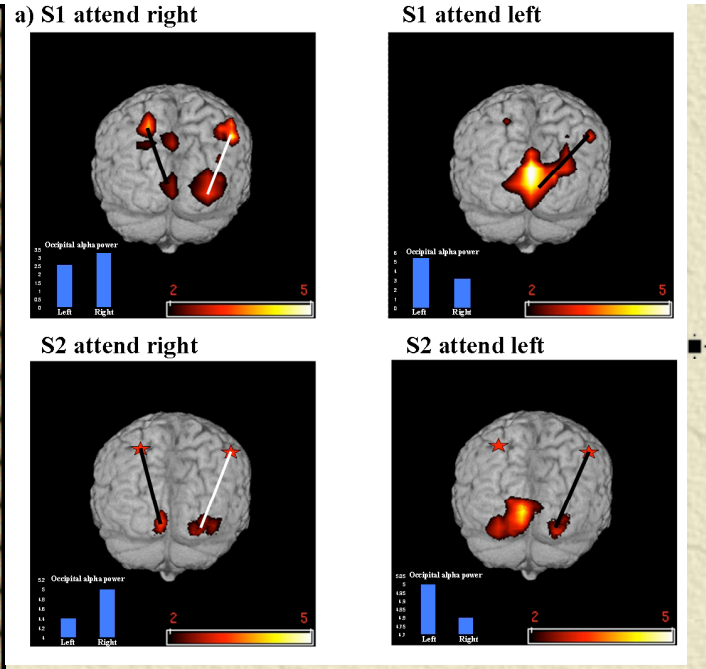
MEG replication

- Beamformer sources projected to cortical surface (star=source in a sulcus so projection done by hand)
- Lateralized increases and decreases in synchrony between parietal and occipital sources in alpha band from 400-800 ms post cue onset (here 800 ms and 14 Hz)
- Occipital 14 Hz power replicates EEG data (blue bars, 800 ms)

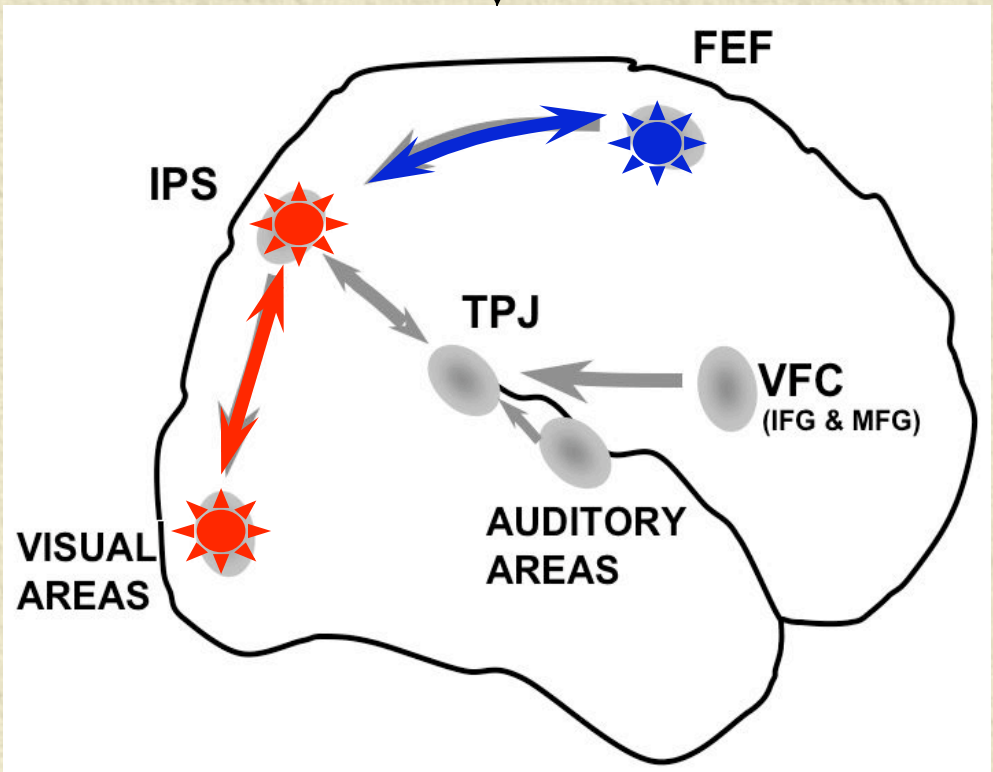


Doesburg, Herdman, Ward, 2007, *Cognitive Neuroscience Society*

MEG Replication

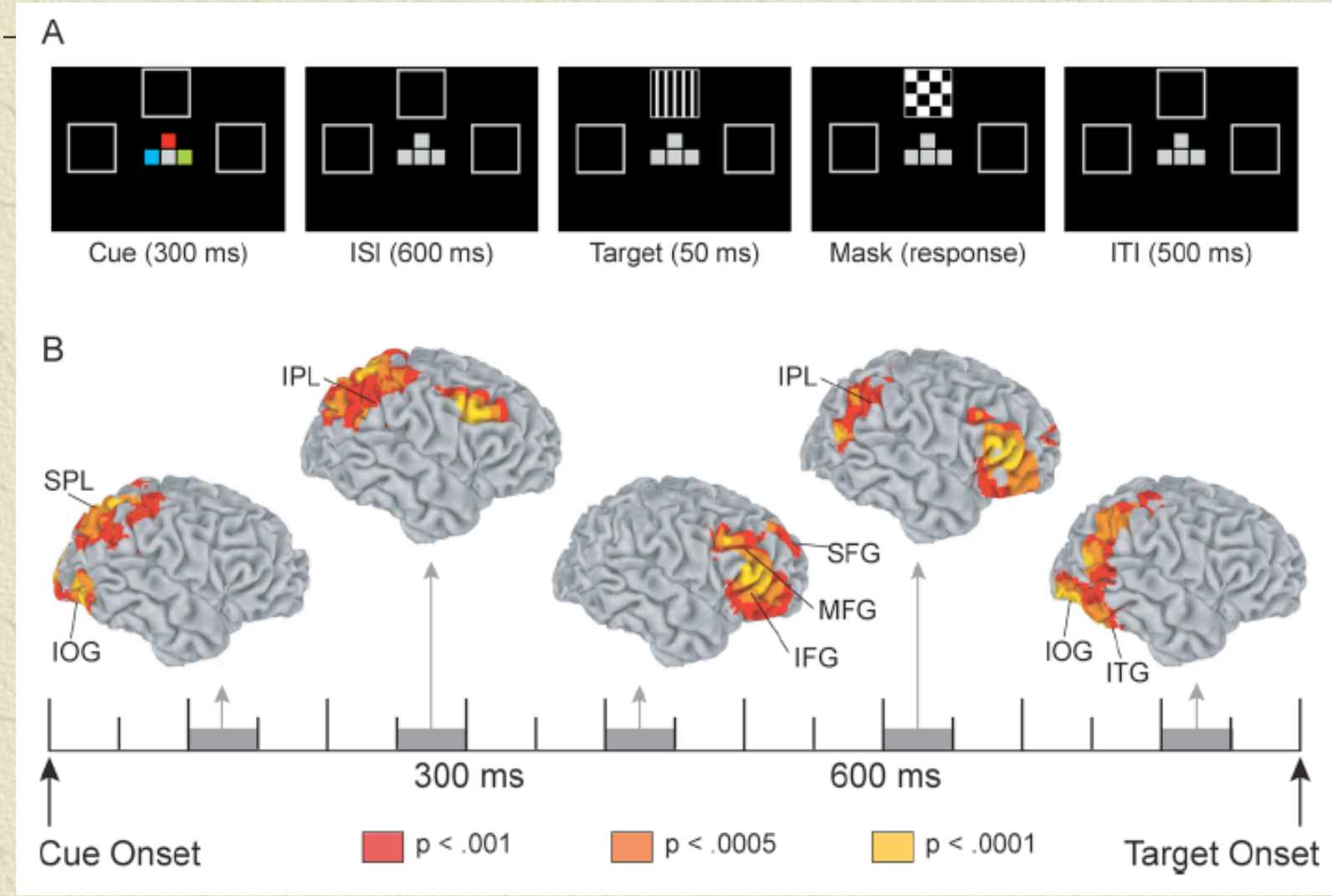


- Endogenous orienting: dorsal fronto- parietal (FEF, IPS, V1/V2)
- We also found FEF sources but not consistent enough for PLV analysis
- Not enough to activate relevant areas - must be synchronized to be functionally effective



Corbetta and Shulman (2002) *Nat Rev Neurosci;* Wright & Ward, 2008, *Orienting of Attention*

EEG source replication: BESA beamformer sources from theta band signals; shift minus neutral => only activity unique to orienting attention



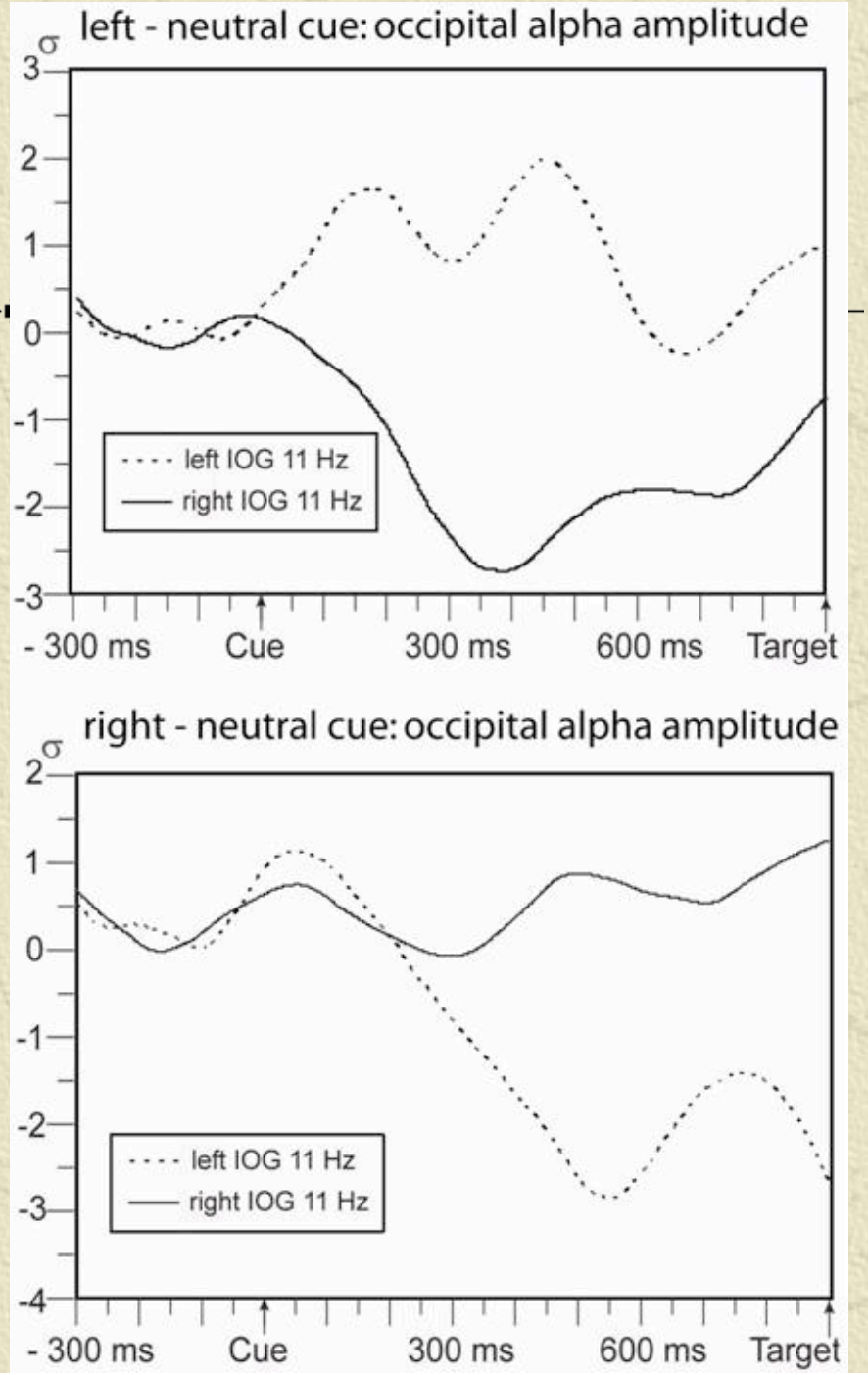
Green & McDonald, 2008, *PLoS Biology*

Synchronization analyses

- BESA beamformer sources in theta band identified
- *Broadband* activity of dipoles at peak voxel locations computed based on EEG recordings
- Broadband signals filtered and analytic signal, PLV etc., computed between sources

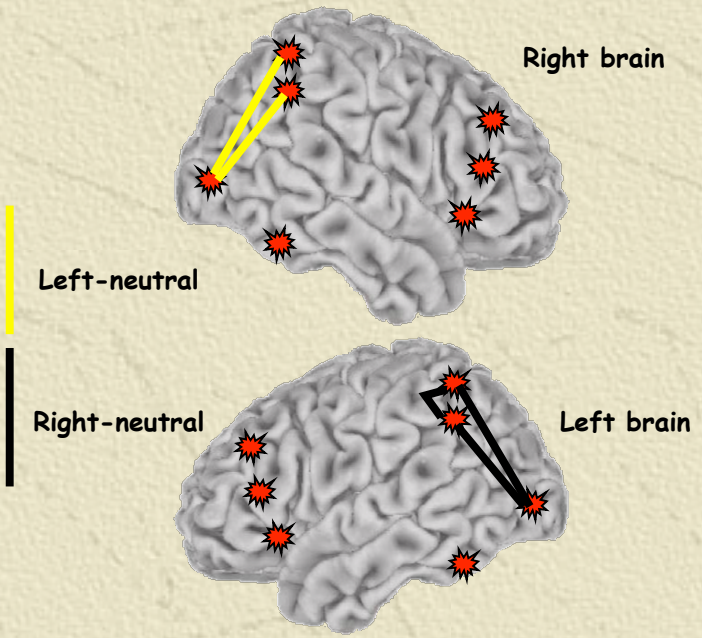
Detailed time course of intra-regional alpha-band amplitude

- Alpha amplitude in occipital cortex contralateral to the shift is decreased from shortly after cue onset until target onset
- Faster response the more ipsilateral occipital alpha power



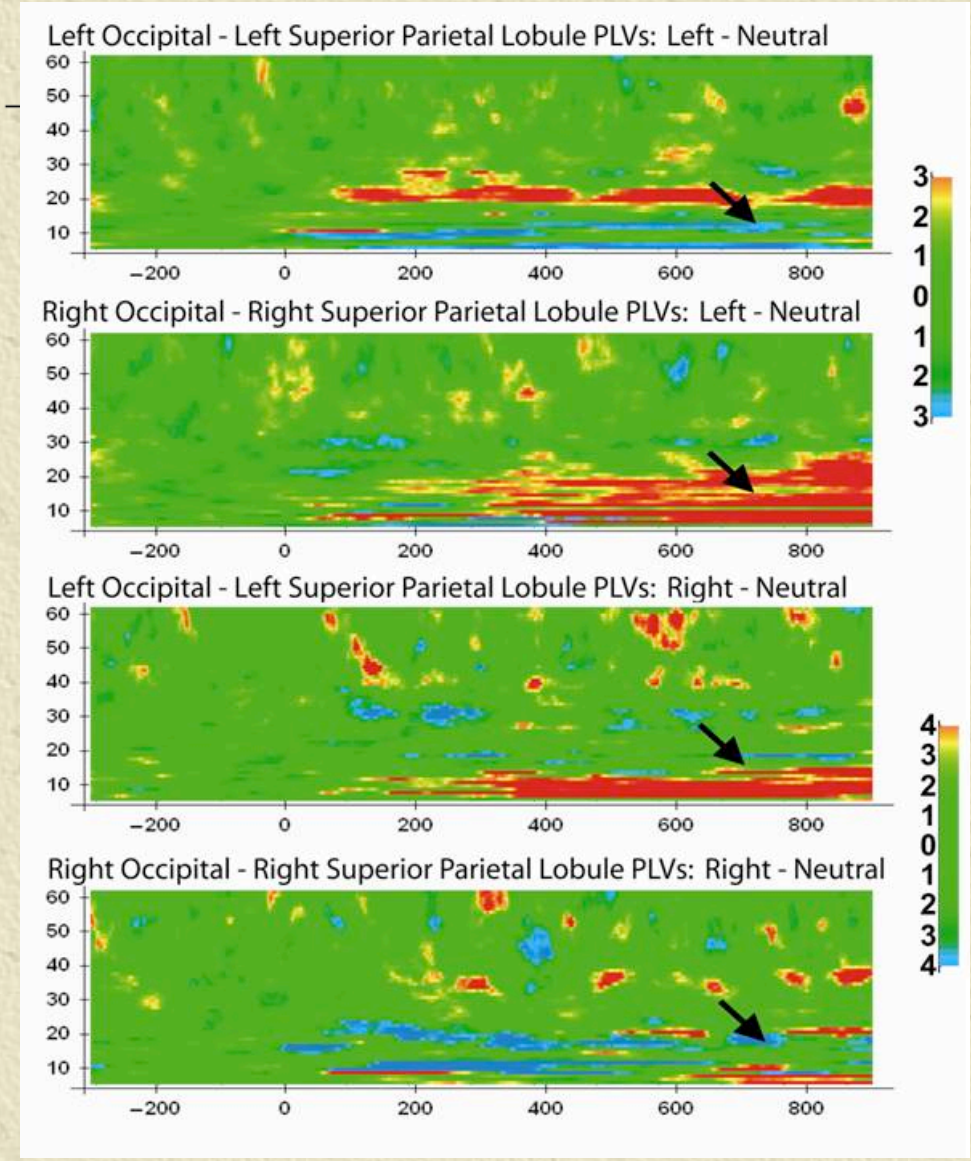
Doesburg, Green, McDonald & Ward, *Brain Research*, 2009

Lateralized increased synchronization in the alpha band

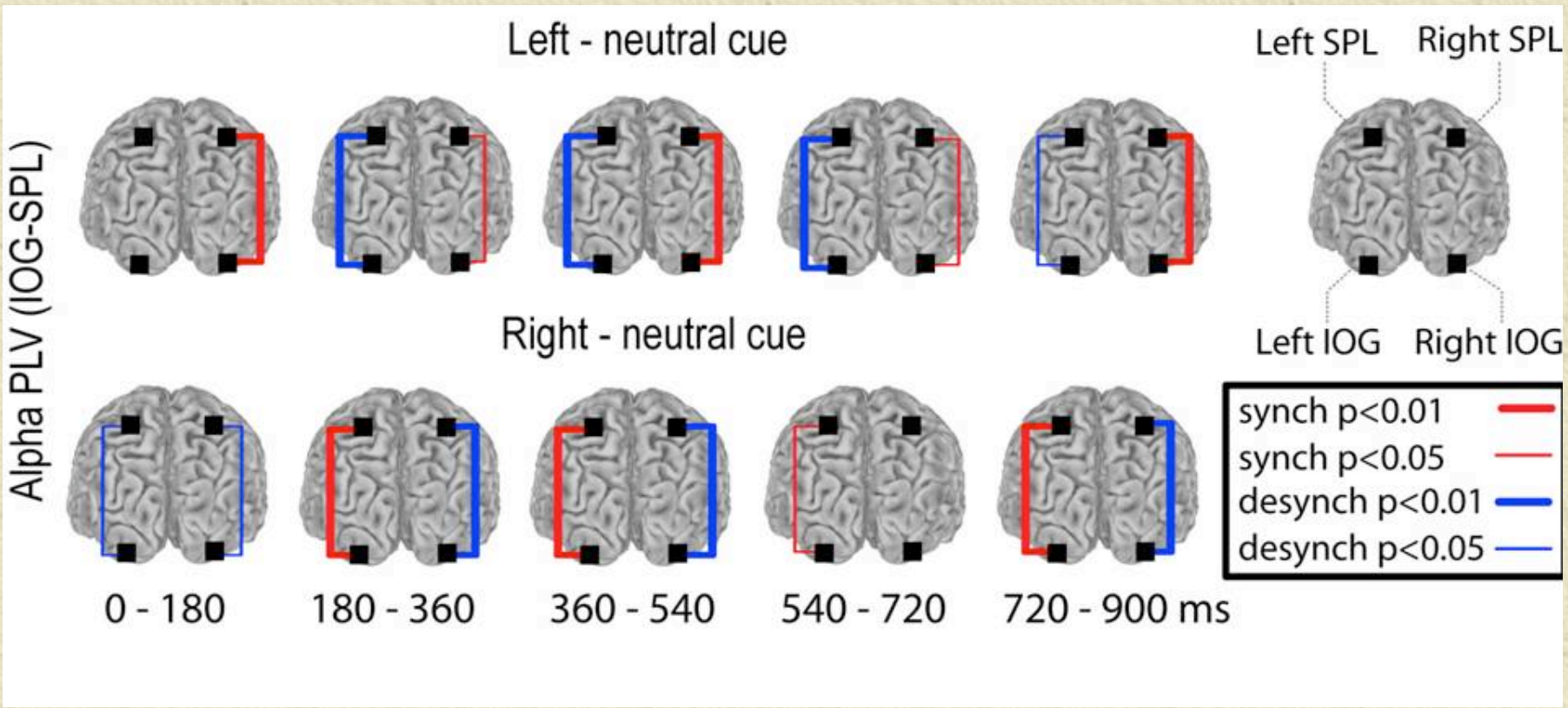


350 ms post cue onset until target onset: maintains attention at cued location

Doesburg, Green, McDonald & Ward, *Brain Research*, 2009



Detailed time course of inter-regional alpha-band synchronization

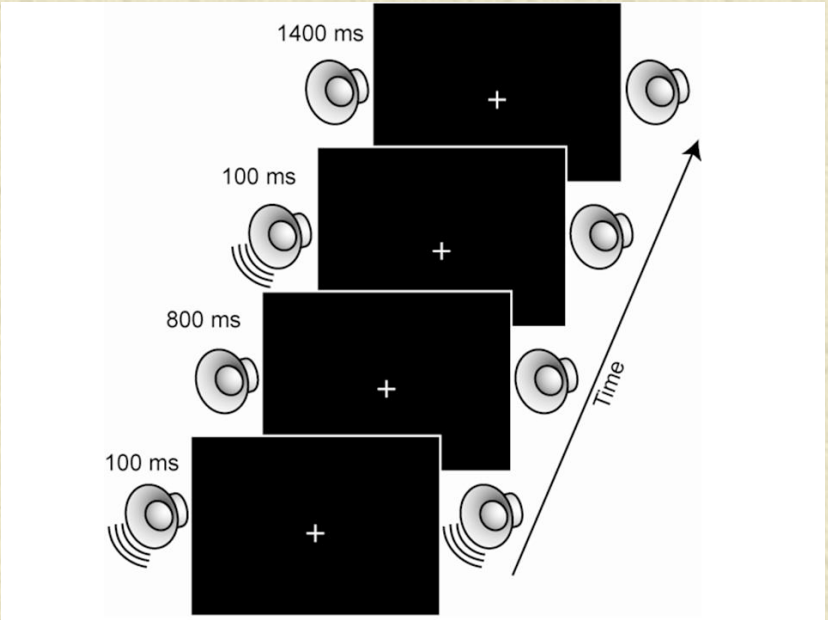


- Inter-regional (occipital-parietal) phase locking is increased contralateral to shift and decreased ipsilateral to shift
- Faster response the greater the contralateral SPL-IOG alpha PLV

Doesburg, Green, McDonald & Ward, *Brain Research*, 2009

Baton-passing in the cerebral cortex?

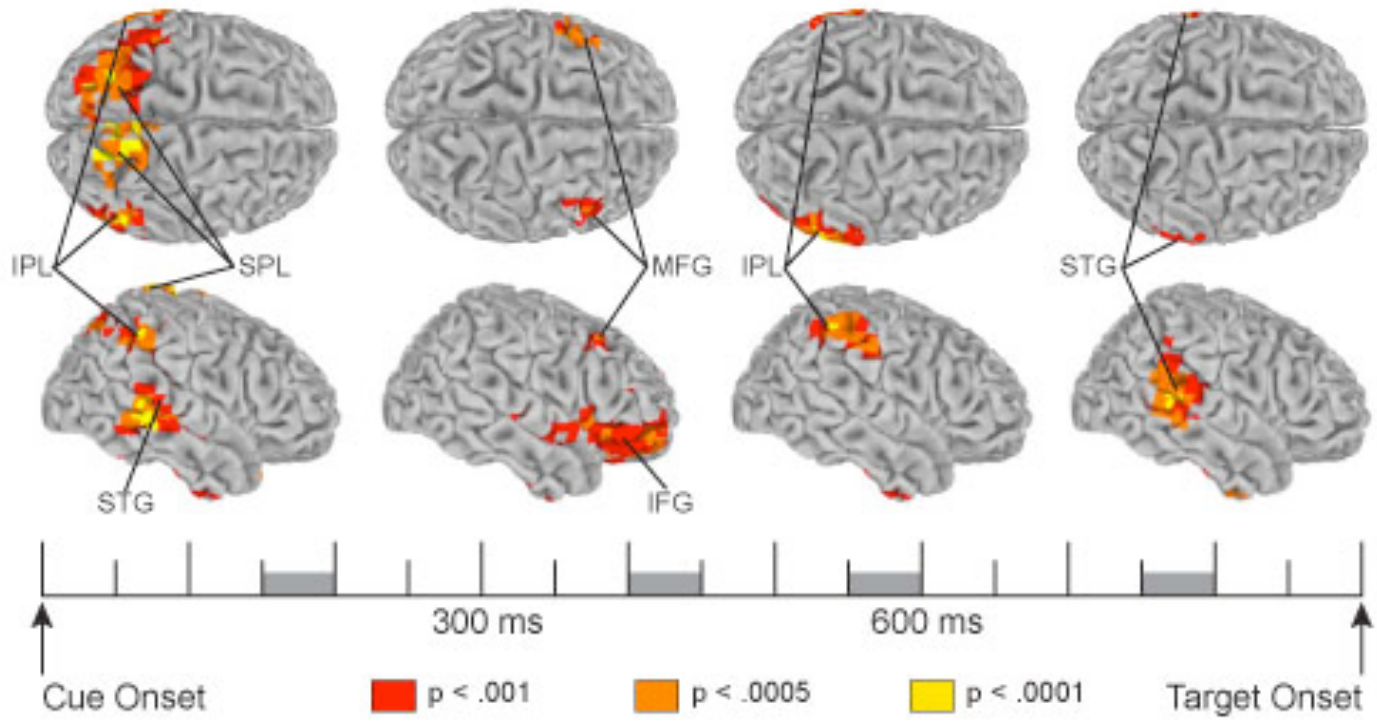
- Auditory cues and targets
- Cue types: up or down glide for orient left or right (or vice versa), both for do not orient; each on 1/3 of trials
- White noise targets (respond to all targets) for gap discrimination presented left (1/3 of trials) or right (1/3 of trials) at random regardless of cue type; probes (respond only if at cued location) presented on 1/3 of trials at random
- BESA beamformer source analyses for theta-band signal



	Valid	Neutral	Invalid
RT (SD)	694 ms (25.5)	718 ms (26.6)	716 ms (26.7)
% Corr (SD)	90.9 (.016)	90.7 (.014)	90.6 (.018)

Green, Doesburg, Ward & McDonald, submitted

Theta-band BESA beamformer source activations

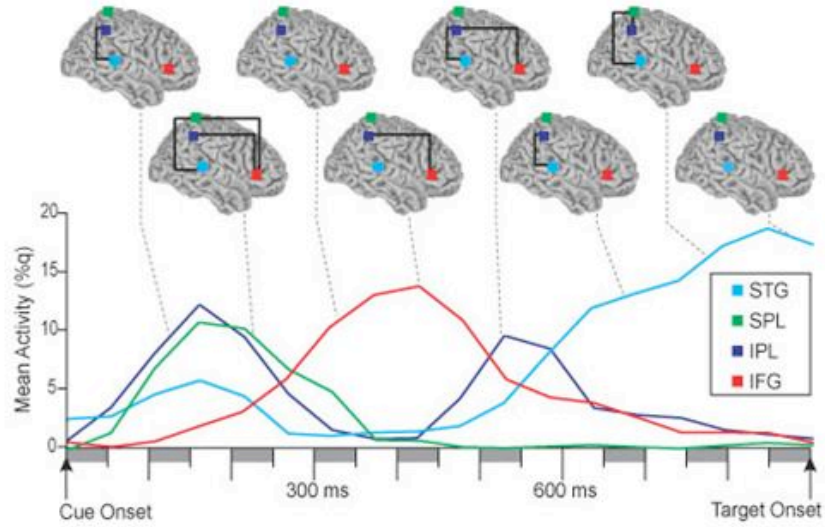


Interpretation of activation sequence:

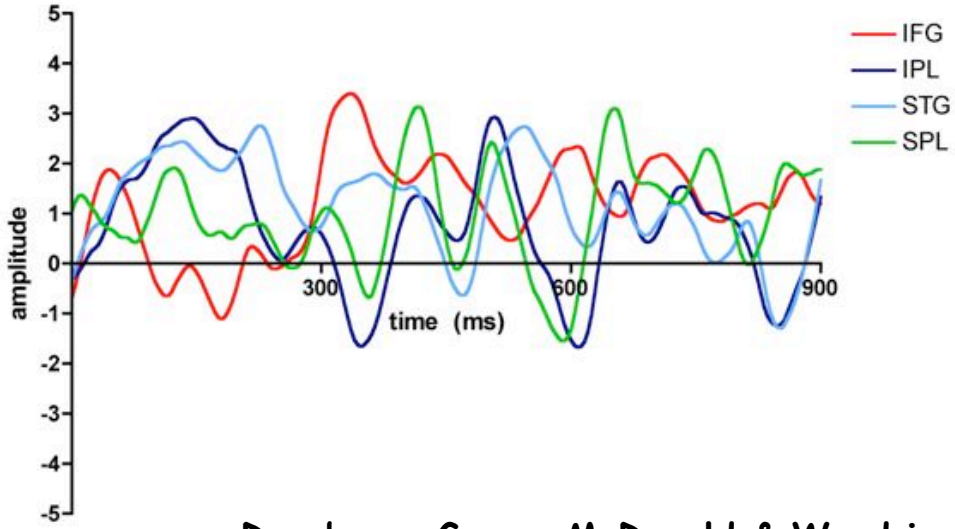
- 1 Cue activates STG which in turn activates IPL and SPL
- 2 IPL/SPL activate MFG/IFG
- 3. IFG/MFG interprets cue
- 4. IFG/MFG tells IPL/SPL where to orient
- 5. IPL/SPL activate relevant STG and maintain activation until target

Green, Doesburg, Ward & McDonald, submitted

Summary of main gamma PLV results as a function of gamma and theta activation => baton passing?



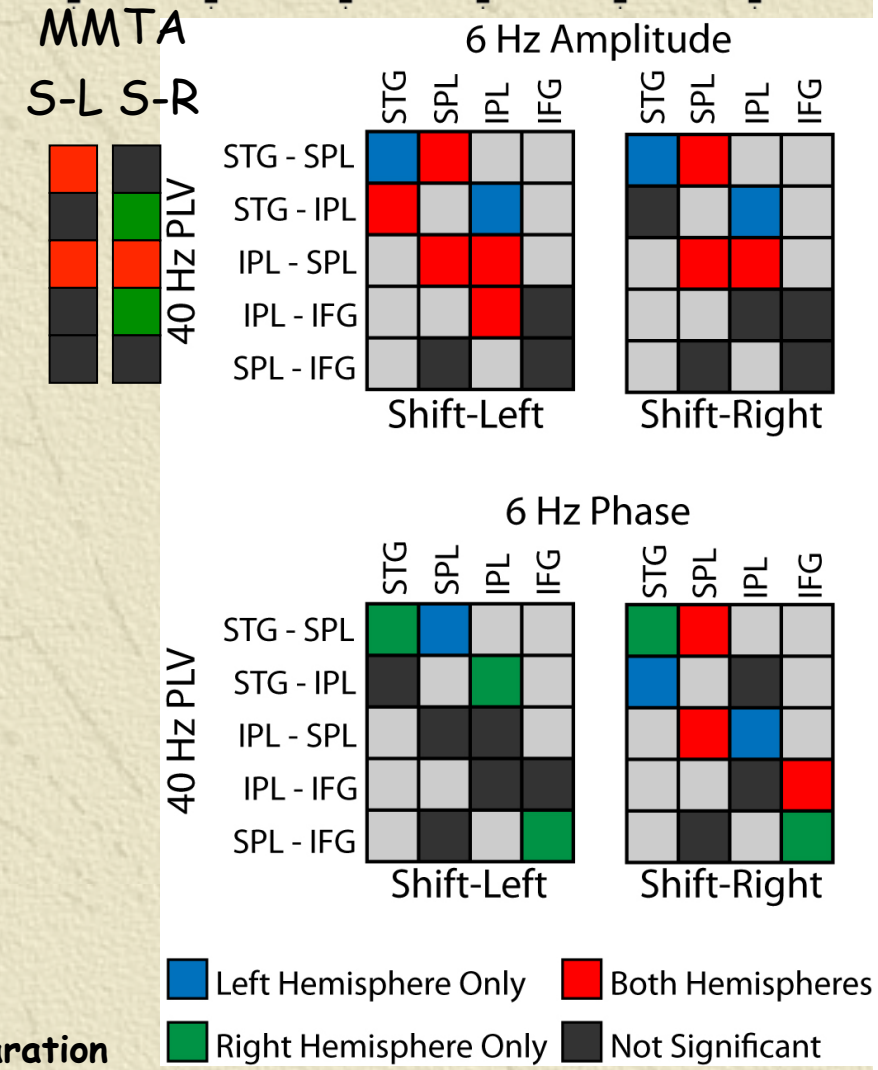
Gamma amplitude



Doesburg, Green, McDonald & Ward in preparation

Across-frequency phase locking

- Significant if beyond 2.5 or 97.5 %ile in 1000 surrogate distribution for 5 bins
- Gamma PLV greater when theta amplitude greater in either or both of relevant regions: all pairs except SPL-IFG
- Gamma PLV significantly modulated by theta phase in either or both relevant regions; all pairs

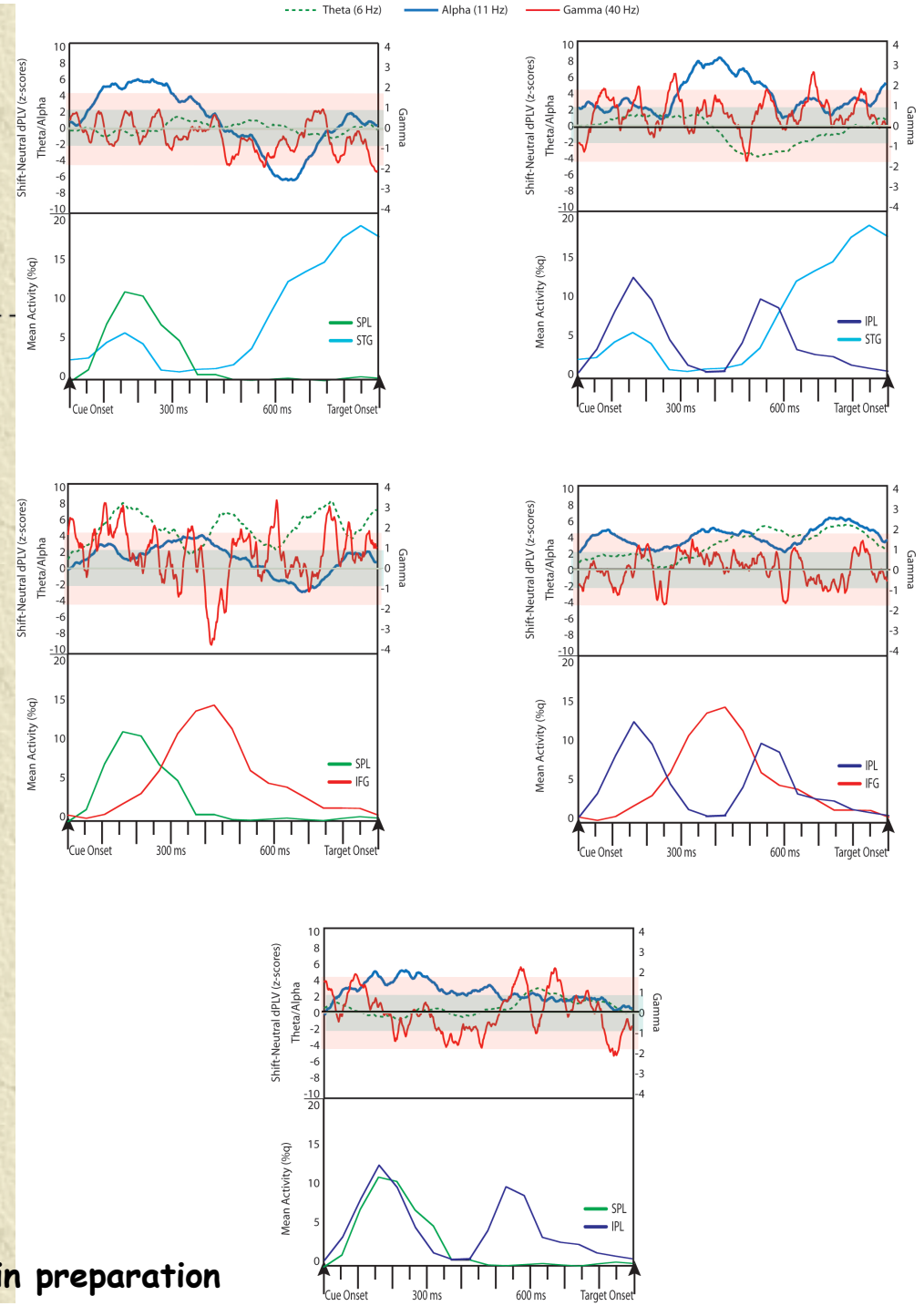


Doesburg, Green, McDonald & Ward in preparation

Gamma-alpha-theta PLV related to theta amplitude?

- SPL-STG: alpha up then down; gamma bursting
- IPL-STG: alpha up and theta down in middle; gamma bursting
- SPL-IFG: theta up and oscillating; alpha up and down; gamma bursting and down when IFG theta power high
- IPL-IFG: theta and alpha up and oscillating; gamma bursting
- SPL-IPL: alpha up at beginning; gamma bursting
- General: significant alpha and theta phase locking between theta-active regions; gamma phase locking transient and often occurring in periods when theta power changing

Doesburg, Green, McDonald & Ward in preparation



Summary: endogenous attention orienting

- Brain (re-)configured to attend to a specific location by simultaneous lateralized modulations of intra-regional alpha power, intra-regional gamma power and inter-regional gamma synchronization at 250 ms post cue
- Attention maintained at specific location by increased inter-regional alpha-band synchrony (at least parietal-visual) that coincides with decreased intra-regional alpha power
- Theta band activation/phase modulates gamma band PLV => information/control signals passed between brain regions by establishing and breaking synchronization in gamma band between those regions?
- Theta, alpha and gamma phase-locking varies across pairs and time-significance?
- Still not understood at all: mechanism of synchronization used (thalamic control?); nature of signals exchanged (control/compliance signals?); how reactivity of sensory cortex is increased by control signals; ……

To come 18, 25 May

3. le mardi 18 mai 2010 à 17 heures:

Neural synchronization and consciousness

4. le mardi 25 mai 2010 à 17 heures:

The role of the thalamus in human consciousness

Pair	MMTA	First-amp	Second-amp	First-phase	Second-phase
Right Shift					
L STG-SPL	yes	yes	yes	no	yes
R STG-SPL	yes	reverse	yes	yes	no
L STG-IPL	yes	yes	yes	no	no
R STG-IPL	no	yes	no	no	yes
L IPL-SPL	yes	yes	yes	yes	no
R IPL-SPL	yes	yes	yes	no	no
L IPL-IFG	no	yes	no	no	no
R IPL-IFG	yes	yes	no	no	no
L SPL-IFG	no	no	no	no	no
R SPL-IFG	no	no	no	no	yes
Left Shift					
L STG-SPL	yes	yes	yes	no	yes
R STG-SPL	yes	no	yes	yes	yes
L STG-IPL	no	reverse	yes	yes	no
R STG-IPL	no	no	no	no	no
L IPL-SPL	yes	yes	yes	yes	yes
R IPL-SPL	yes	yes	yes	yes	no
L IPL-IFG	no	no	no	no	yes
R IPL-IFG	no	no	no	no	yes
L SPL-IFG	no	no	no	no	no
R SPL-IFG	no	no	no	no	yes

Table X: First column: Modulation of 40 Hz standardized DPLV (Shift – Neutral) by 6 Hz Minimum Mutual Theta Activation (MMTA). Second-fifth columns: Modulation of shift only 40 Hz PLV by 6 Hz amplitude (significantly modulated by First- or Second-listed member of pair), and by 6 Hz phase (significantly modulated by First- or Second-listed member of pair). PLV was considered to be significantly modulated if it was greater than the 97.5th percentile of the surrogate distribution (top dotted line in Figure y) for at least five successive bins within 30 bins of the maximum *and* less than the 2.5th percentile for at least five successive bins within 30 bins of the minimum for both 6 Hz MMTA and amplitude, or greater than or equal to the 97.5th or less than or equal to the 2.5th percentiles for at least five bins anywhere in the 6 Hz phase.