

*Frequency-domain EEG
applications and methodological
considerations*

Announcements

- Papers: 1 or 2 paragraph prospectus due no later than Monday March 28
- 3x5s

A wee bit more on
Digital Signal Processing

The Problem of Aliasing

➤ Definition

- To properly represent a signal, you must sample at a fast enough rate.
- Nyquist's (1928) theorem
 - a sample rate twice as fast as the highest signal frequency will capture that signal perfectly
 - Stated differently, the highest frequency which can be accurately represented is one-half of the sampling rate
 - This frequency has come to be known as the Nyquist frequency and equals $\frac{1}{2}$ the sampling rate

➤ Comments

- Wave itself looks distorted, but frequency is captured adequately.
- Frequencies faster than the Nyquist frequency will not be adequately represented
- Minimum sampling rate required for a given frequency signal is known as Nyquist sampling rate



Harry Nyquist

Aliasing and the Nyquist Frequency

- In fact, frequencies above Nyquist frequency represented as frequencies lower than Nyquist frequency
 - $F_{Ny} + x \text{ Hz}$ will be seen as $F_{Ny} - x \text{ Hz}$
 - “folding back”
 - frequency $2F_{Ny}$ seen as 0,
 - frequency $3F_{Ny}$ will be seen as F_{Ny}
 - accordion-like folding of frequency axis

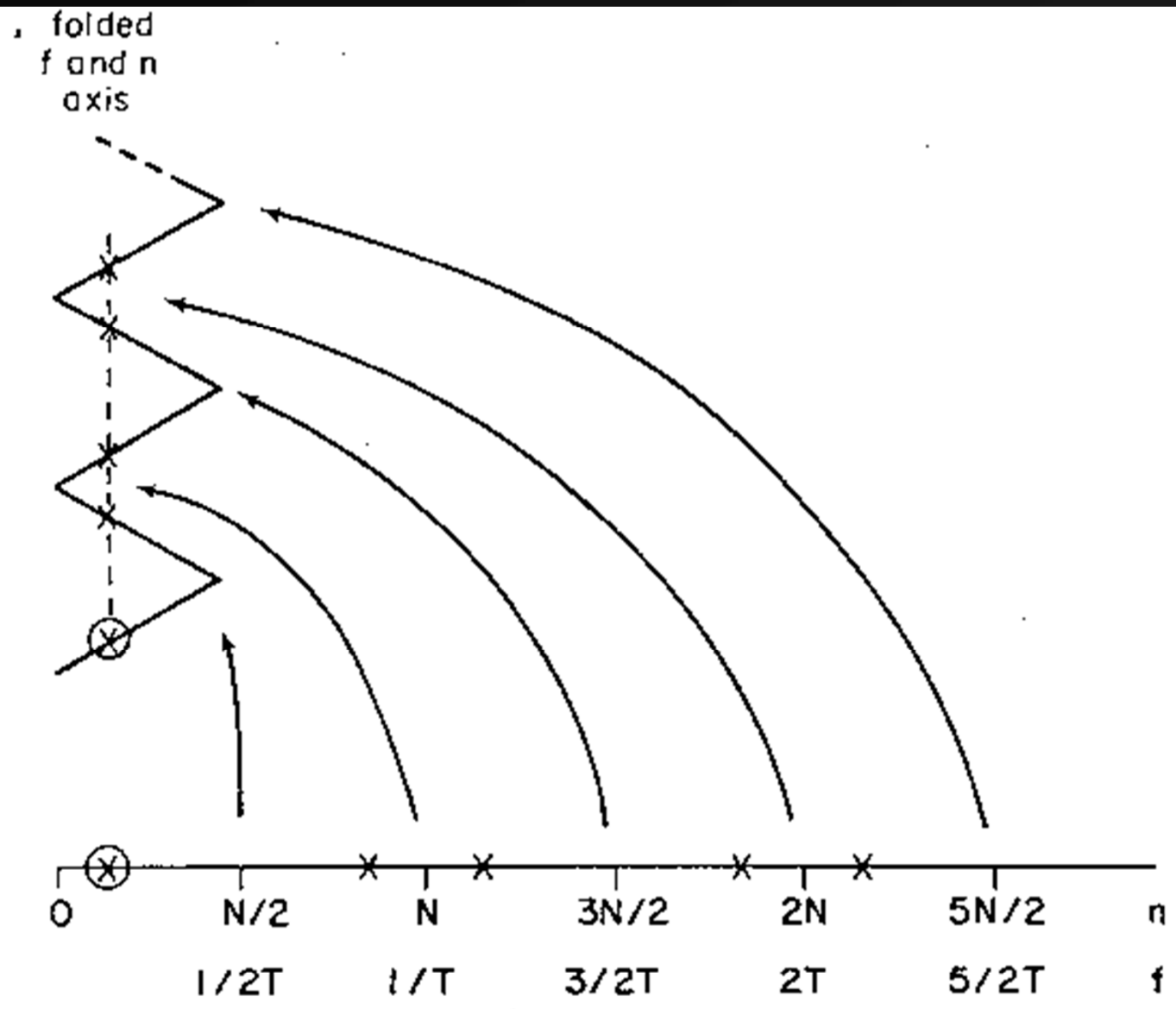
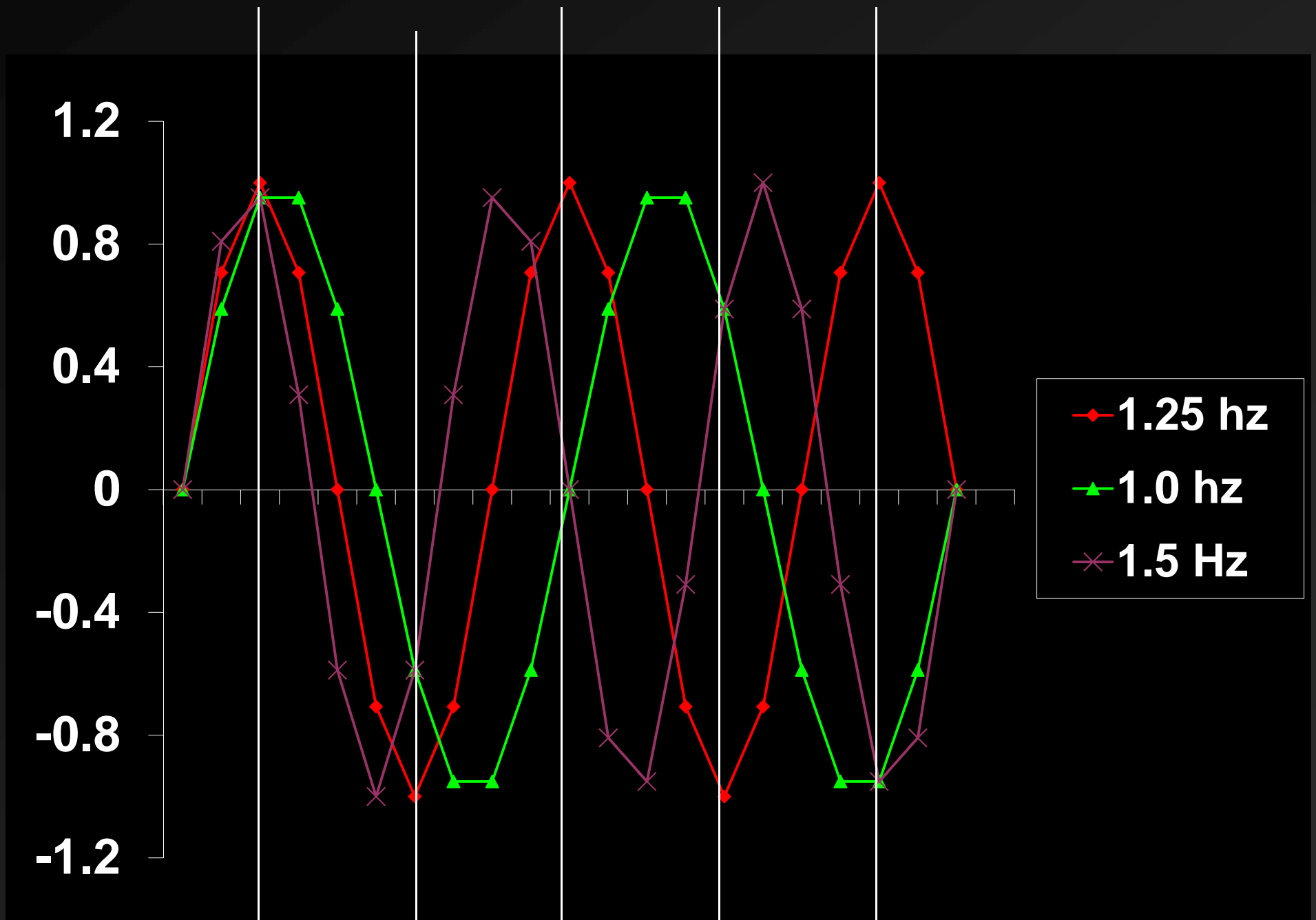
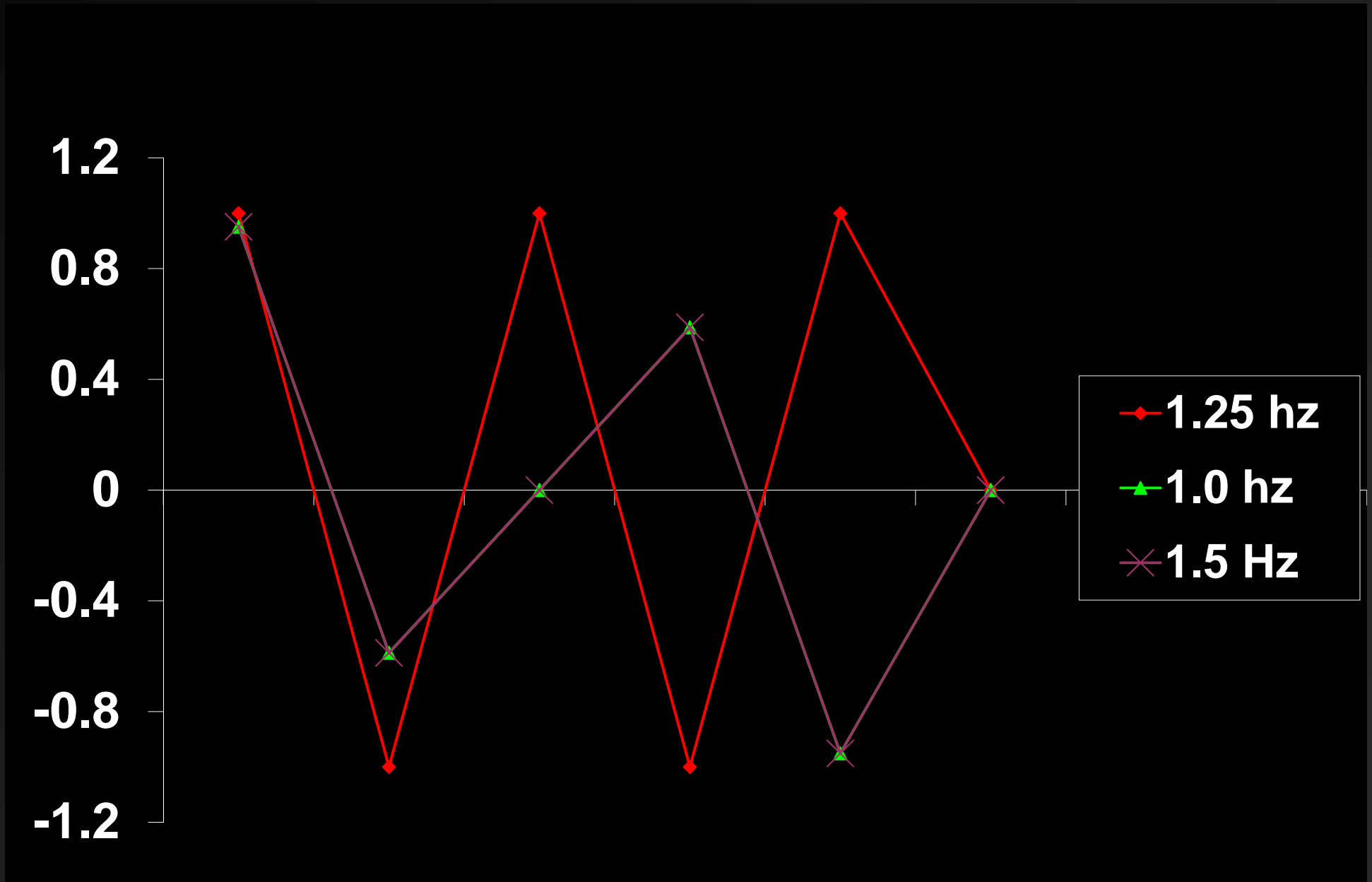


Fig. 3.2. The accordionlike folding of the frequency (or n) axis due to sampling of a continuous signal. Frequency components of the original signal marked with x 's on the f axis are interpreted in the sampled version as belonging to the lowest frequency, an encircled x .

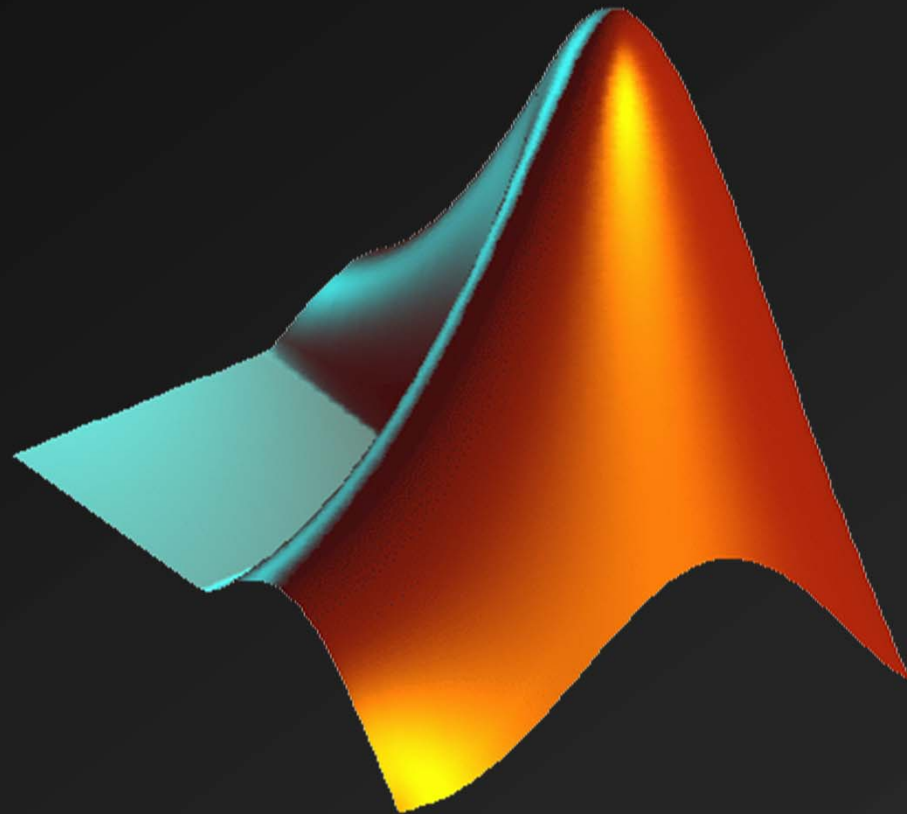
Aliasing Demo (Part 1, 10 Hz Sampling Rate)



Aliasing Demo (Part 2, 2.5 Hz Sampling Rate)



Matlab Demo of Aliasing



Solutions to Aliasing

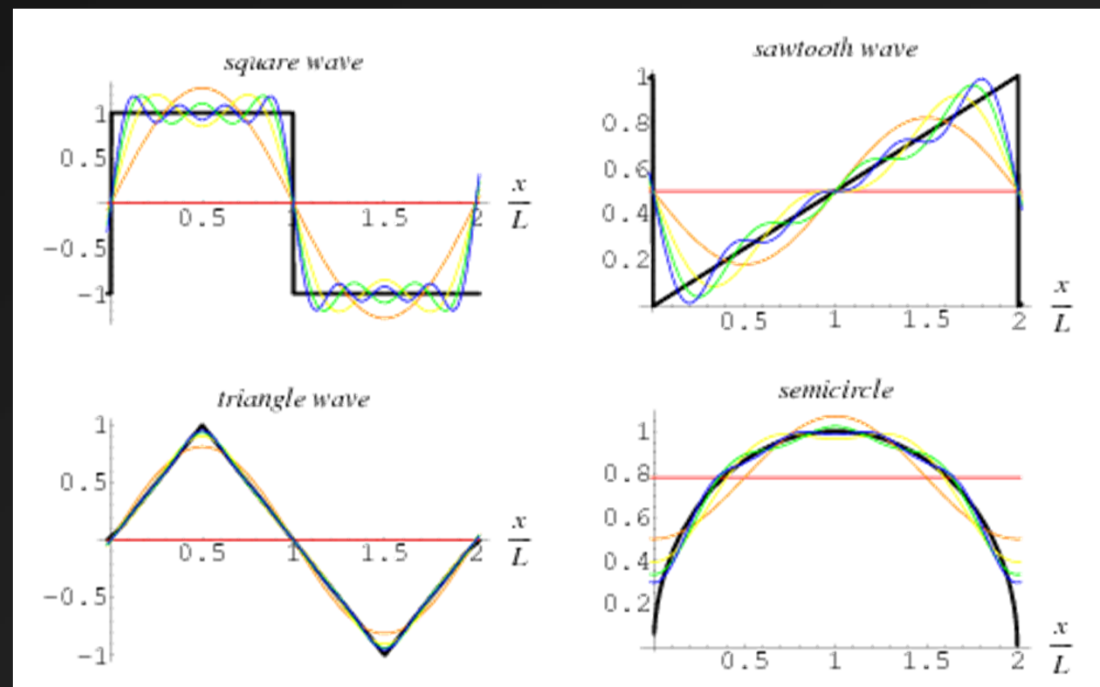
- Sample very fast
- Use anti-aliasing filters
- **KNOW YOUR SIGNAL!**

Time Domain Vs Frequency Domain Analysis

- Frequency Domain Analysis involves characterizing the signal in terms of its component frequencies
 - Assumes periodic signals
- Periodic signals (definition):
 - Repetitive
 - Repetitive
 - Repetition occurs at uniformly spaced intervals of time
- Periodic signal is assumed to persist from infinite past to infinite future

Fourier Series Representation

- If a signal is periodic, the signal can be expressed as the sum of sine and cosine waves of different amplitudes and frequencies
- This is known as the Fourier Series Representation of a signal



For nice demo, see <http://www.falstad.com/fourier/>

Fourier Series Representation

➤ Pragmatic Details

- Lowest Fundamental Frequency is $1/T$
- Resolution is $1/T$

➤ Phase and Power

- There exist a phase component and an amplitude component to the Fourier series representation
 - Using both, it is possible to completely reconstruct the waveform.

➤ Psychophysicist often interested in amplitude component:

- Power spectrum; for each frequency n/T

$$|\text{Amp}_{\cos}^2 + \text{Amp}_{\sin}^2|$$

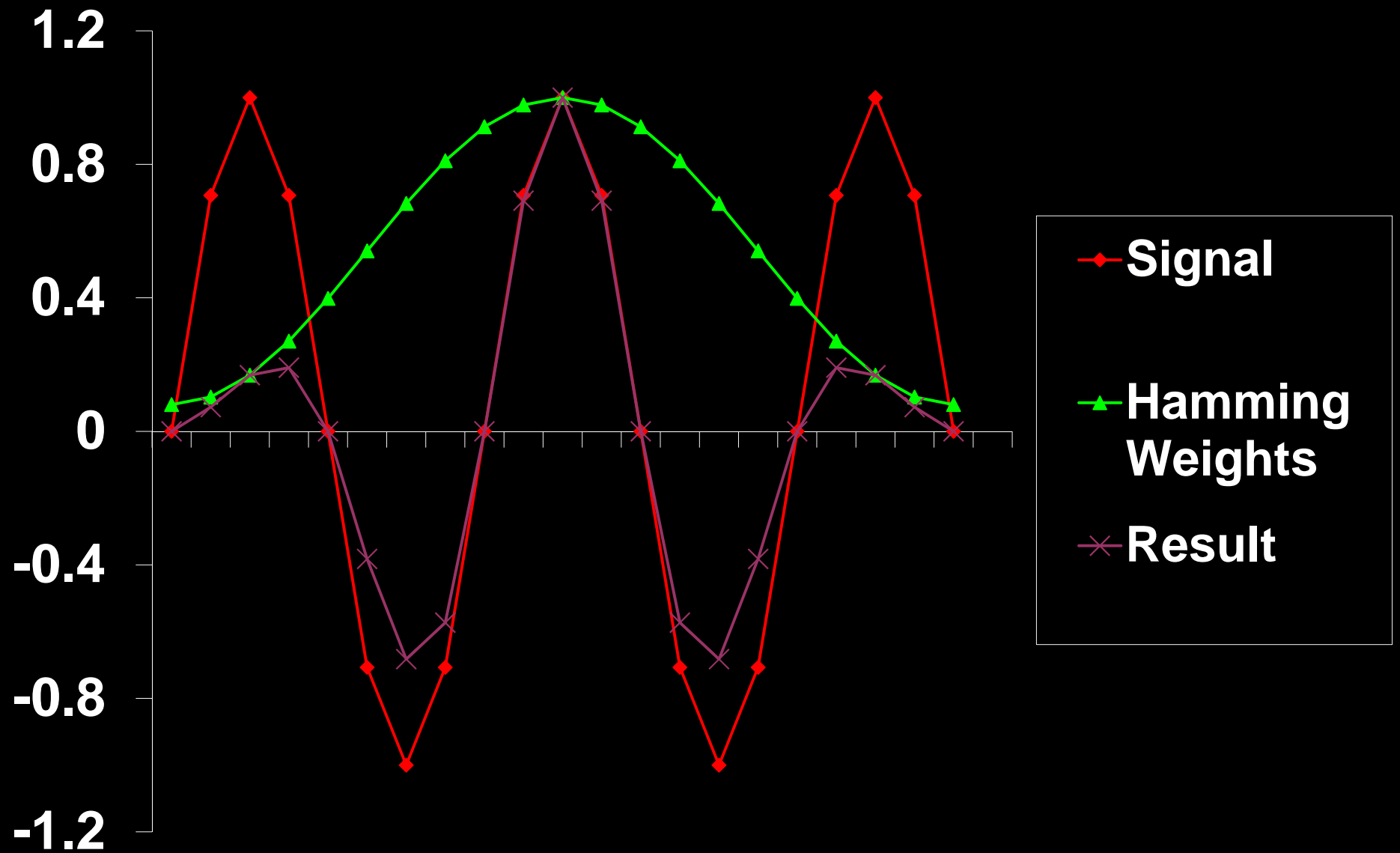
- Amplitude Spectrum (may conform better to assumptions of statistical procedures); for each frequency n/T

$$|\text{Amp}_{\cos}^2 + \text{Amp}_{\sin}^2|^{1/2}$$

Preventing Spectral Leakage

- Use windows
 - not Micro\$oft Windows
 - Hamming
 - Hann
 - Cosine
 - Etc.

Hamming Demo



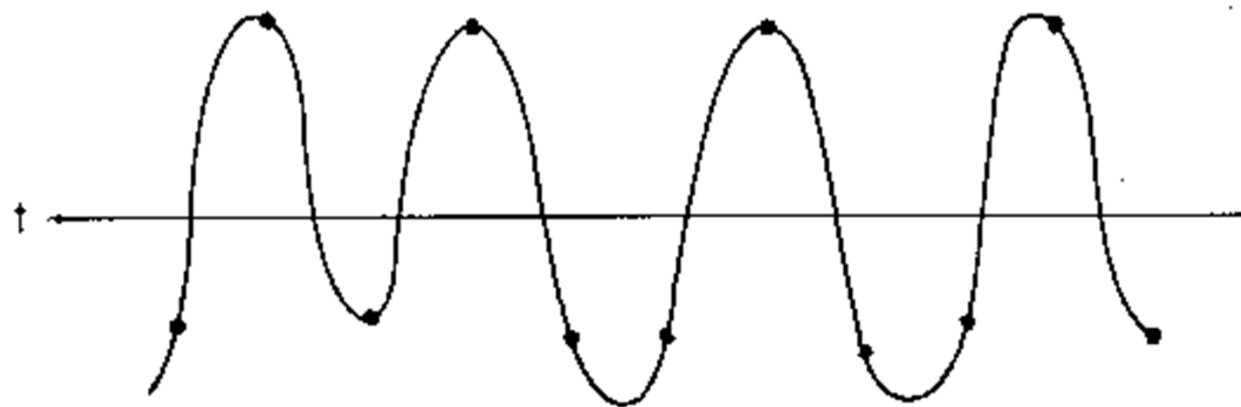
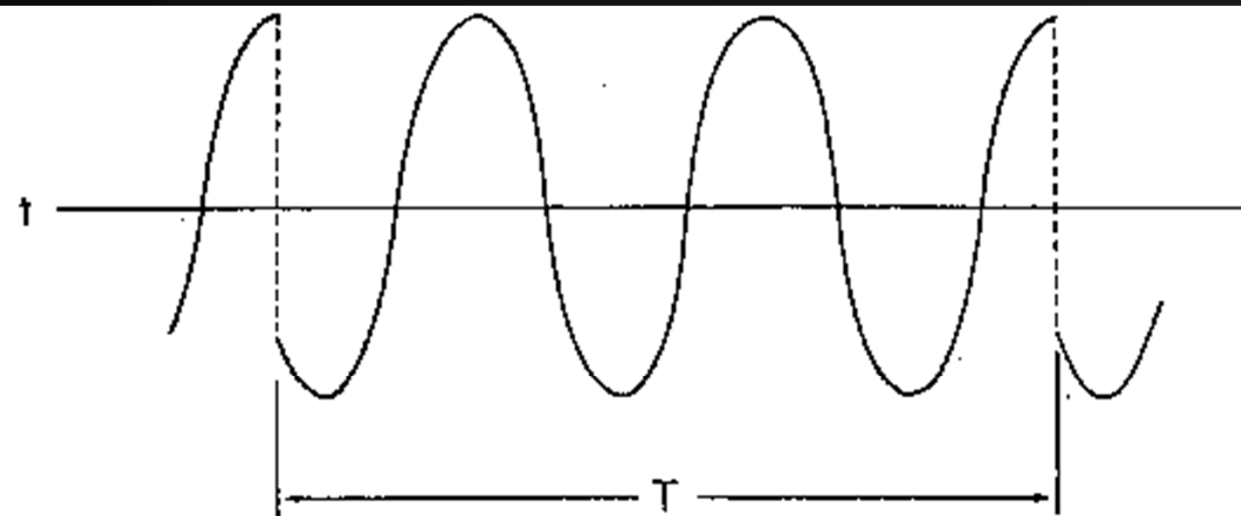
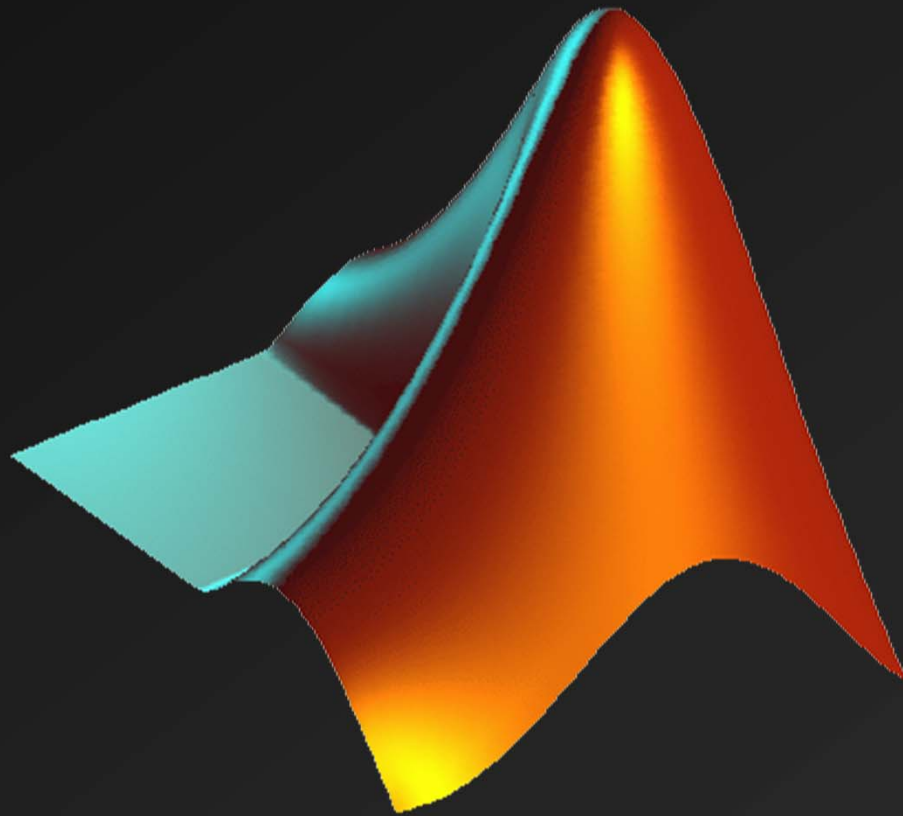


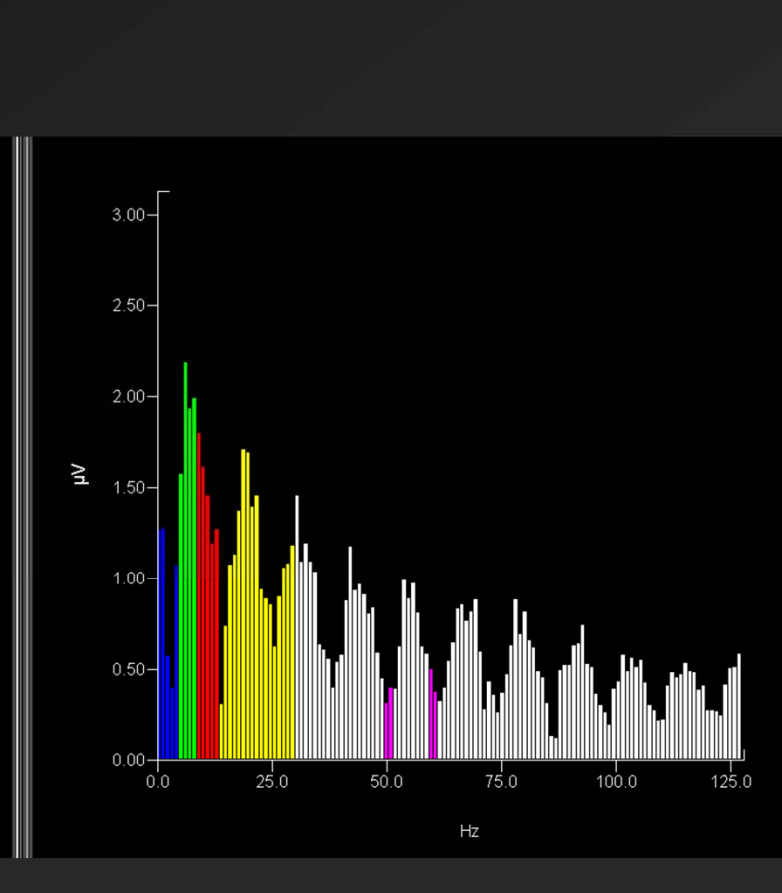
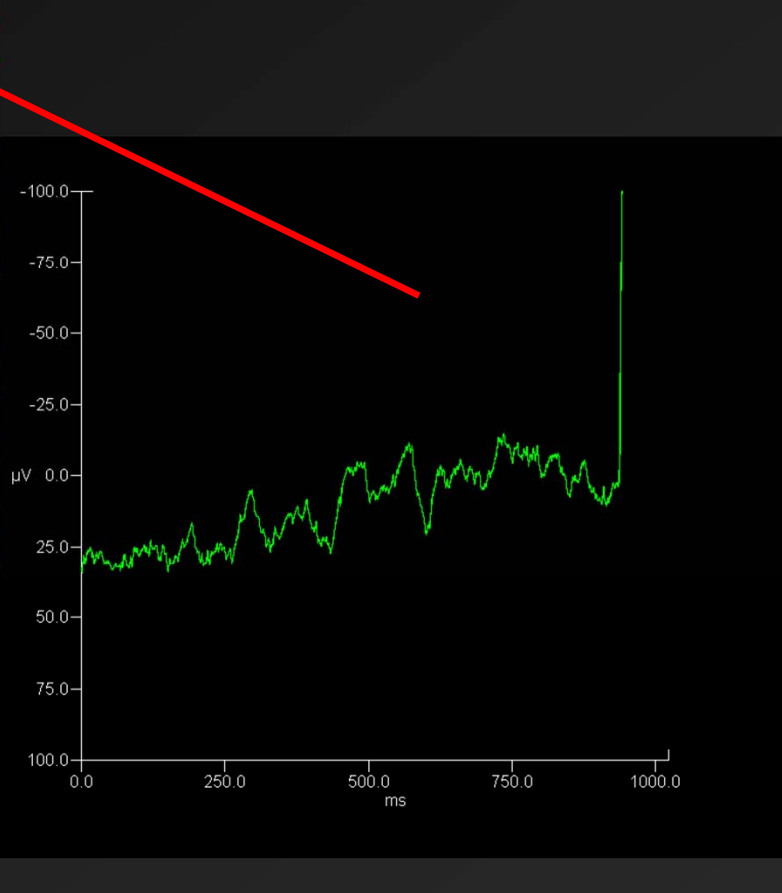
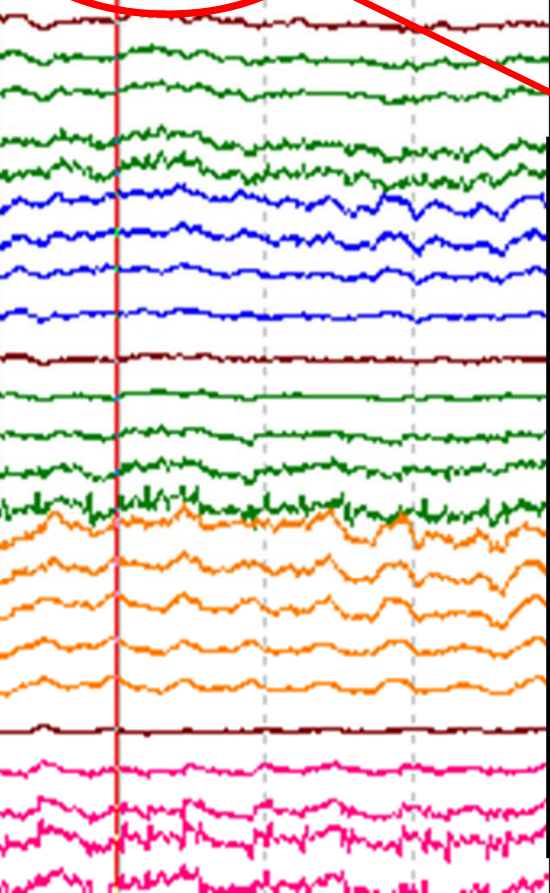
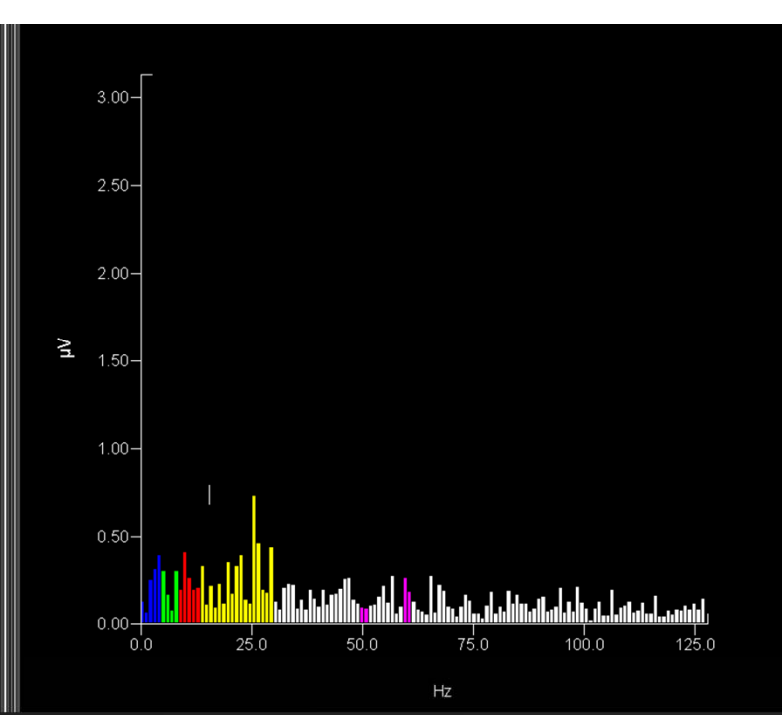
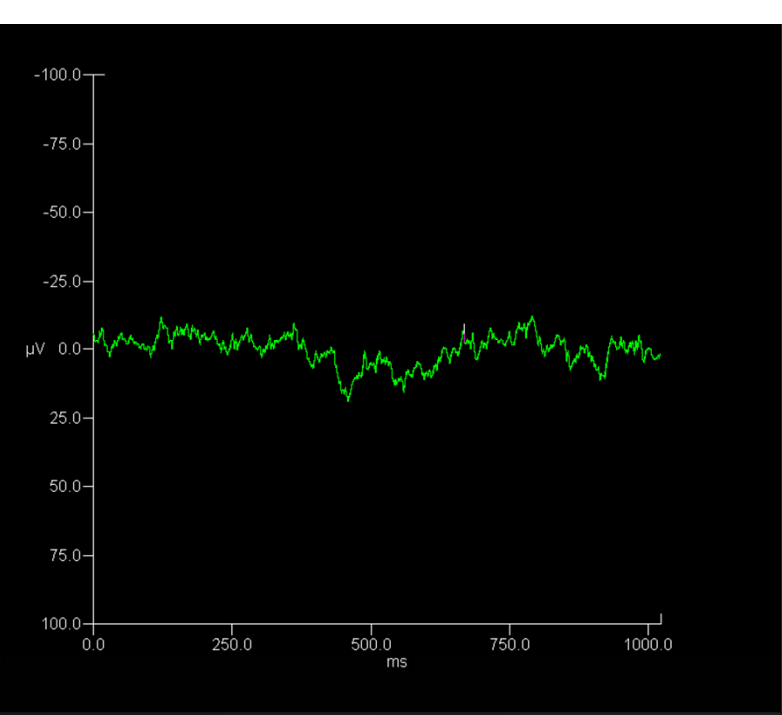
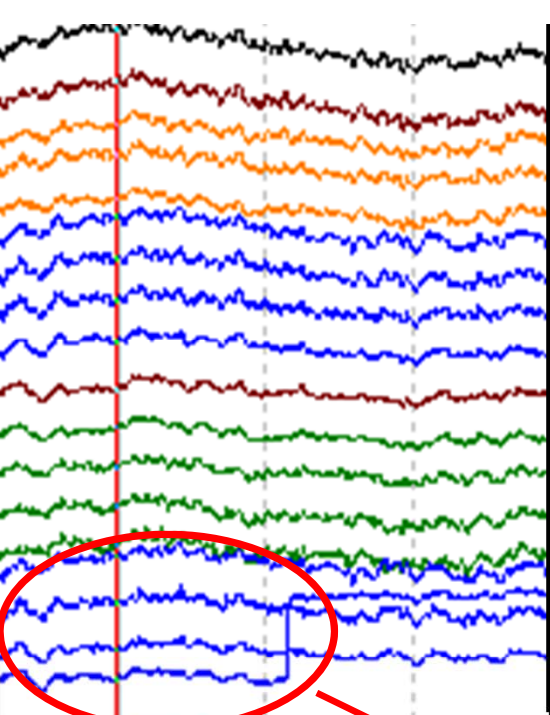
Fig. 3.3. Top, a periodicized segment of a cosine wave. T is the observation time and $3T/8$ the period of the wave. Note the discontinuities at 0 and T . Bottom, a continuous and periodic band-limited wave drawn through the sample points $\Delta = T/16$ sec apart.

Matlab Demo of Hamming Window



Pragmatic Concerns

- Sample fast enough so no frequencies exceed Nyquist
 - signal bandwidth must be limited to less than Nyquist
 - Violation = **ERROR**
- Sample a long enough epoch so that lowest frequency will go through at least one period
 - Violation = **ERROR**
- Sample a periodic signal
 - if subject engaging in task, make sure that subject is engaged during entire epoch
 - Violation = ??, probably introduce some additional frequencies to account for change



Demo of EEG Data

- CNT Data to Frequency Domain Representation

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Applications

- Emotion Asymmetries
 - Lesion findings
 - Catastrophic reaction (LH)
 - RH damage show a belle indifference
 - EEG studies
 - Trait (80+ studies)
 - State (30 + studies)

Types of Studies

➤ Trait

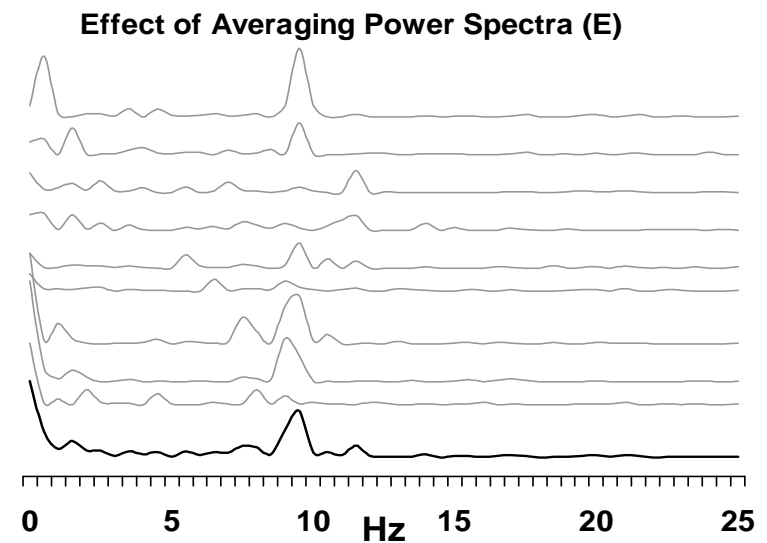
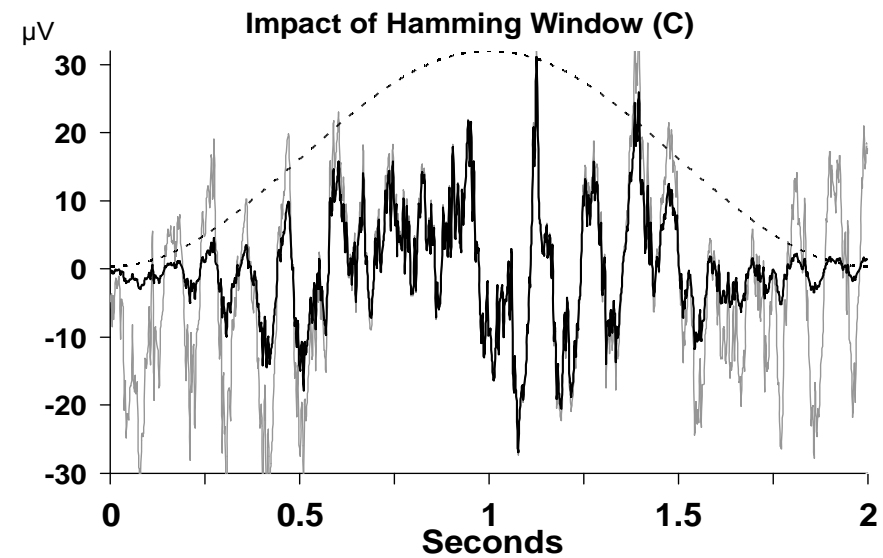
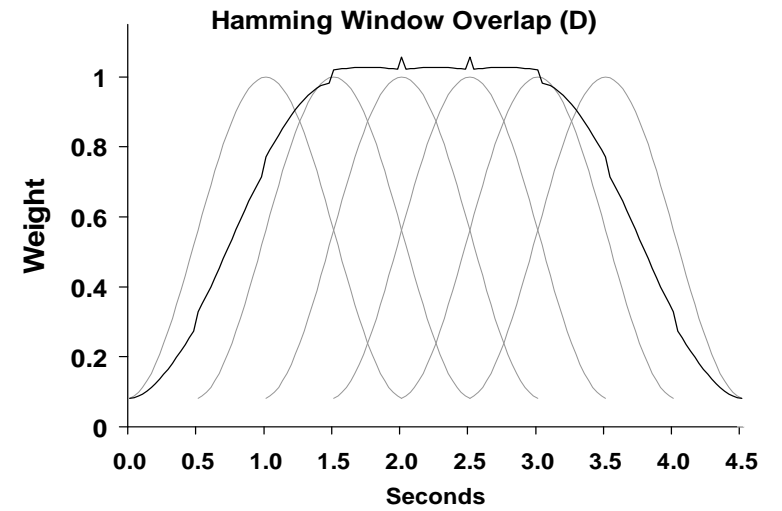
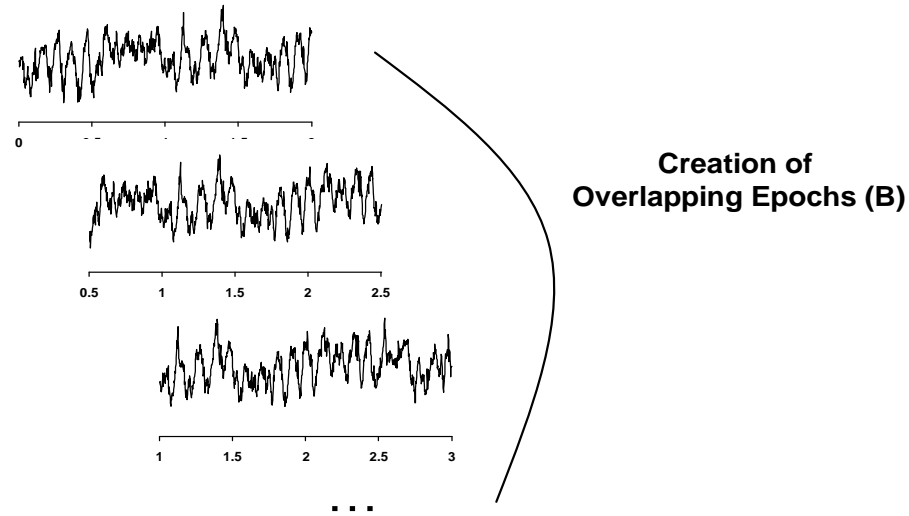
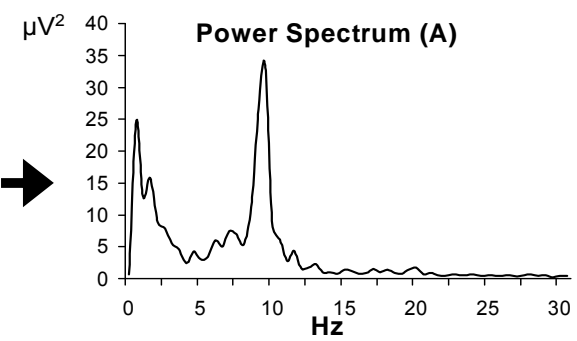
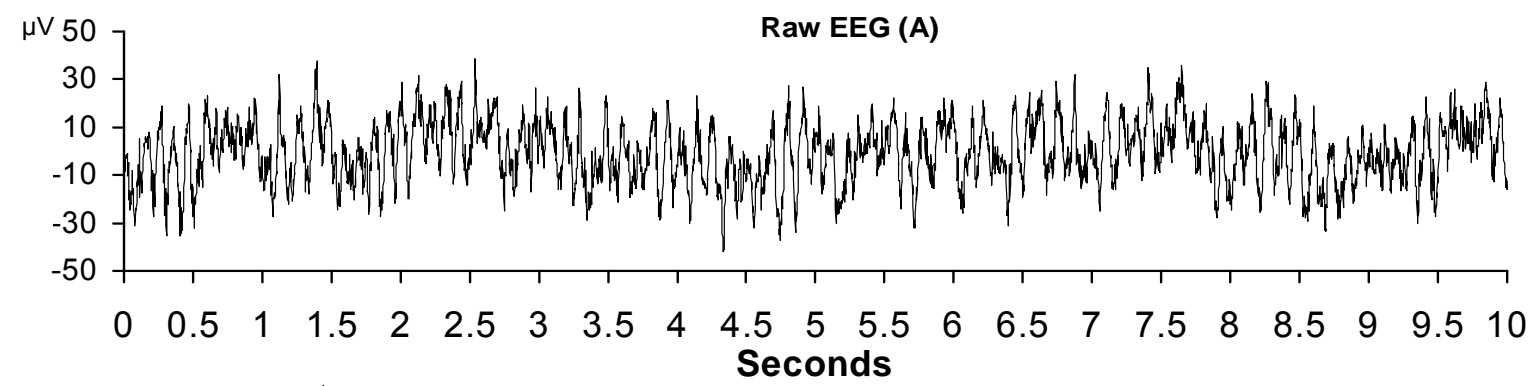
- Resting EEG asymmetry related to other traits (e.g. BAS)
- Resting EEG asymmetry related to psychopathology (e.g. depression)
- Resting EEG asymmetry predicts subsequent emotional responses (e.g. infant/mom separation)

➤ State

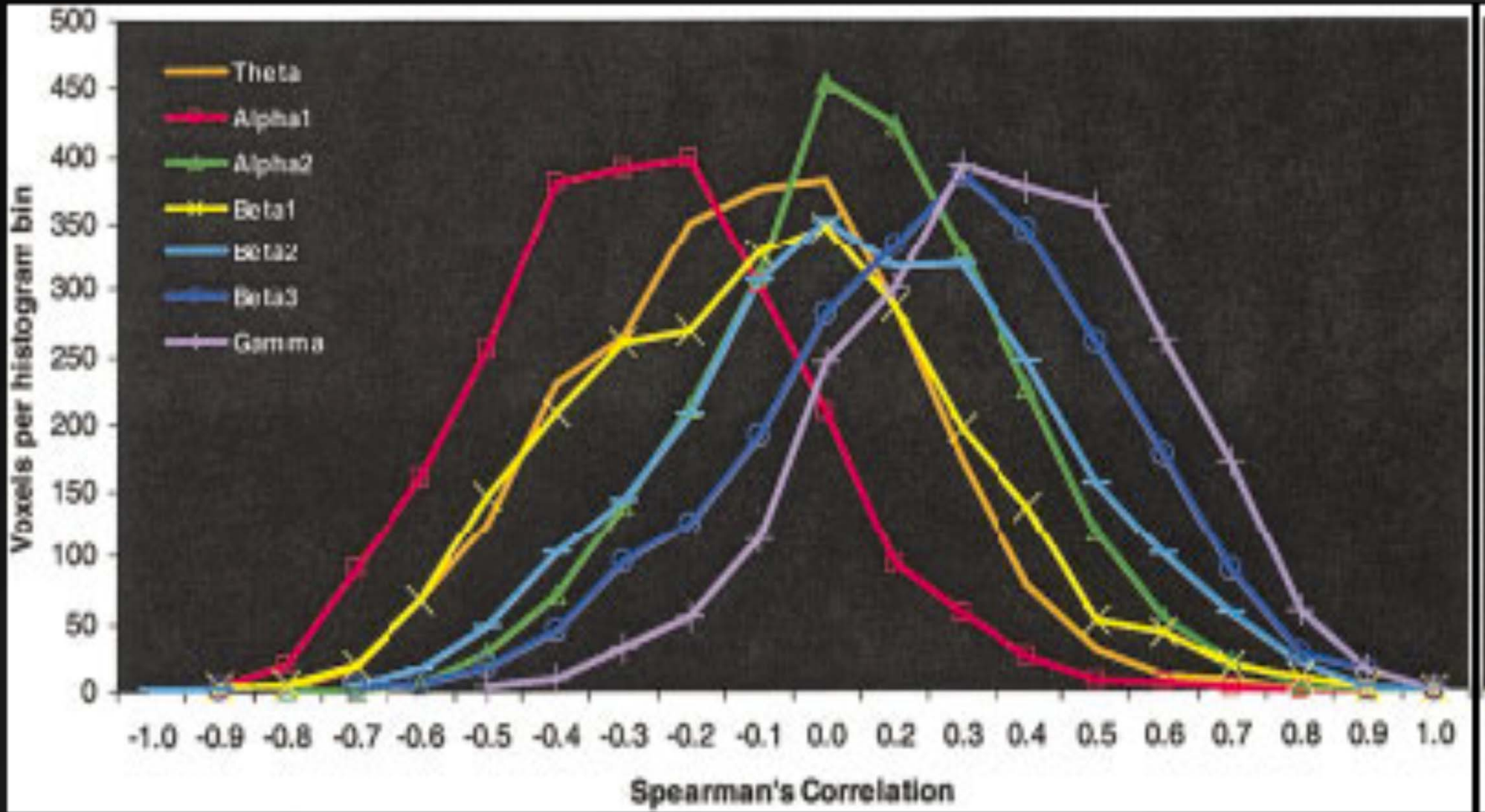
- State EEG asymmetry covaries with current emotional state (e.g., self report, spontaneous emotional expressions)

Trait, Occasion, and State variance

- Three sources of reliable variance for EEG Asymmetry
 - *Stable trait consistency* across multiple assessments
 - *Occasion-specific* variance
 - reliable variations in frontal asymmetry across multiple sessions of measurement
 - may reflect systematic but unmeasured sources such as current mood, recent life events and/or factors in the testing situation.
 - *State-specific* variance
 - changes within a single assessment that characterize
 - the difference between two experimental conditions
 - the difference between baseline resting levels and an experimental condition.
 - conceptualized as proximal effects in response to specific experimental manipulations
 - should be reversible and of relatively short duration
- Unreliability of Measurement (small)



Alpha Vs Activity Assumption (AAA)



Left Hypofrontality in Depression

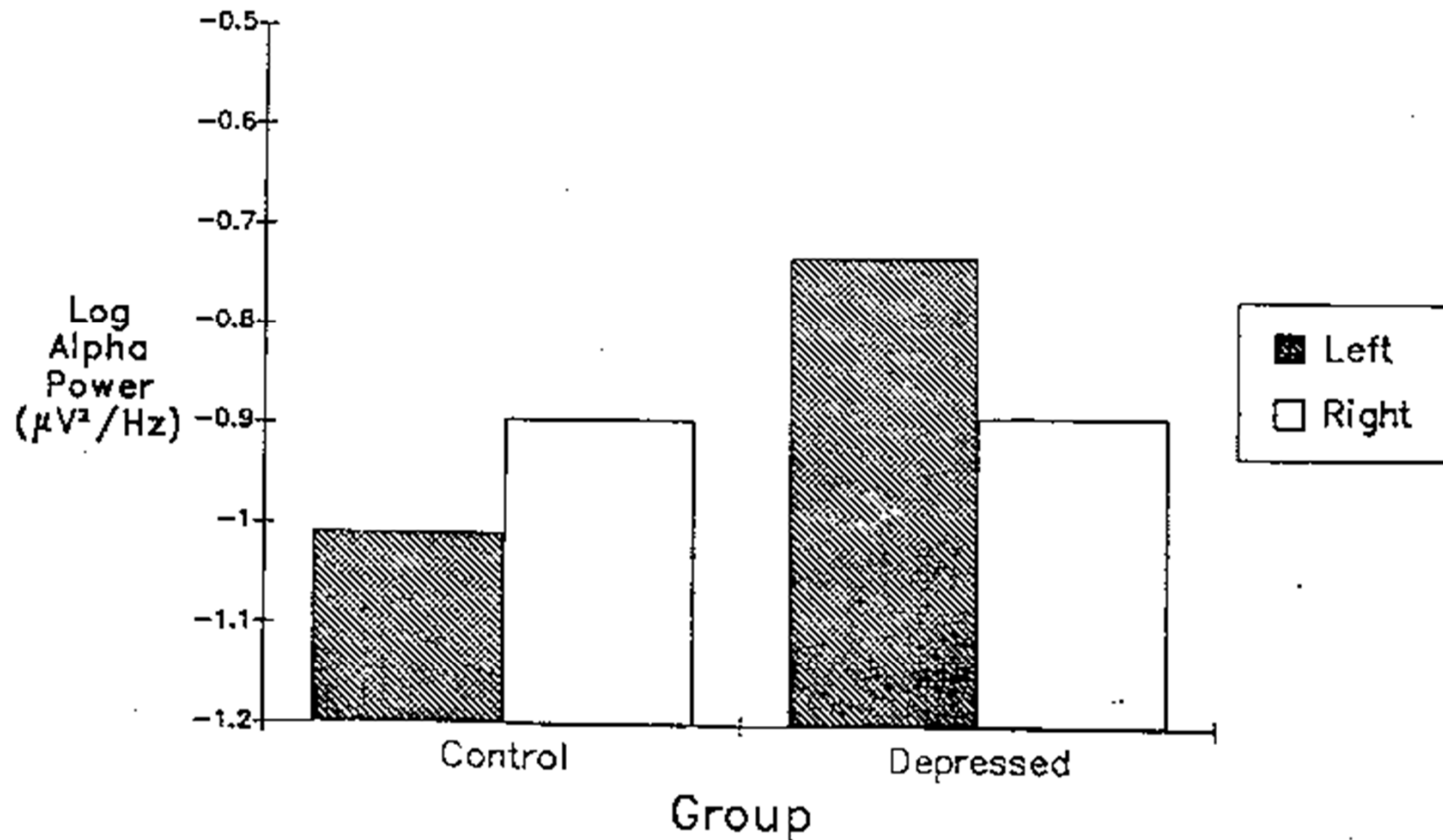
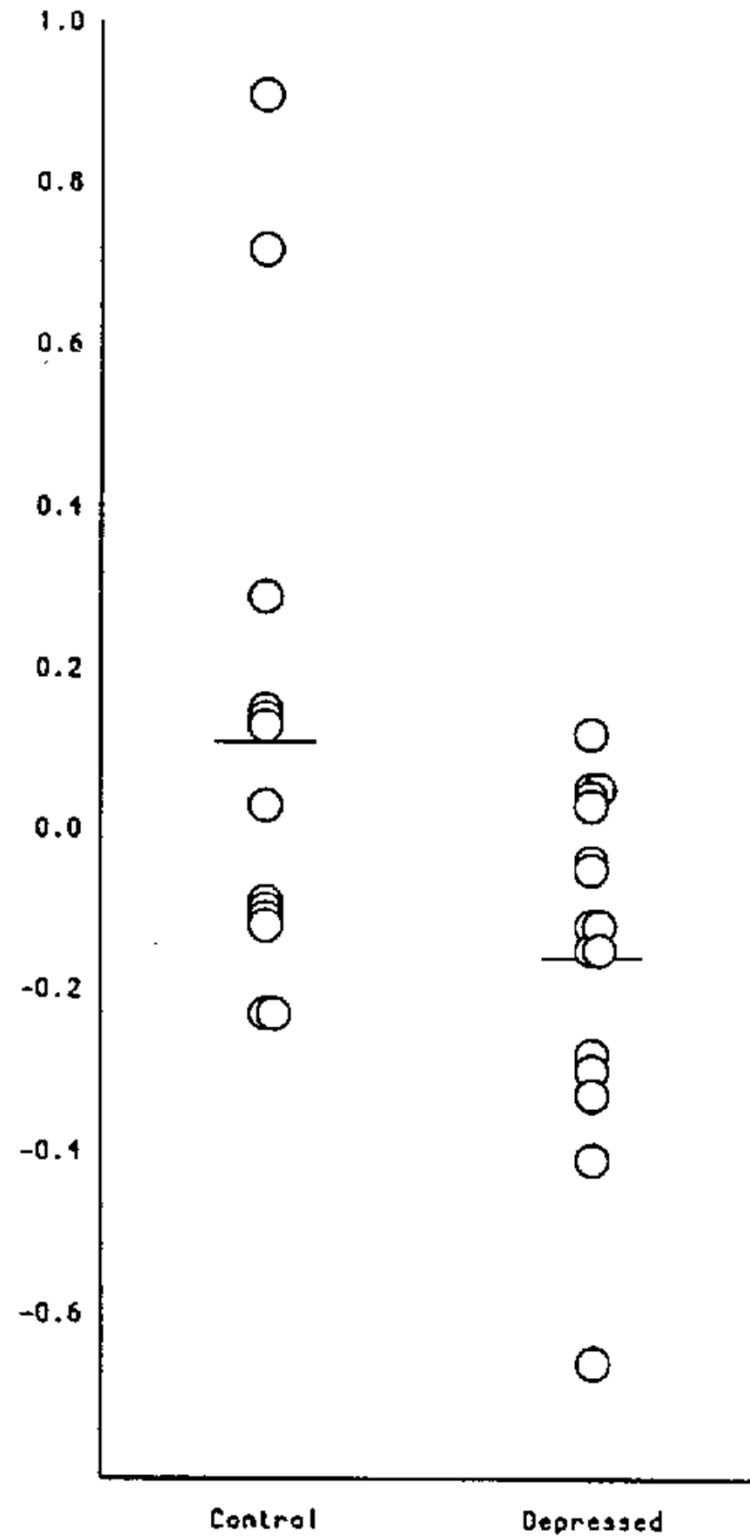


Figure 1. Mean log-transformed alpha (8–13 Hz) power (in $\mu V^2/Hz$) for Cz-referenced electroencephalograms (averaged across eyes-open and eyes-closed baselines), split by group and hemisphere, for the mid-frontal region. (Decreases in alpha power are indicative of increased activation.)

Henriques & Davidson (1991); see also, Allen et al. (1993), Gotlib et al. (1998);
Henriques & Davidson (1990); Reid Duke and Allen (1998); Shaffer et al (1983)

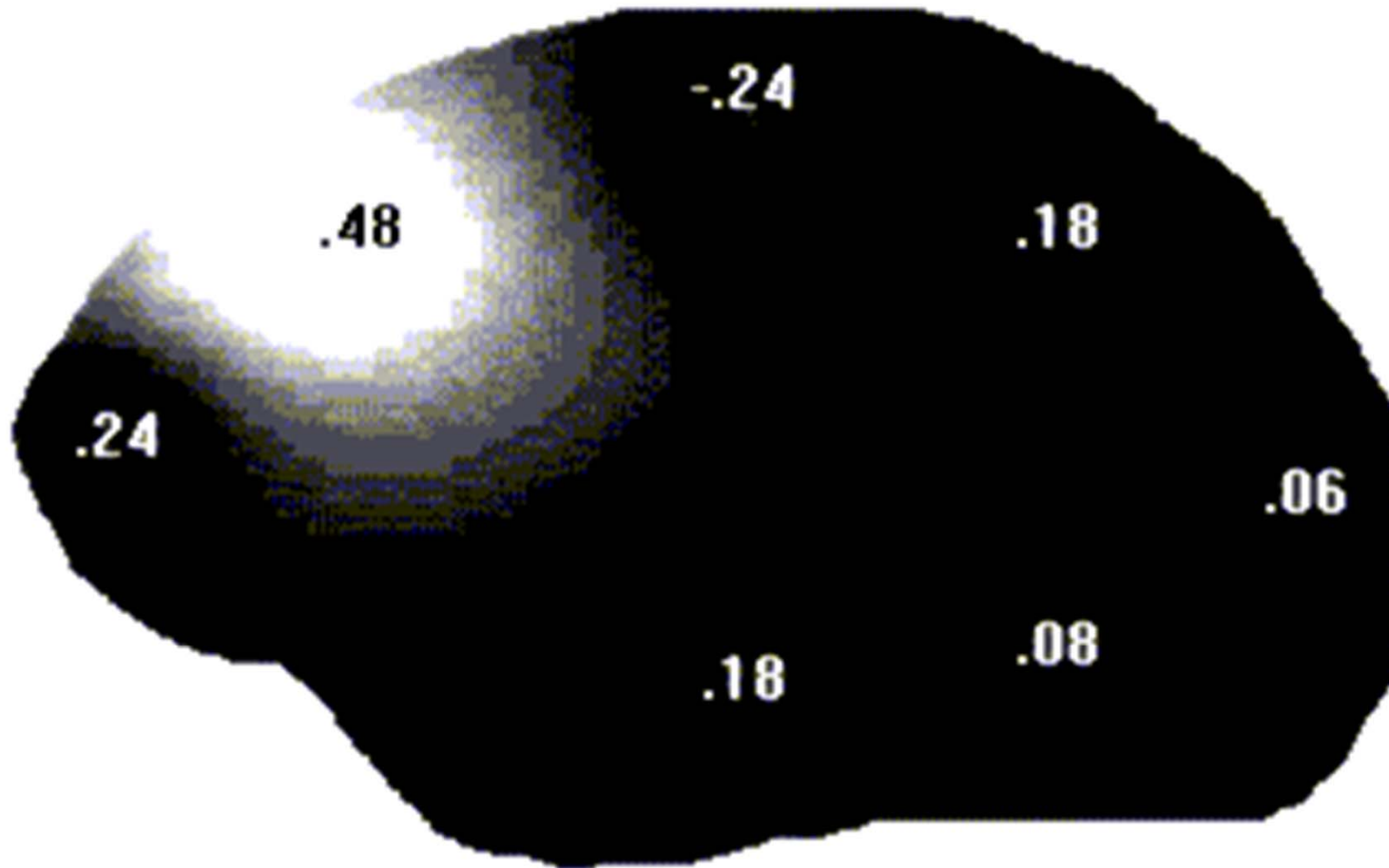
Individual Subjects' Data

Log R-Log L
Alpha Power



Valence Vs Motivation

- Valence hypothesis
 - Left frontal is positive
 - Right frontal is negative
- Motivation hypothesis
 - Left frontal is Approach
 - Right frontal is Withdrawal
- Hypotheses are confounded
 - With possible exception of Anger



Correlation with alpha asymmetry ($\ln[\text{right}] - \ln[\text{left}]$) and trait anger. Positive correlations reflect greater left activity (less left alpha) is related to greater anger. After Harmon-Jones and Allen (1998).

State Anger and Frontal Asymmetry

- Would situationally-induced anger relate to relative left frontal activity?

Method

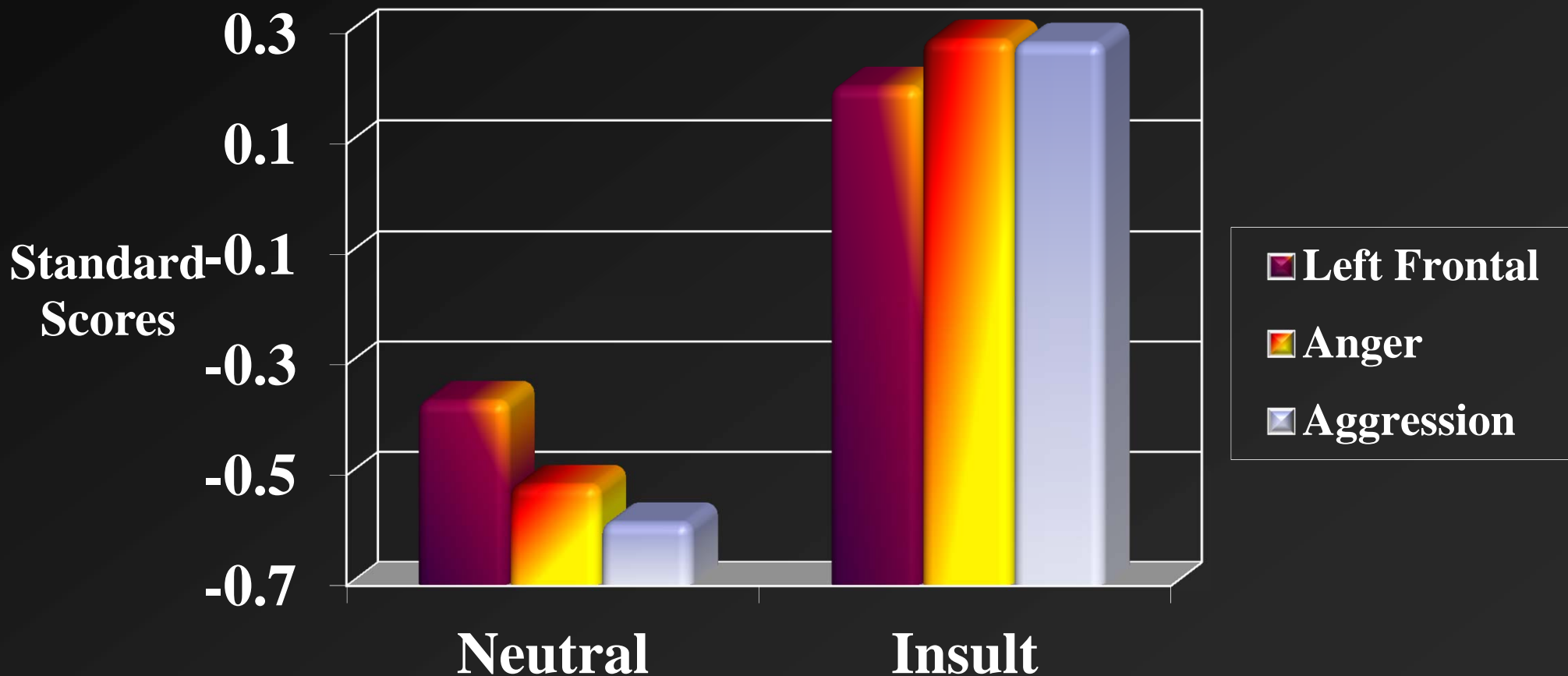
- Cover story: two perception tasks – person perception & taste perception
- Person perception task – participant writes essay on important social issue; another ostensible participant gives written feedback on essay
- Feedback is neutral or insulting
 - negative ratings + “I can’t believe an educated person would think like this. I hope this person learns something while at UW.”

- Record EEG immediately after feedback
- Then, taste perception task, where participant selects beverage for other participant, “so that experimenter can remain blind to type of beverage.”
- 6 beverages; range from pleasant-tasting (sweetened water) to unpleasant-tasting (water with hot sauce)
 - Aggression measure



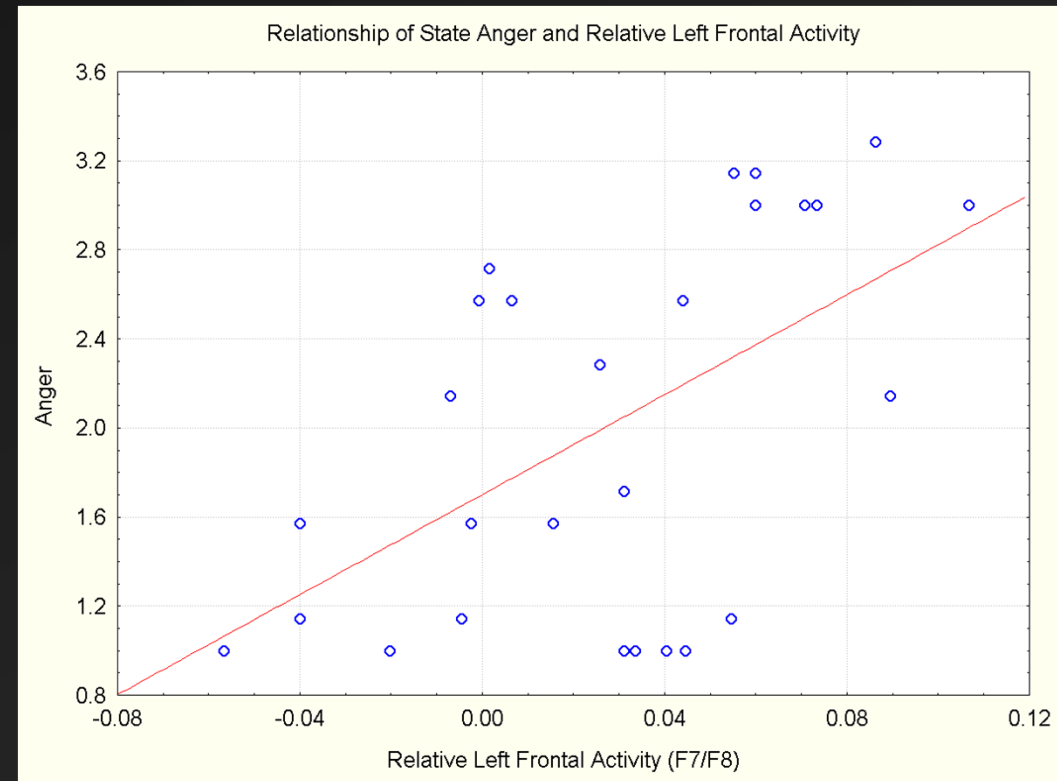
Harmon-Jones & Sigelman, *JPSP*, 2001

Relative Left Frontal, Anger, & Aggression as a Function of Condition



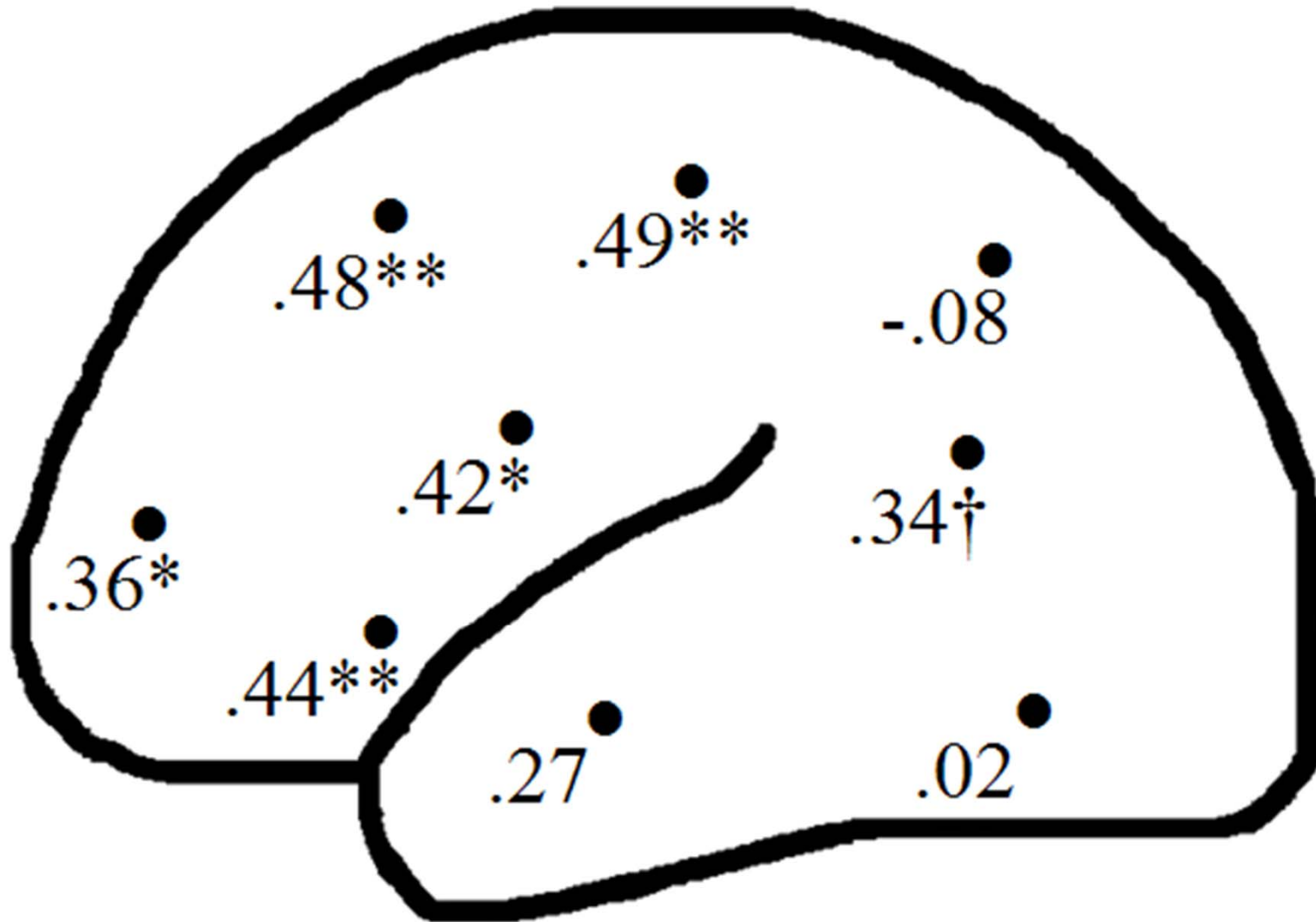
Frontal EEG asymmetry predicts Anger and Aggression

- Not in Neutral condition
... no relationship
- Strongly in Insult condition
 - $r = .57$ for anger
 - $r = .60$ for aggression
 - Note: partial r adjusting for baseline indiv diffs in asymmetry and affect



The BAS/BFS/Approach System

- **sensitive to signals of**
 - **conditioned reward**
 - **nonpunishment**
 - **escape from punishment**
- **Results in:**
 - **driven pursuit of appetitive stimuli**
 - **appetitive or incentive motivation**
 - **Decreased propensity for depression (Depue & Iacono, 1989; Fowles 1988)**



Correlations with alpha asymmetry ($\ln[\text{right}] - \ln[\text{left}]$) and self-reported Behavioral Activation Sensitivity. Positive correlations reflect greater left activity (less left alpha) is related to greater BAS scores. From Coan and Allen (2003); see also Harmon-Jones and Allen (1997).

L>R Activity (R>L Alpha) characterizes:

- an approach-related motivational style (e.g. Harmon-Jones & Allen, 1997; Sutton & Davidson, 1997)
- higher positive affect (e.g. Tomarken, Davidson, Wheeler, & Doss, 1992)
- higher trait anger (e.g. Harmon-Jones & Allen, 1998)
- lower shyness and greater sociability (e.g. Schmidt & Fox, 1994; Schmidt, Fox, Schulkin, & Gold, 1999)
- and greater defensiveness (e.g. Kline, Allen, & Schwartz, 1998; Kline, Knapp-Kline, Schwartz, & Russek, in press; Tomarken & Davidson, 1994)

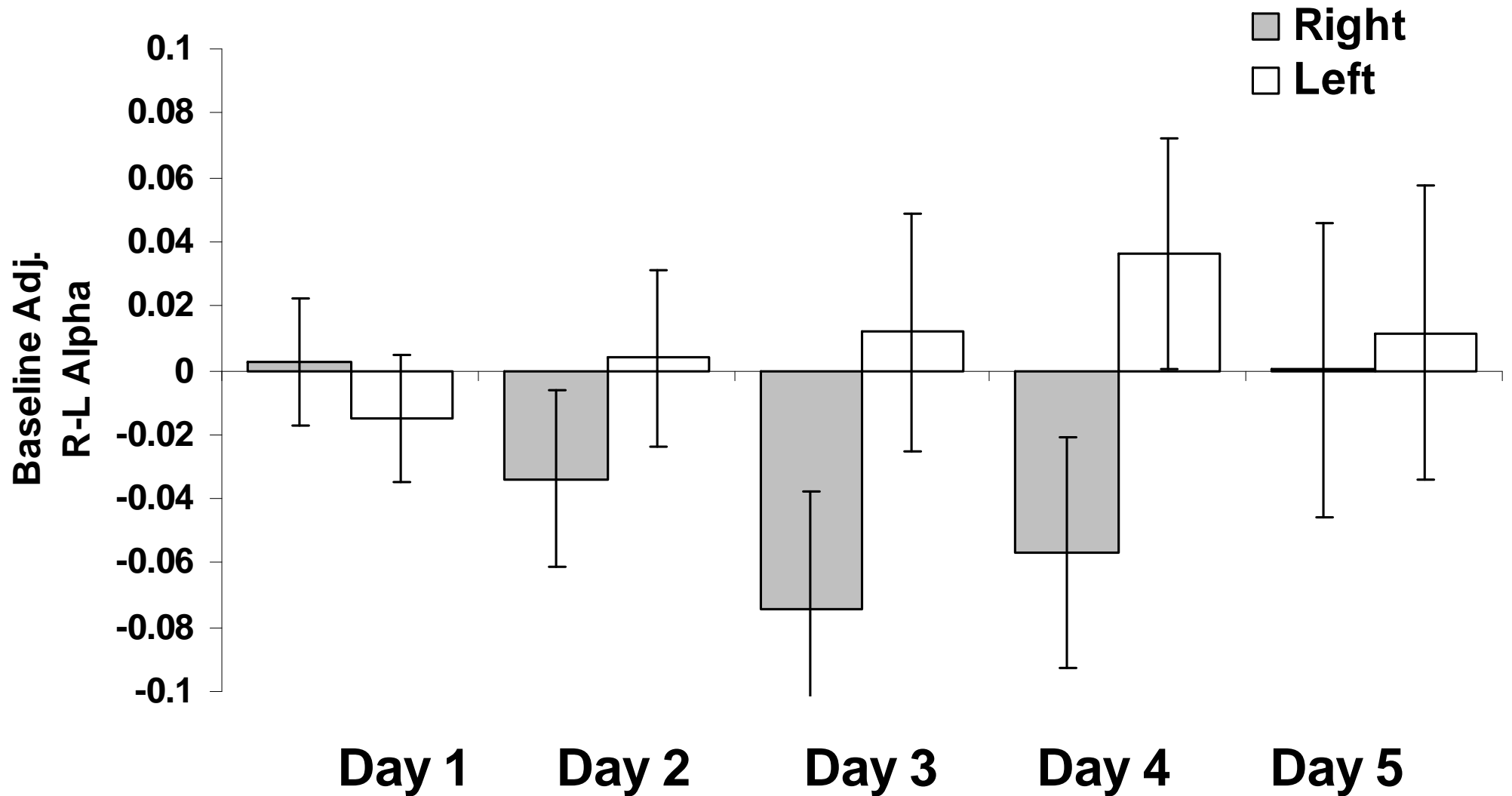
R>L Activity (L>R Alpha) characterizes:

- depressive disorders and risk for depression (e.g. Allen, Iacono, Depue, & Arbisi, 1993; Gotlib, Ranganath, & Rosenfeld, 1998; Henriques & Davidson, 1990; Henriques & Davidson, 1991 **but see also Reid, Duke, & Allen, 1998**)
- certain anxiety disorders (e.g. Davidson, Marshall, Tomarken, & Henriques, 2000; Wiedemann et al., 1999)

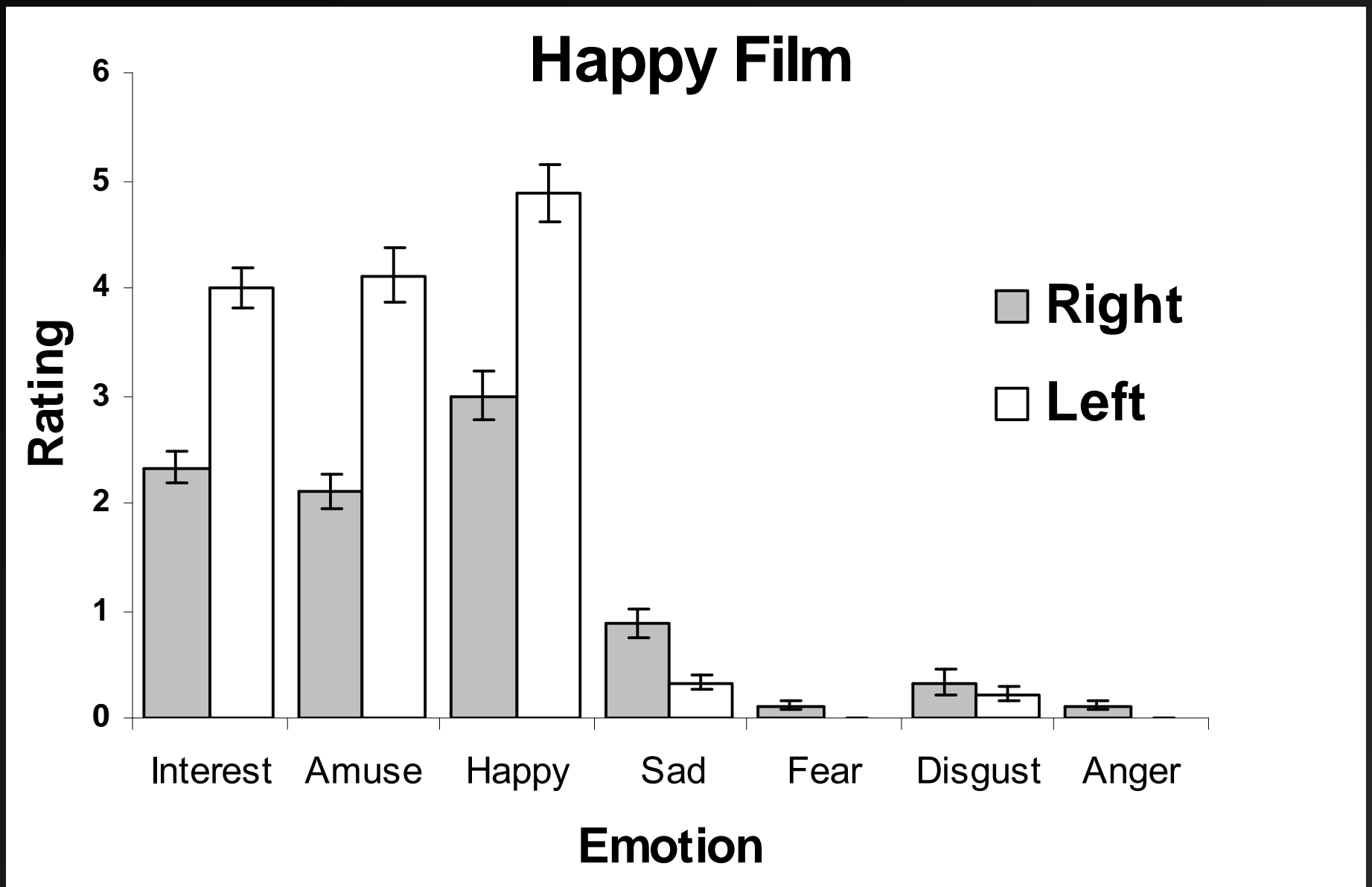
Correlations \neq Causality

- Study to manipulate EEG Asymmetry
- Five consecutive days of biofeedback training (R vs L)
 - Nine subjects trained “Left”; Nine “Right”
 - Criterion titrated to keep reinforcement equal
- Tones presented when asymmetry exceeds a threshold, adjusted for recent performance
- Films before first training and after last training

Training Effects: Asymmetry Scores



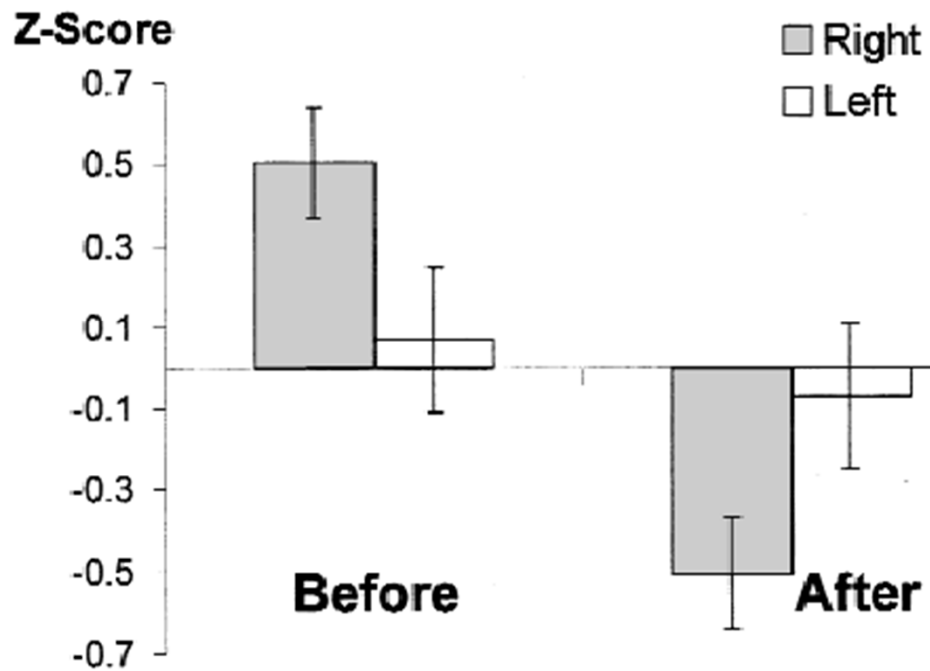
Manipulation of EEG asymmetry with biofeedback produced differential change across 5 days of training; Regression on Day 5



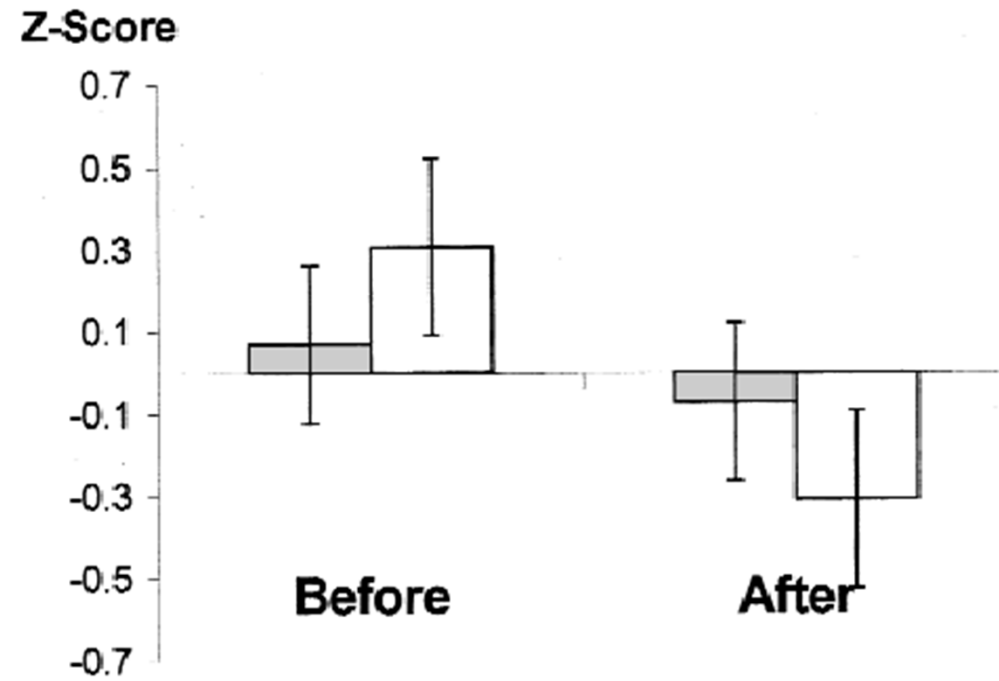
Despite no differences prior to training, following manipulation of EEG asymmetry with biofeedback subjects trained to increase left frontal activity report greater positive affect.

From Allen, Harmon-Jones, and Cavender (2001)

Zygomatic



Corrugator

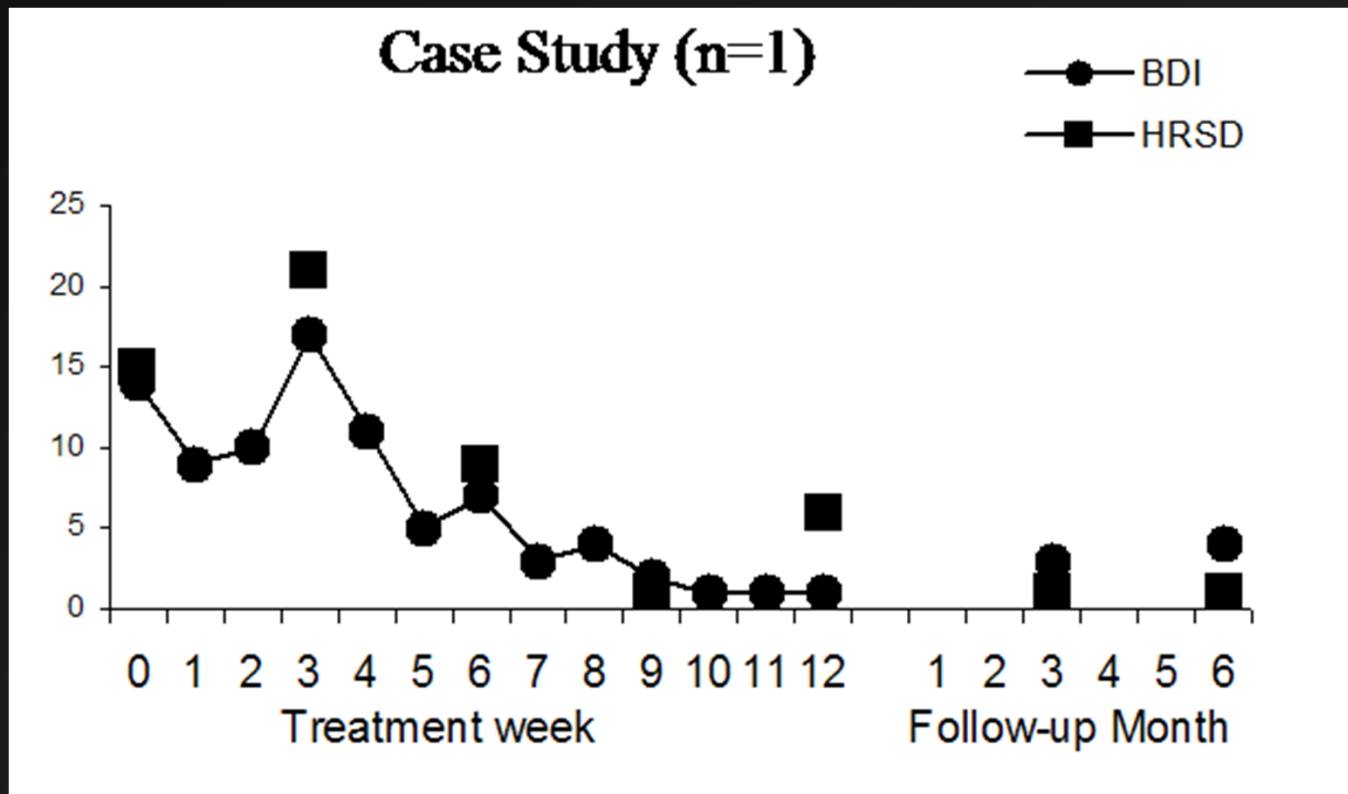


From Allen, Harmon-Jones, and Cavender (2001)

Manipulation of Asymmetry using Biofeedback

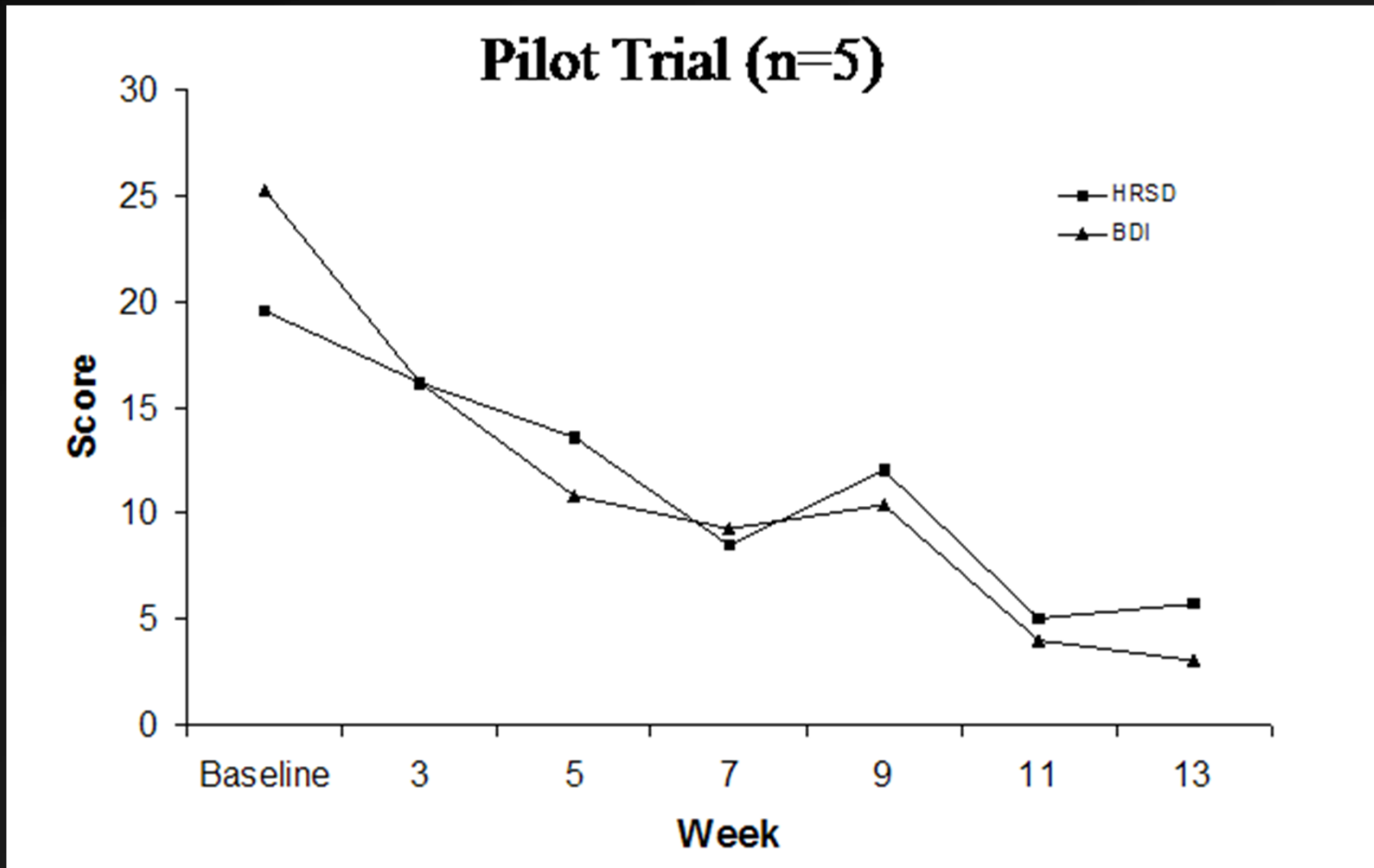
- Phase 1: Demonstrate that manipulation of EEG asymmetry is possible
- Phase 2: Determine whether EEG manipulation has emotion-relevant consequences
- Phase 3: Examine whether EEG manipulation produces clinically meaningful effects
- Phase 4: Conduct efficacy trial

Phase 3a



Biofeedback provided 3 times per week for 12 weeks

Phase 3b



“Open Label” pilot trial, with biofeedback provided 3 times per week for 12 weeks

Phase 4: Randomized Control Trial

- Depressed subjects ages 18-60 to be recruited through newspaper ads
- Ad offers treatment for depression but does not mention biofeedback
- Participants meet DSM-IV criteria for Major Depressive Episode (nonchronic)

Design

- Contingent-noncontingent yoked partial crossover design
- Participants randomly assigned to:
 - *Contingent Biofeedback*: tones presented in response to subject's EEG alpha asymmetry
 - *Noncontingent Yoked*: tones presented that another subject had heard, but tones not contingent upon subject's EEG alpha asymmetry
- Treatments 3 times per week for 6 weeks
- After 6 weeks, all subjects receive contingent biofeedback 3 times per week for another 6 weeks

Results



A Different Manipulation

Peterson, Shackman, Harmon-Jones (2008)

- Hand contractions to activate contralateral premotor cortex
- Insult about essay (similar to Harmon-Jones & Sigelman, *JPSP*, 2001) followed by chance to give aversive noise blasts to the person who insulted them
- Hand contractions:
 - altered frontal asymmetry as predicted
 - Altered subsequent aggression (noise blasts)
- Asymmetry during hand contractions predicted aggression

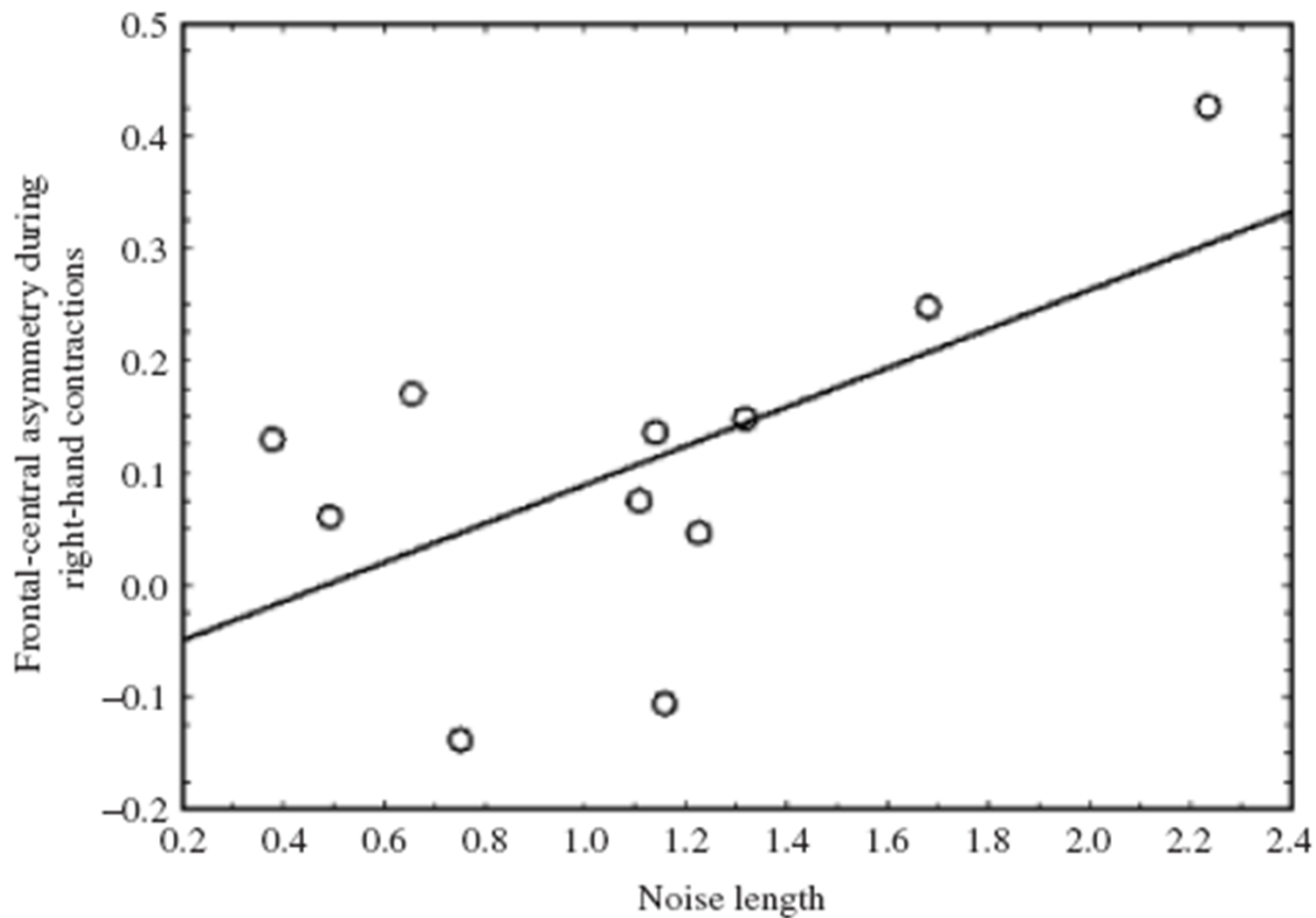


Figure 1. Relation between noise length and frontal-central asymmetry during right-hand contractions. Higher asymmetry scores indicate greater relative left than right activation.

State Changes

➤ Infants

- Stanger/Mother paradigm (Fox & Davidson, 1986)
- Sucrose Vs water (Fox & Davidson, 1988)
- Films of facial expressions (Jones & Fox, 1992; Davidson & Fox, 1982)

➤ Primates

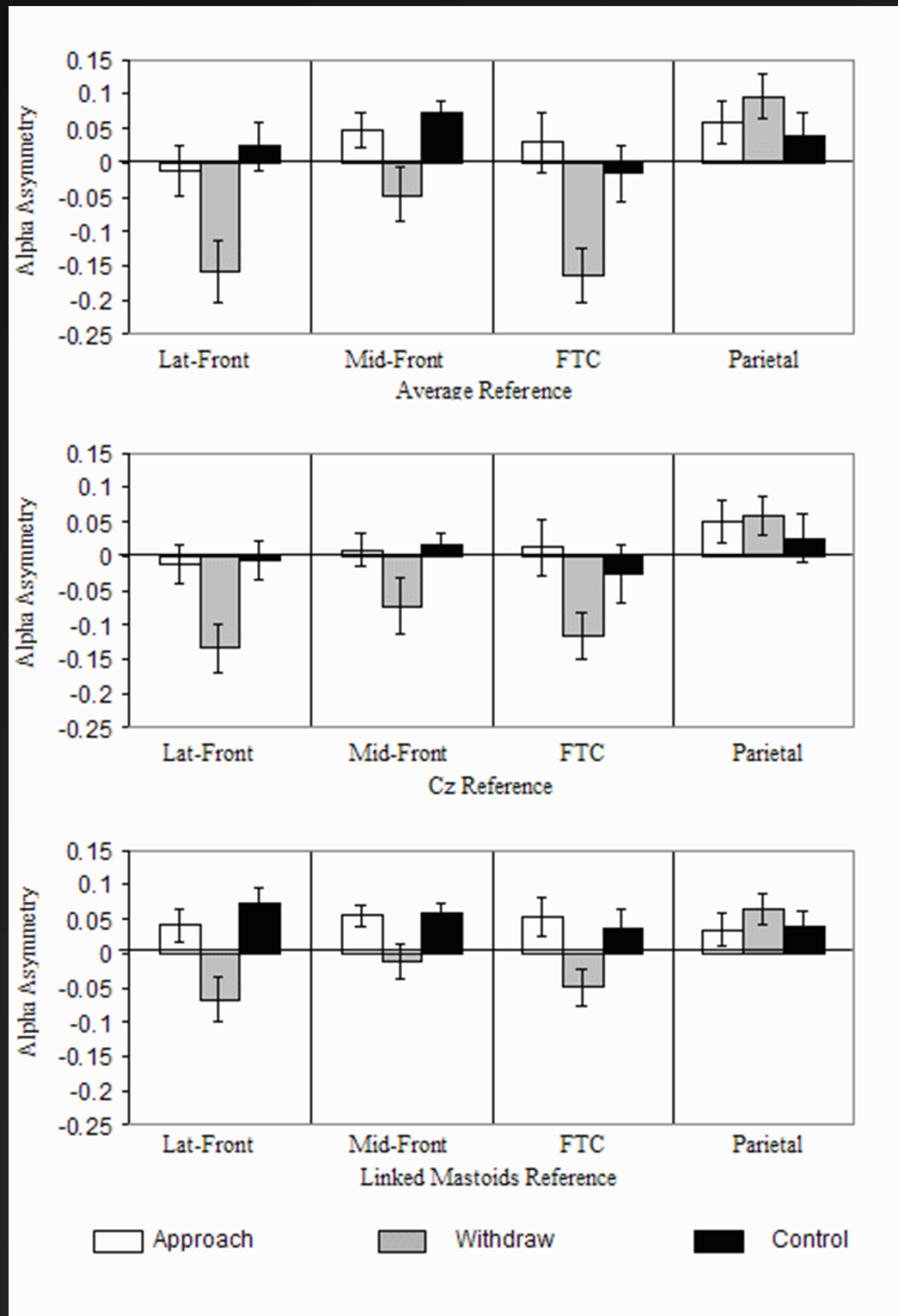
- Benzodiazepines increases LF (Davidson et al., 1992)

State Changes

- Adults
 - Spontaneous facial expressions (Ekman & Davidson, 1993; Ekman et al., 1990; Davidson et al., 1990)
 - Directed facial actions (Coan, Allen, & Harmon-Jones, 2001)

EEG responds to directed facial actions

From Coan, Allen, and Harmon-Jones (2001)



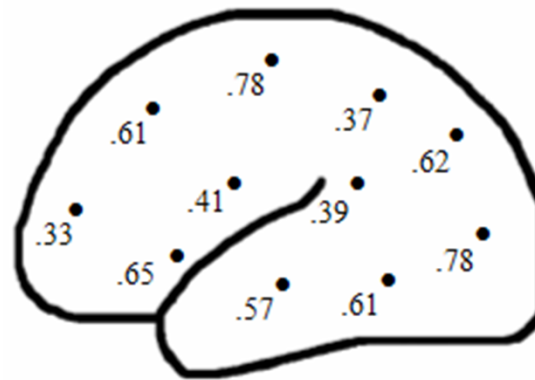
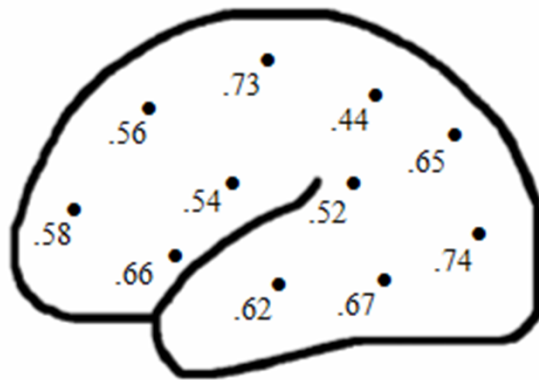
Can EEG Asymmetry serve as Trait Indicator of Risk for _____ ?

- test-retest stability in nonclinical populations
 - ICCs .53 to .72 across three weeks (Tomarken et al., 1992)
 - ICC of .57 for five sessions across two years (Tomarken et al., 1994)
 - Correlation of .66 between asymmetry at 3 months and asymmetry at 3 years of age (Jones et al., 1997)
 - 52-64% of variance across 4 sessions due to temporally stable latent trait (Hagemann et al., 2002)
- Test-retest stability in depressed folks (Allen et al., 2004)
 - median ICC across three assessments was .56, .76, .41 for AR, Cz, and LM referenced data
 - across five assessments, the comparable medians were .61, .60, and .61 for AR, Cz, and LM referenced data.

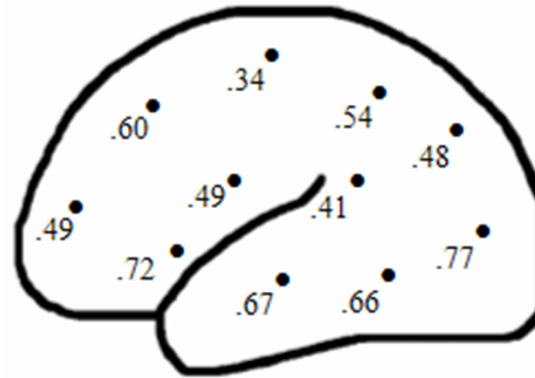
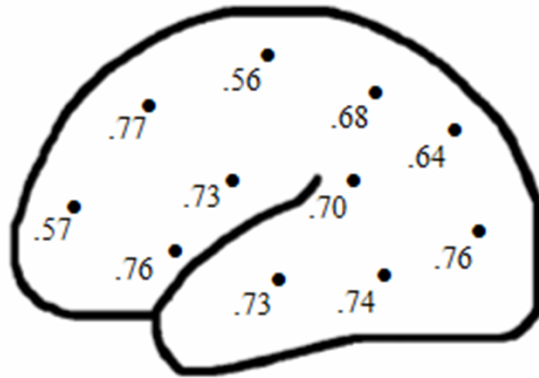
Three Assessments

Five Assessments

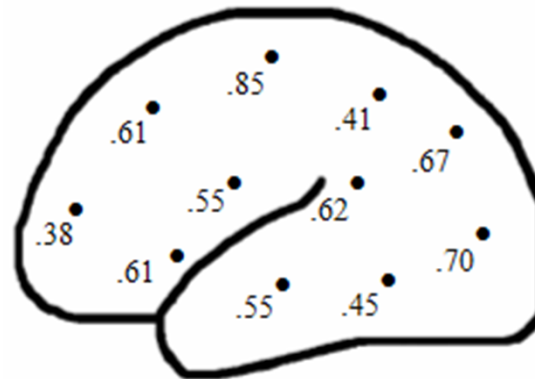
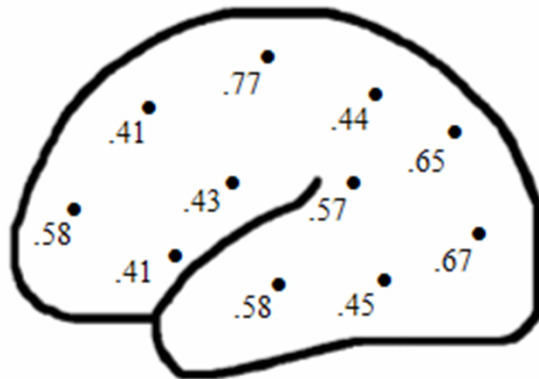
**Average
Reference**



**Cz
Reference**



**“Linked”
Mastoids
Reference**



Allen, Urry, Hitt, &
Coan (2004),
Psychophysiology

Episode	Liability	Genetic
Characterizes most depressed persons (sensitivity) ^{1,4,5,8,-9,11}	Characterizes most depressed persons (sensitivity) ^{1,4,5,8,-9,11}	Characterizes most depressed persons (sensitivity) ^{1,4,5,8,-9,11}
Differentiates depressed from nondepressed (specificity) ^{1,-3,4,5-6,-13}	Differentiates depressed from nondepressed, not only in episode but in remission as well ^{1,-3,7}	Differentiates depressed from nondepressed, not only in episode but in remission as well ^{1,-3,7}
Changes with variations in clinical state ¹⁰	Demonstrates stability in both depressed and nondepressed individuals ^{1,-4,12,present report}	Demonstrates stability in both depressed and nondepressed individuals ^{1,-4,12,present report}
	Predicts the future development of depression in individuals currently not depressed ^{NA}	Predicts the future development of depression in individuals currently not depressed ^{NA}
		Is heritable within the normal population ²
		Is more common in depressed persons with a strong family history of depression than those without a such a history ^{NA}
		Is more prevalent in families of depressed individuals than in families of nondepressed individuals ^{NA}
		Identifies those family members at risk for depression ^{NA}

¹Allen et al., 1993

²Allen, Reiner, Katsanis, & Iacono, 1997

³Davidson et al., 2000

⁴Debener et al., 2000

⁵Gotlib et al., 1998

⁶Heller et al., 1997

⁷Henriques & Davidson, 1990

⁸Henriques & Davidson, 1991

⁹Reid et al., 1998

¹⁰Rosenfeld, Baehr, Baehr, Gotlib, & Ranganath, 1996

¹¹Schaffer et al., 1983

¹²Tomarken, Davidson, Wheeler, & Kinney, 1992

¹³Wiedemann et al., 1999

Heritability of EEG Power Spectra

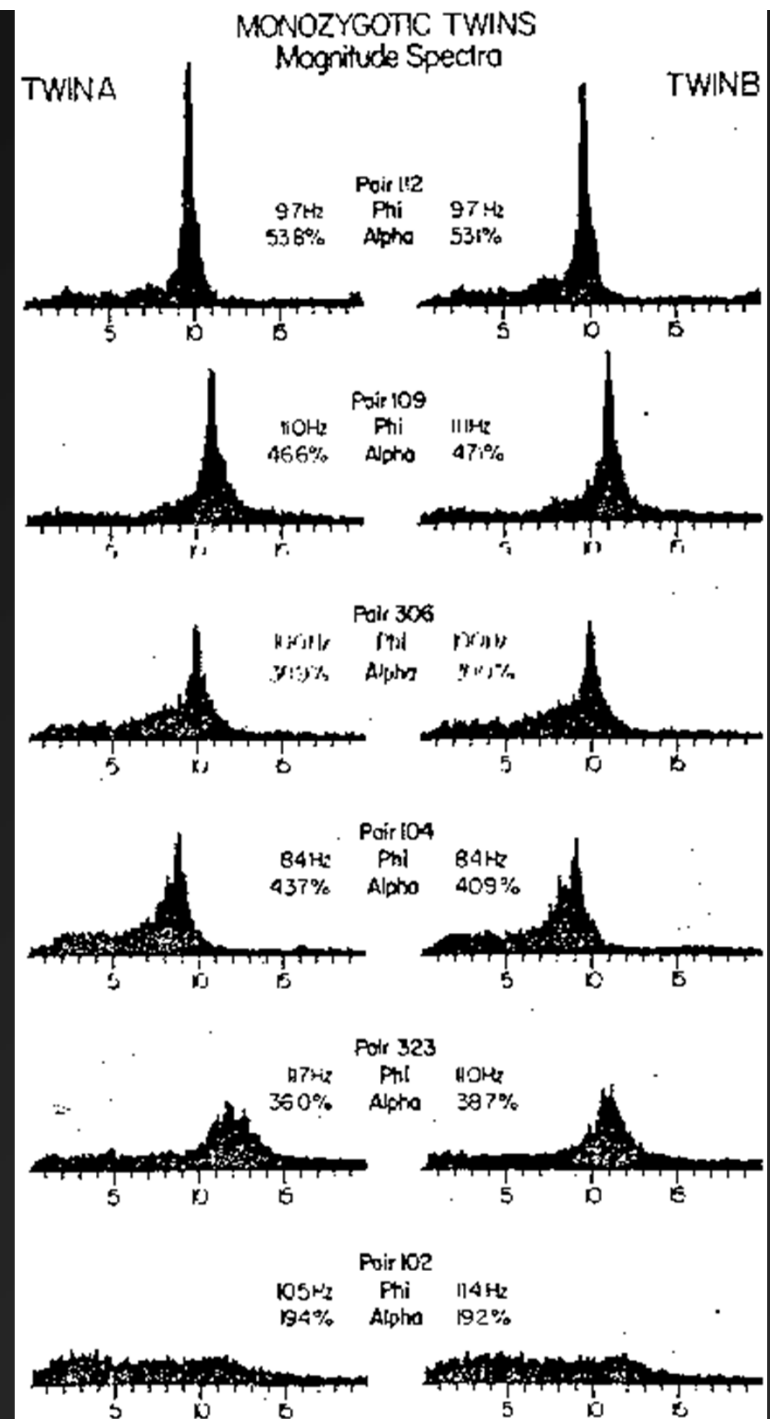


Figure 1. EEG spectra from 6 of the 39 monozygotic (MZ) twin pairs studied in 1974, selected to show the range of amount of alpha activity. Phi is the median frequency in a 3-Hz band centered on the central peak. All spectra are standardized to unit area. (Reprinted from Lykken, Tellegen, & Thorkelson, 1974.)

Resting brain asymmetry as an endophenotype for depression

Endophenotypes

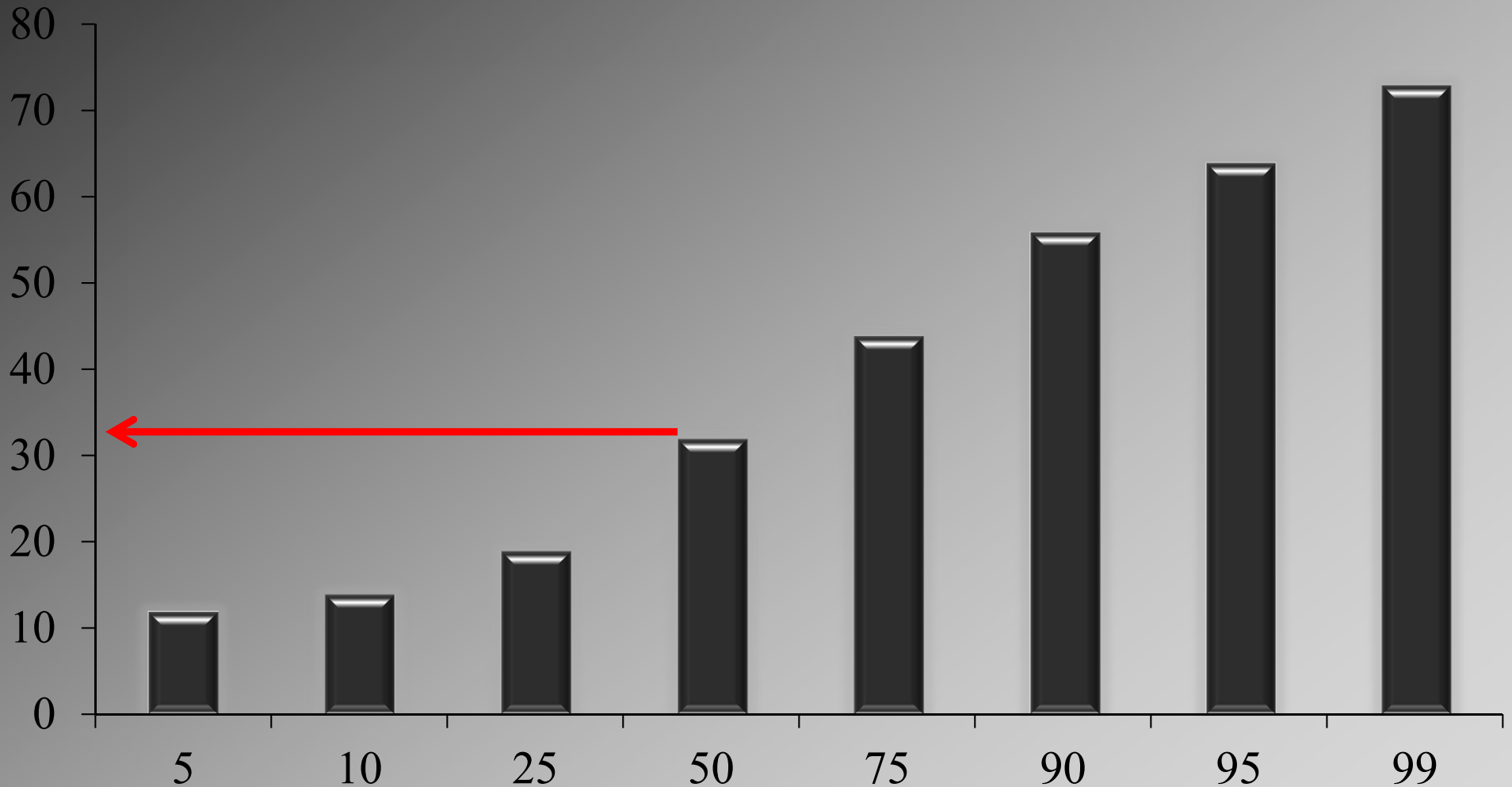
- Intermediate-level measure of characteristics related to risk for disorder
- Less complex phenotype for genetic association
- Can include, biochemical and imaging measures, among others
- Desiderata
 - Specificity
 - Heritability
 - State-independence
 - Familial Association
 - Co-segregation within families
 - Predicts development of disorder

Depression as a Heterogeneous Phenotype

- Variable Age of Onset
- Variable Symptom Presentation
- Variable Course
- Variable Response to Treatment

Depression: Variable Age Onset

Age at Select Percentiles for Onset of MDD



Data from Kessler et al., Arch Gen Psychiatry, 2005, 62:593-602

Depression: Variable Age Onset

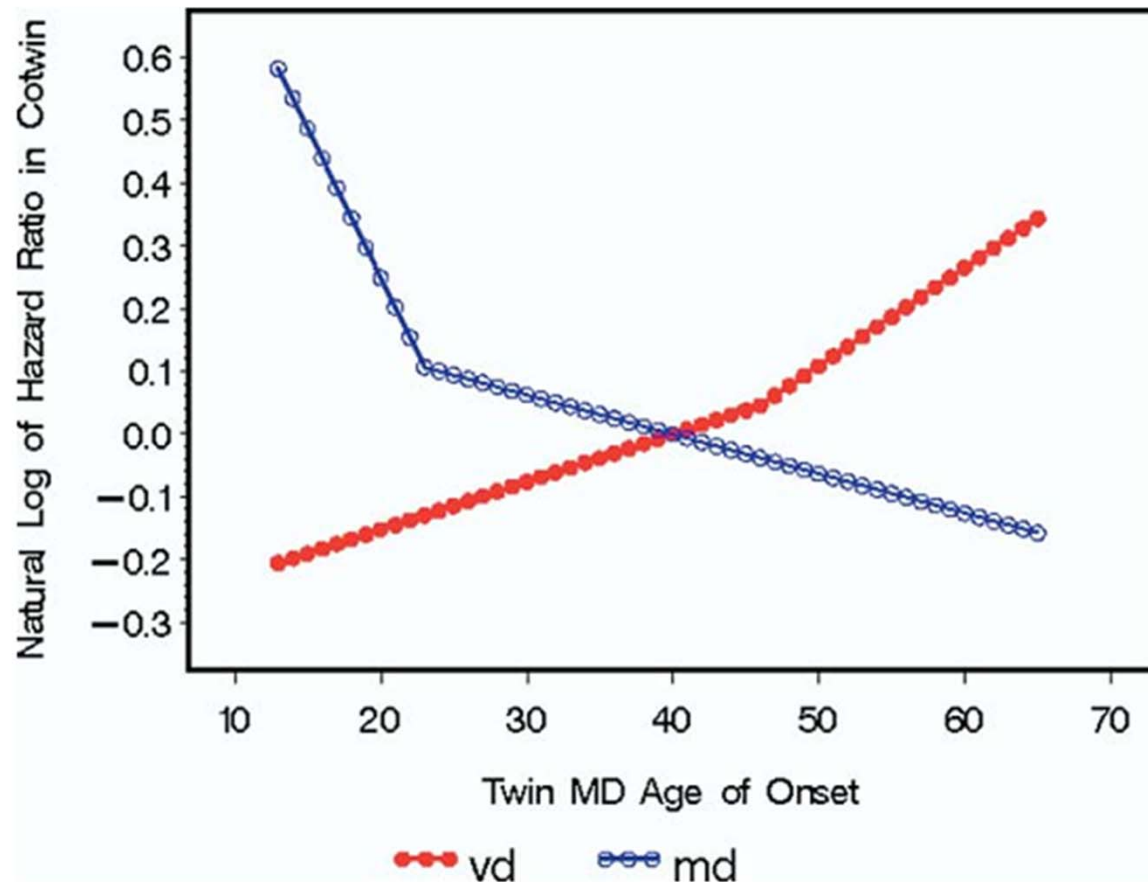
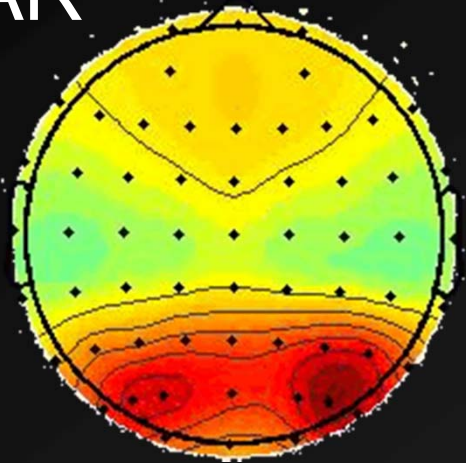


Figure 1. The relationship between the age at onset of major depression (MD) in an affected twin and the natural logarithm of the hazard ratio in the cotwin for MD (in open circles) and vascular disease (VD) (in filled-in circles). These results are obtained from a Cox proportional hazard model controlling for age, sex, and birth cohort. We fitted to these results piecewise models with a single inflection point using a grid search to find the single inflection point that maximized the model's $-2 \log$ likelihood.

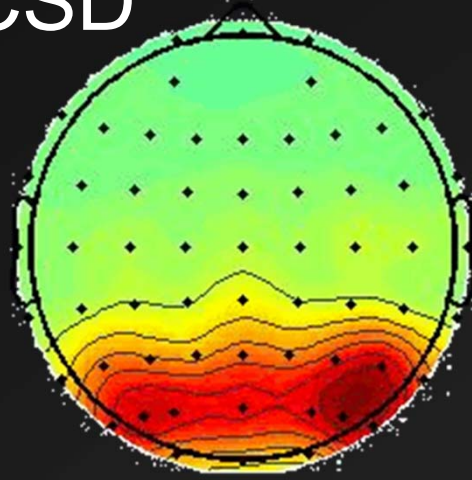
Reference Effects

Resting
Eyes Closed
Alpha Power

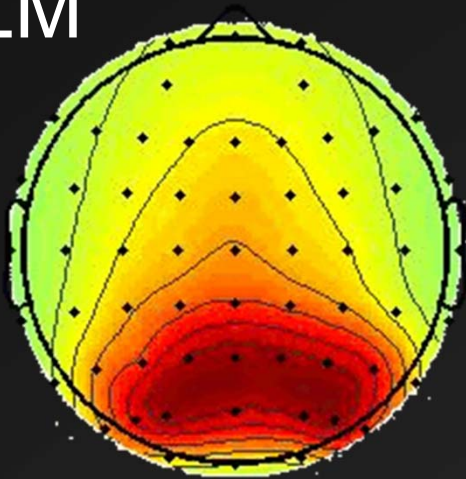
AR



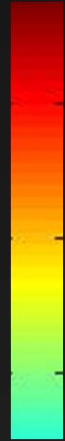
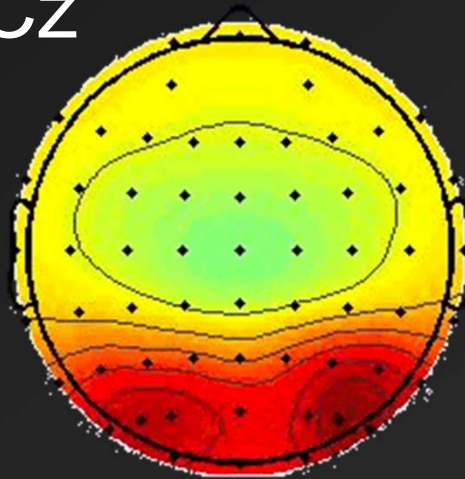
CSD



LM

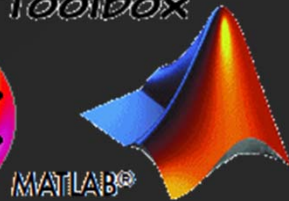
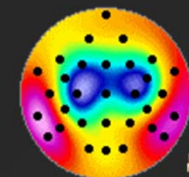


Cz

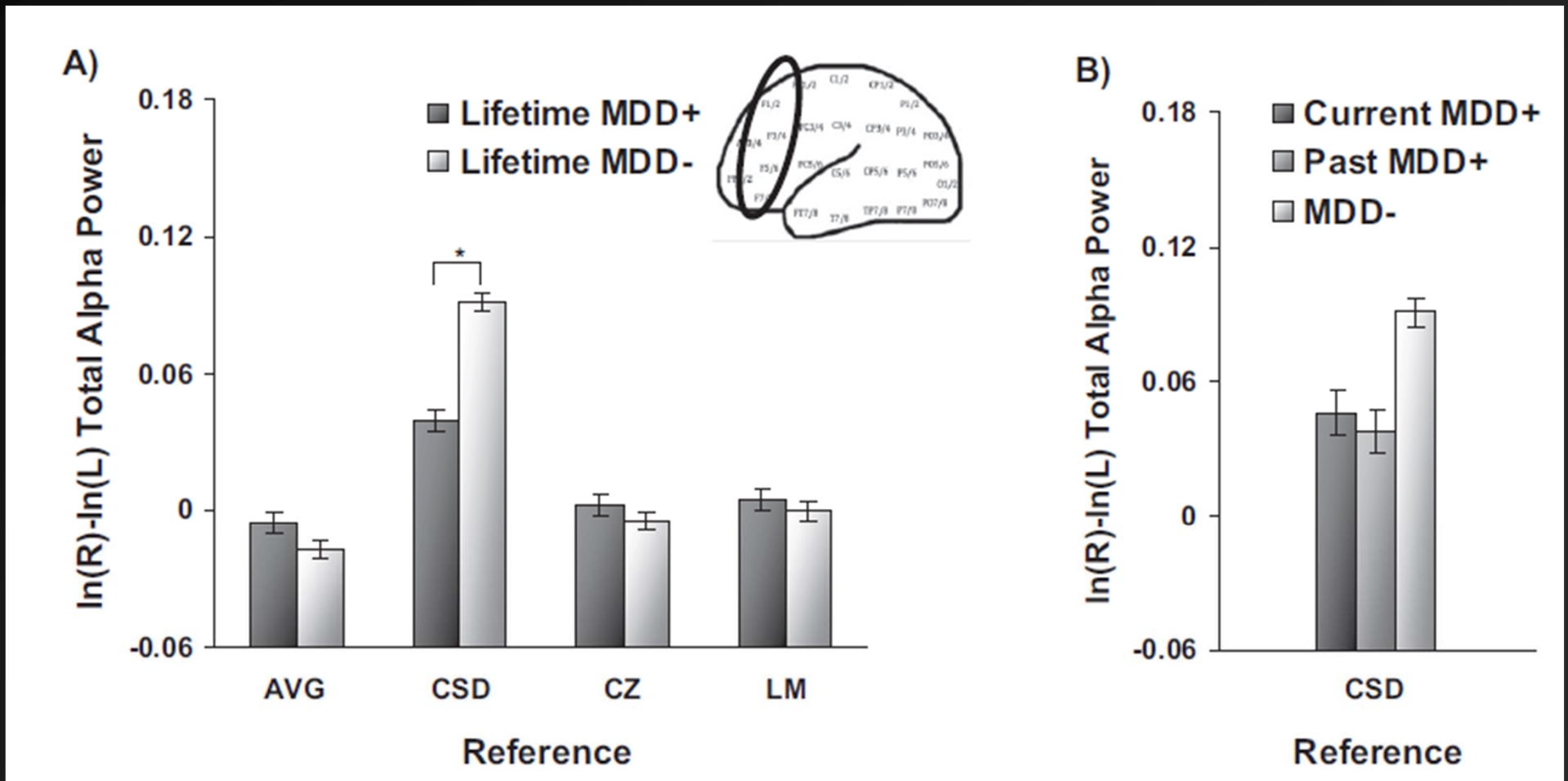


Jürgen Kayser

CSD Toolbox



The effect of reference

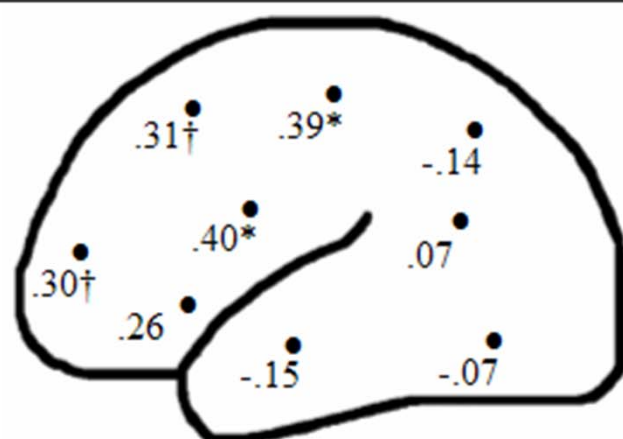


Asymmetry Metric Vs Individual Sites

- Is it left or is it right?
- Can assess using ANOVA with hemisphere as a factor
 - Removes overall power before testing for interaction of emotion/temperament/psychopathology with hemisphere
 - But not easily amenable for assessing relationship of EEG at given site to continuous variables

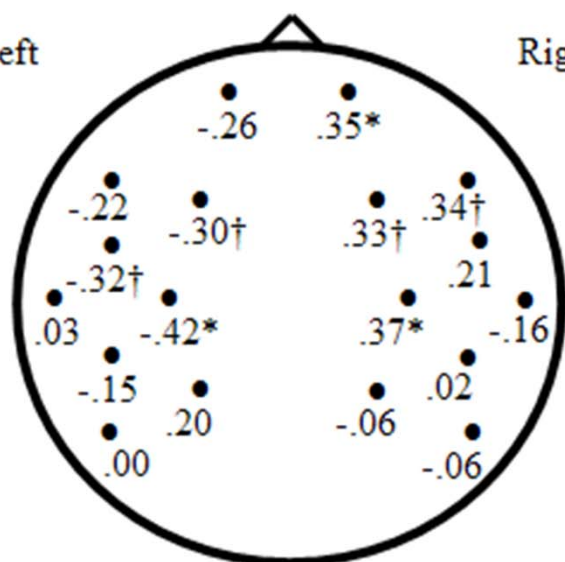
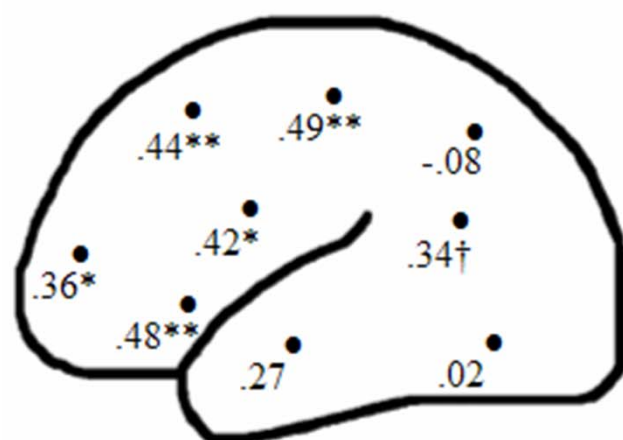
Asymmetry Metric Vs Individual Sites

- The Problem:
 - Power at an individual site reflects:
 - Underlying neural activity
 - Scalp thickness
- An early (nonoptimal) solution
 - Residualize power at each lead based on
 - Whole head power (reasonable)
 - Homologous lead power (troublesome)

Ln(Right)-Ln(Left)**Residualized Power****Average Reference**

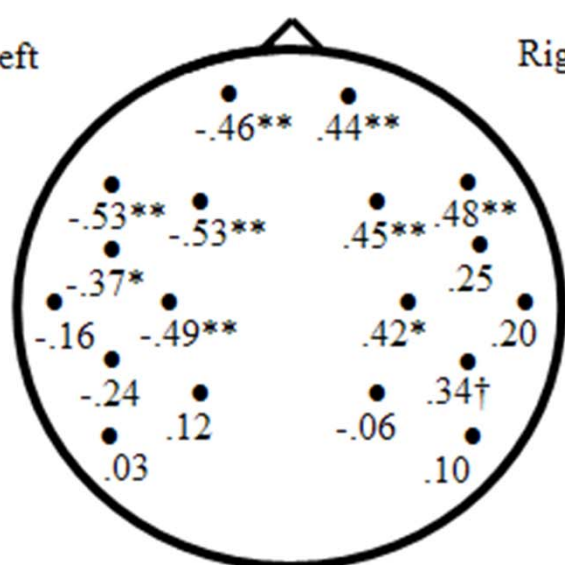
Left

Right

**Linked Mastoids Reference**

Left

Right



†p < .10; *p < .05; ** p < .01

Why does it do *that*?!

- This double residualization results in correlations with the outcome variable similar in magnitude to the difference score, but with opposite signs for the two hemispheres.
- This is actually to be expected when the predictor and criterion variable are highly correlated

Alpha Power at Homologous Sites is *Highly* Correlated

Sites	Reference	
	AR	LM
FP1 .. FP2	.997	.998
F7 .. F8	.983	.971
F3 .. F4	.990	.992
FTC1 .. FTC2	.975	.943
C3 .. C4	.977	.981
T3 .. T4	.918	.891
TCP1 .. TCP2	.944	.948
P3 .. P4	.965	.982
T5 .. T6	.907	.932

Consider residualized left lead power when $L \approx R$

$$L_{resid} = L - \hat{L}$$

$$\hat{L} = a + b(R)$$

In limiting case where $r_{lr} \rightarrow 1.0$

$$\hat{L} = 0 + 1(R) = R$$

$$L_{resid} = L - \hat{L} = L - R$$

Fancy That!

- Residual values for left hemisphere leads approaches $L - R$ as the correlation between left and right leads approaches 1.0.
- Residual values for right hemisphere approaches the value $R - L$ as the correlation between left and right leads approaches 1.0.
- Therefore, this procedure will make it appear that right hemisphere leads correlate with a criterion variable in the same direction and magnitude as the $R - L$ difference score, and that left hemisphere leads correlate with a criterion variable in the opposite direction but same magnitude as the $R - L$ difference score.
- Therefore, *don't do that!*

What to do?

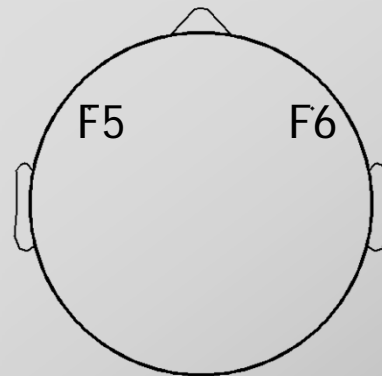
- Residualize only on whole head power, not additionally on homologous lead power
- Use hierarchical general linear models
 - can include both categorical and continuous predictors
 - can be constructed to test a variety of specific hypotheses of interest, including those related to overall power, hemisphere, and even reference scheme, all in a single model

Deconstructing the “resting”
state:

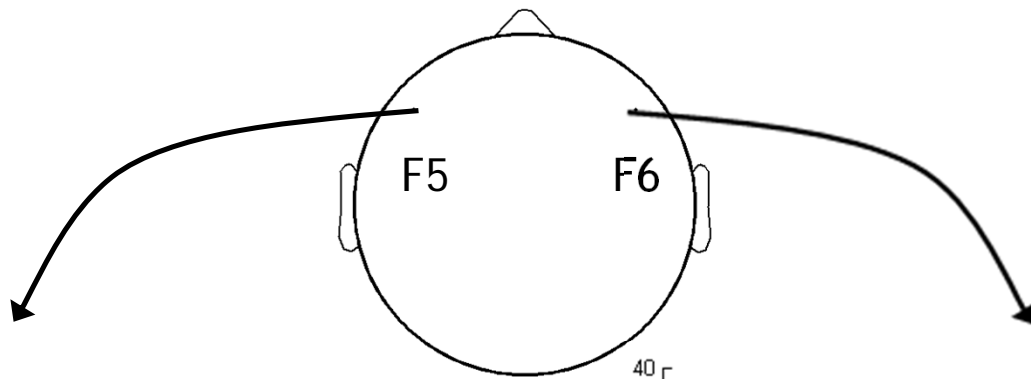
Exploring the temporal dynamics
of resting frontal brain
asymmetry as an endophenotype
for depression

The Conventional Approach

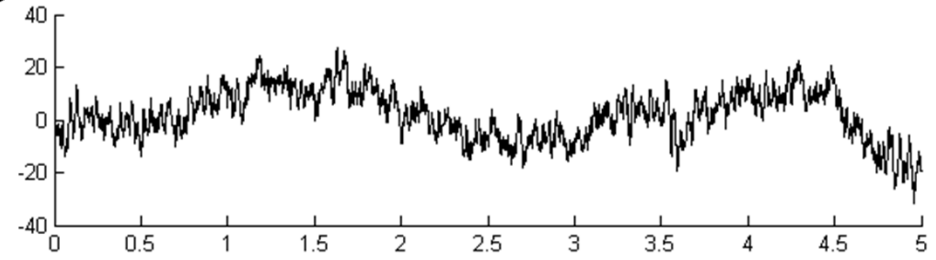
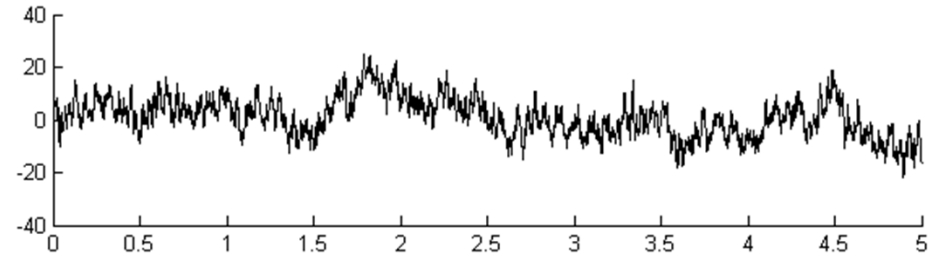
- ◆ One number to summarize several minutes of resting data
- ◆ Good reliability, but...
 - ◆ Lacks temporal specificity
 - ◆ Confuses “more” with “more often”



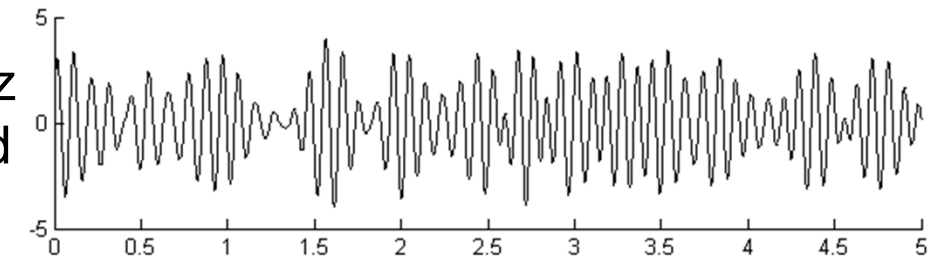
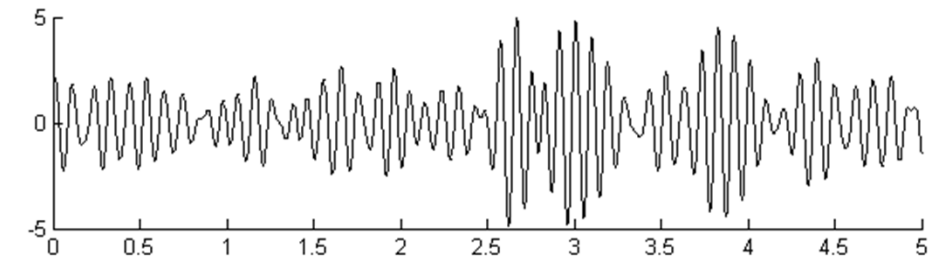
$$\text{Asym} = \ln(\text{Right}) - \ln(\text{Left}) \text{ Alpha Power}$$



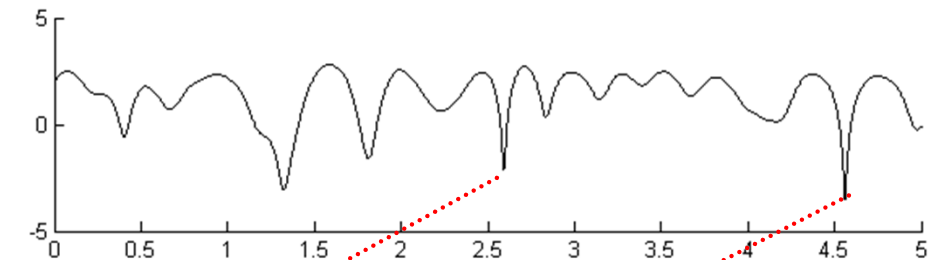
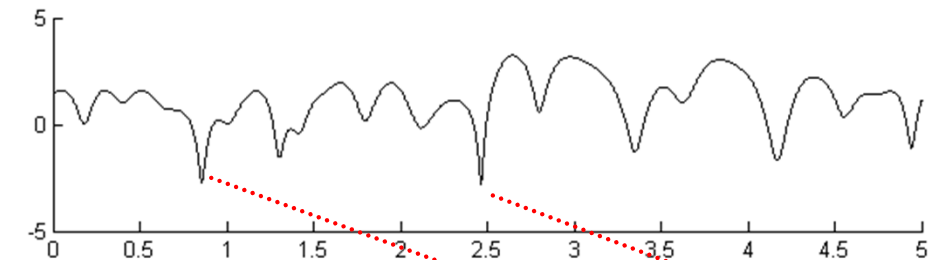
Raw



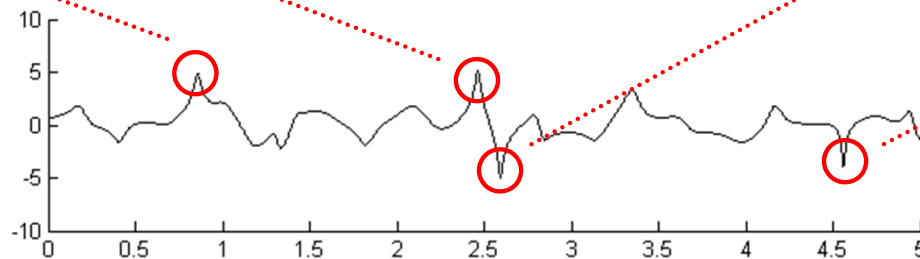
8-13 Hz
Filtered



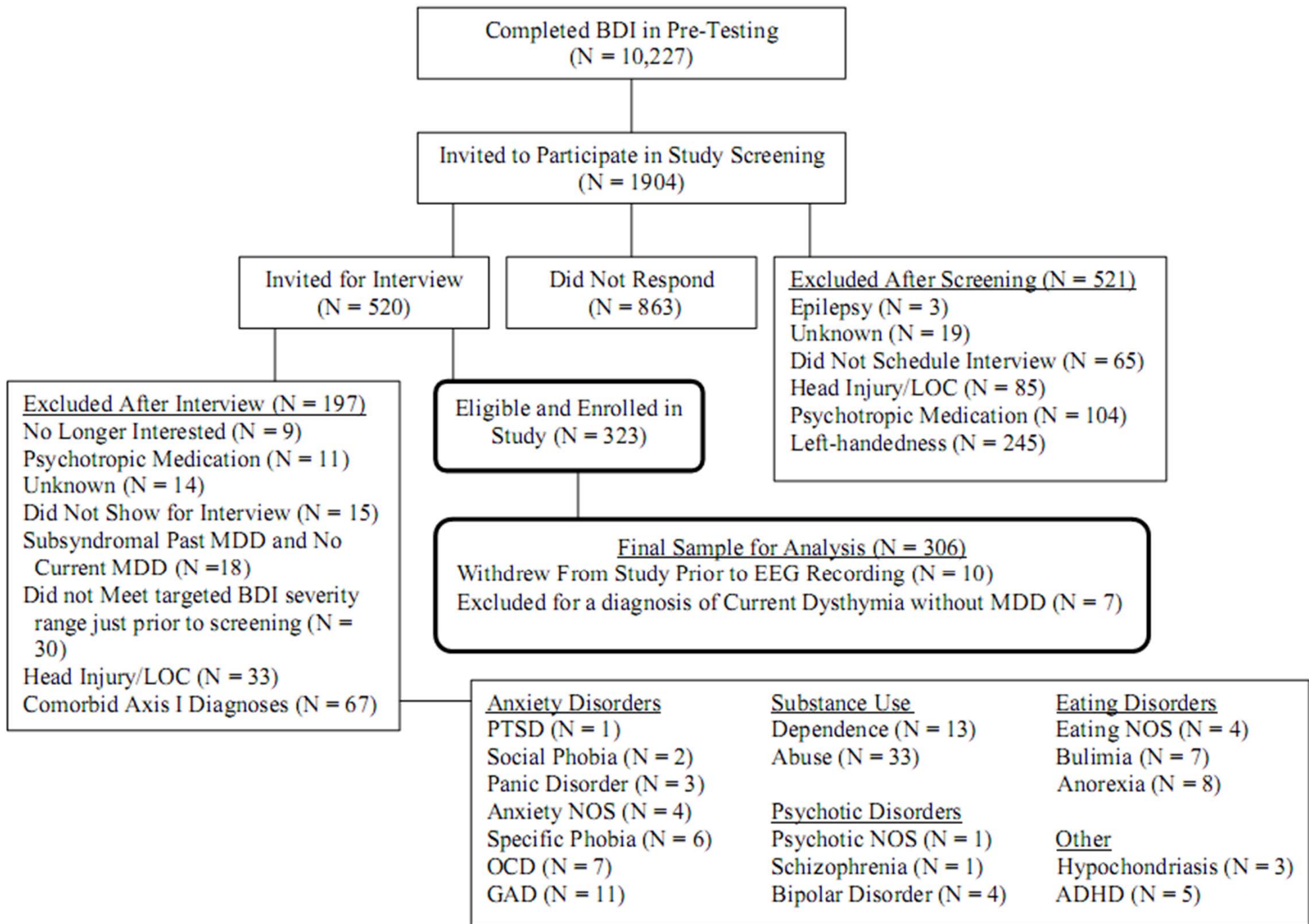
Ln
Power



1%



Continuous R-L
Difference



Three Central Questions

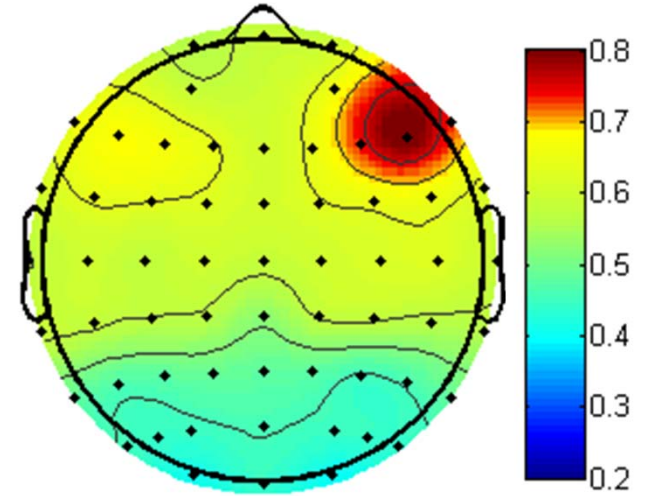
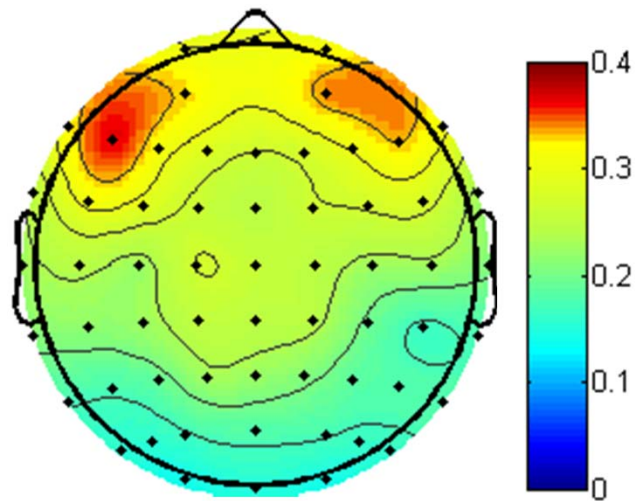
- ◆ How do the novel peri-burst metrics of dynamic asymmetry compare to the conventional FFT-based metrics?
- ◆ Do the peri-burst metrics adequately differentiate depressed and non-depressed participants
- ◆ What EEG dynamics surround the asymmetry bursts that are captured by the novel peri-burst metrics?

Three Central Questions

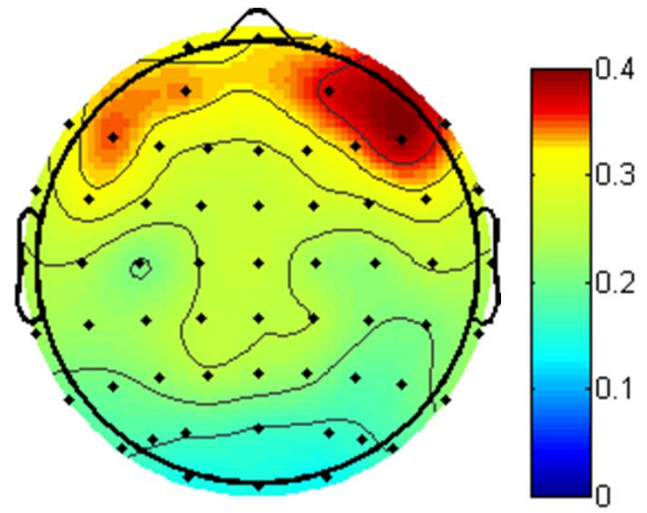
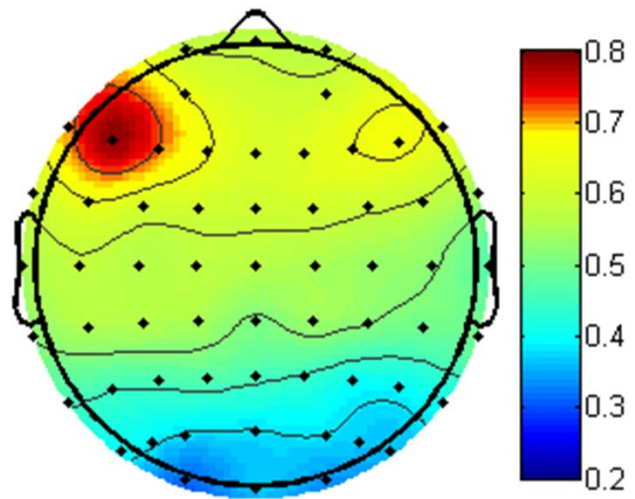
- ◆ How do the novel peri-burst metrics of dynamic asymmetry compare to the conventional FFT-based metrics?
- ◆ Do the peri-burst metrics adequately differentiate depressed and non-depressed participants
- ◆ What EEG dynamics surround the asymmetry bursts that are captured by the novel peri-burst metrics?

Relationship of Peri-Burst Alpha Power with Conventional FFT-Derived Power

POS



NEG

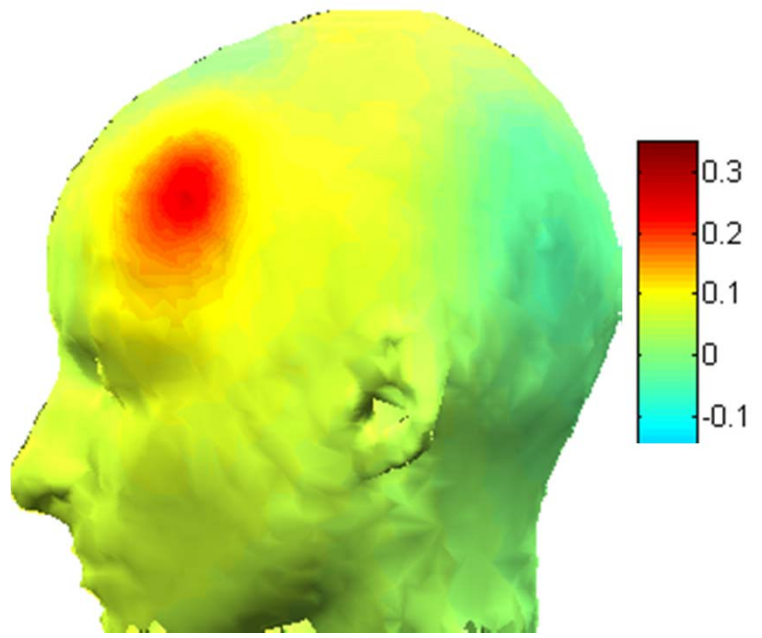


F5

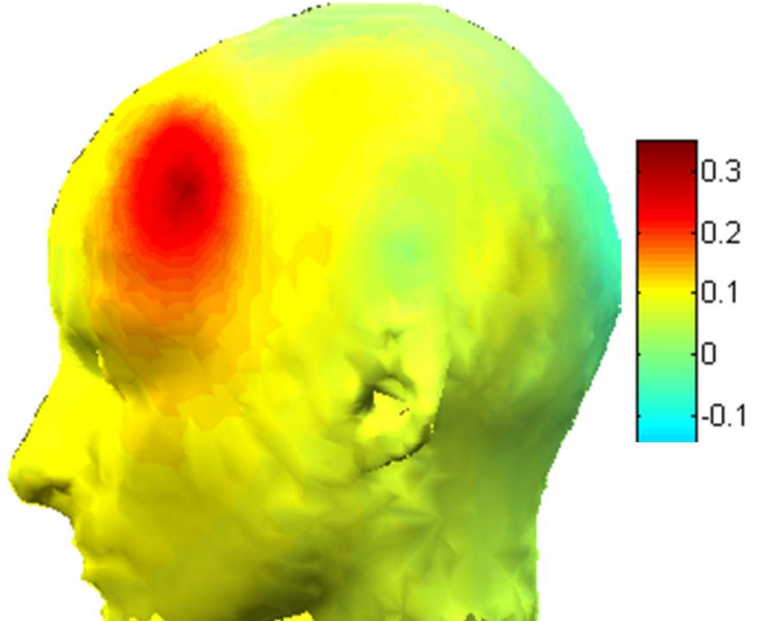
F6

Relationship of Peri-Burst Alpha Asymmetry at F6-F5 with Conventional FFT-Derived Alpha Asymmetry across the scalp

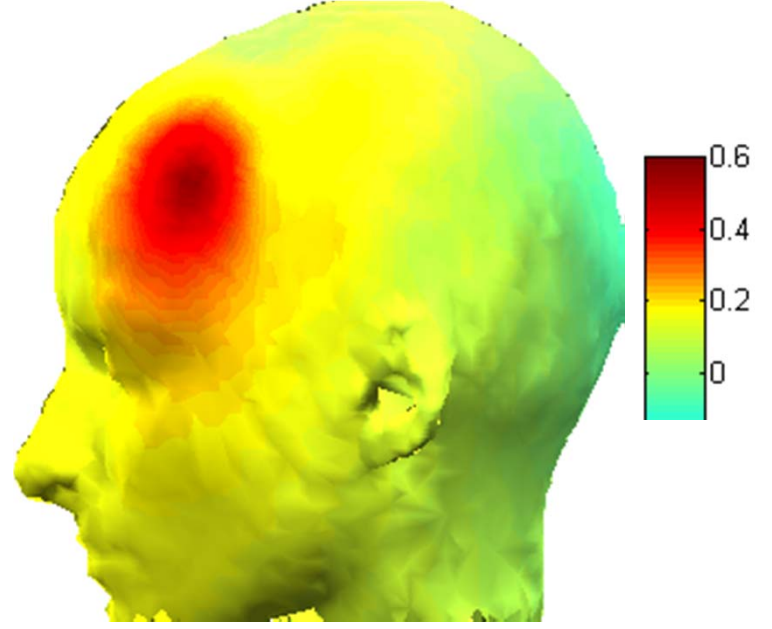
POS



NEG



COMBINED

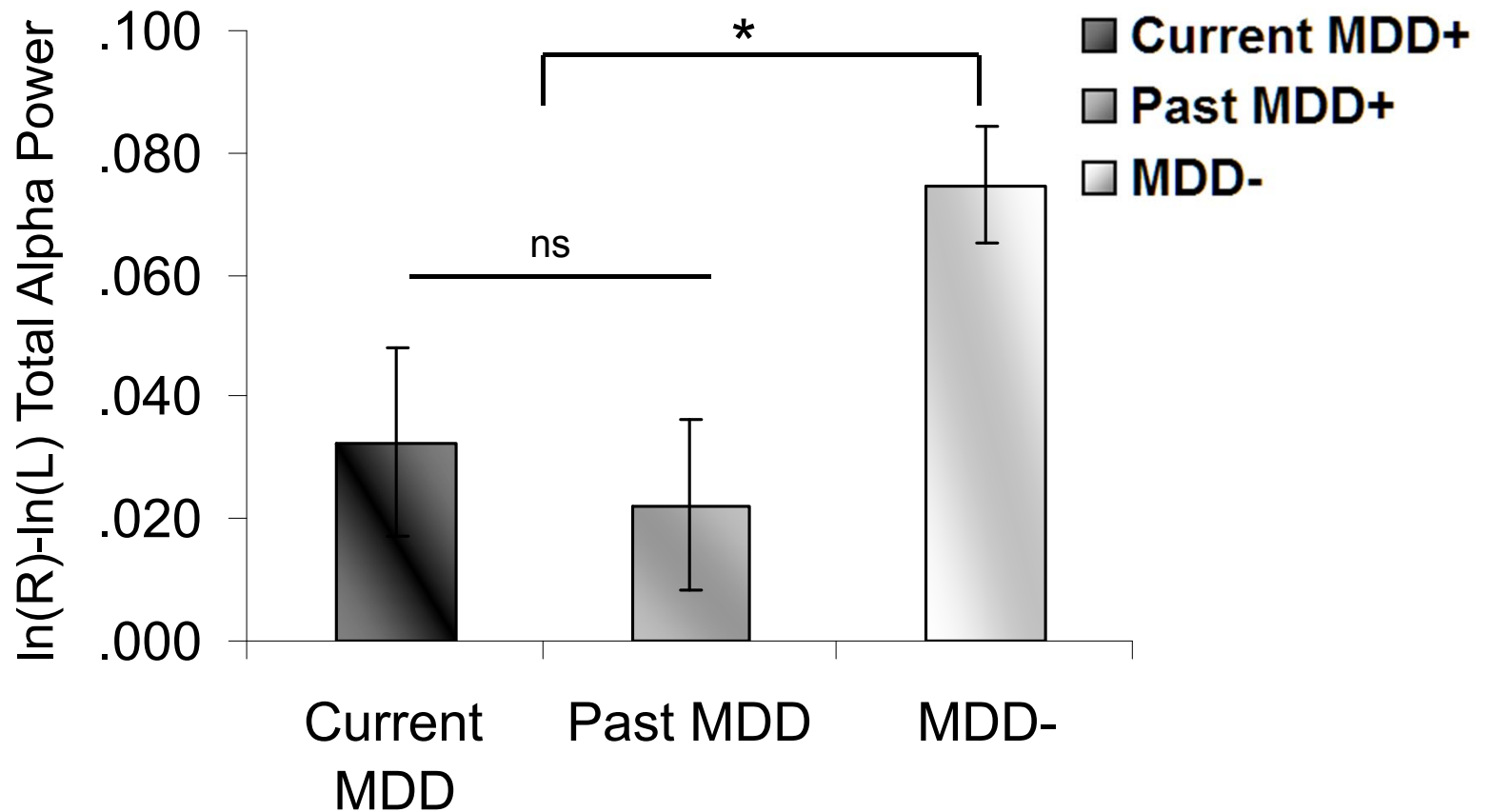


$r^2 = .42!$
(1%)

Three Central Questions

- ◆ How do the novel peri-burst metrics of dynamic asymmetry compare to the conventional FFT-based metrics?
- ◆ Do the peri-burst metrics adequately differentiate depressed and non-depressed participants
- ◆ What EEG dynamics surround the asymmetry bursts that are captured by the novel peri-burst metrics?

Conventional Frontal EEG Alpha Asymmetry by MDD status



Peri-burst Frontal EEG Alpha Power Asymmetry by MDD status

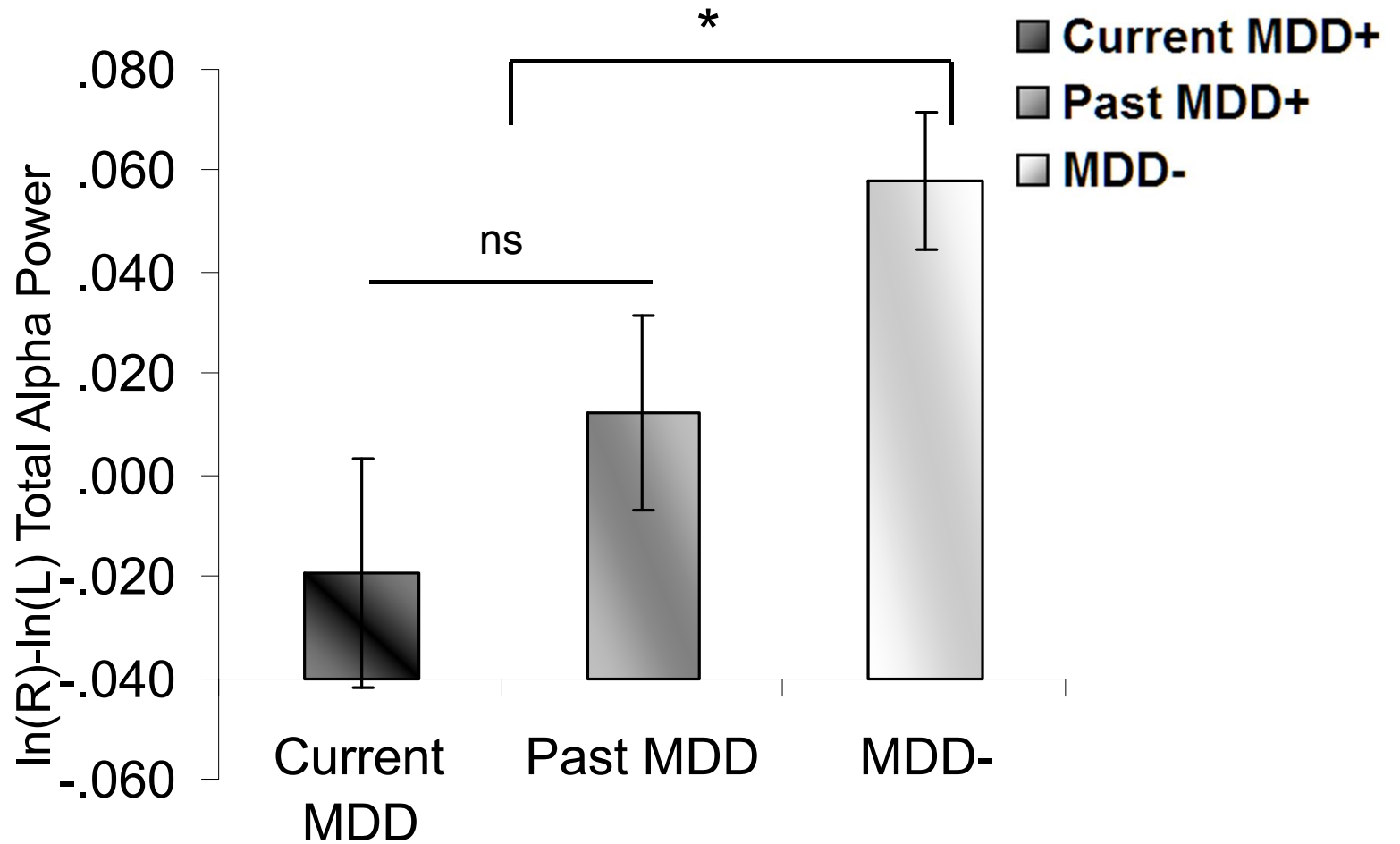


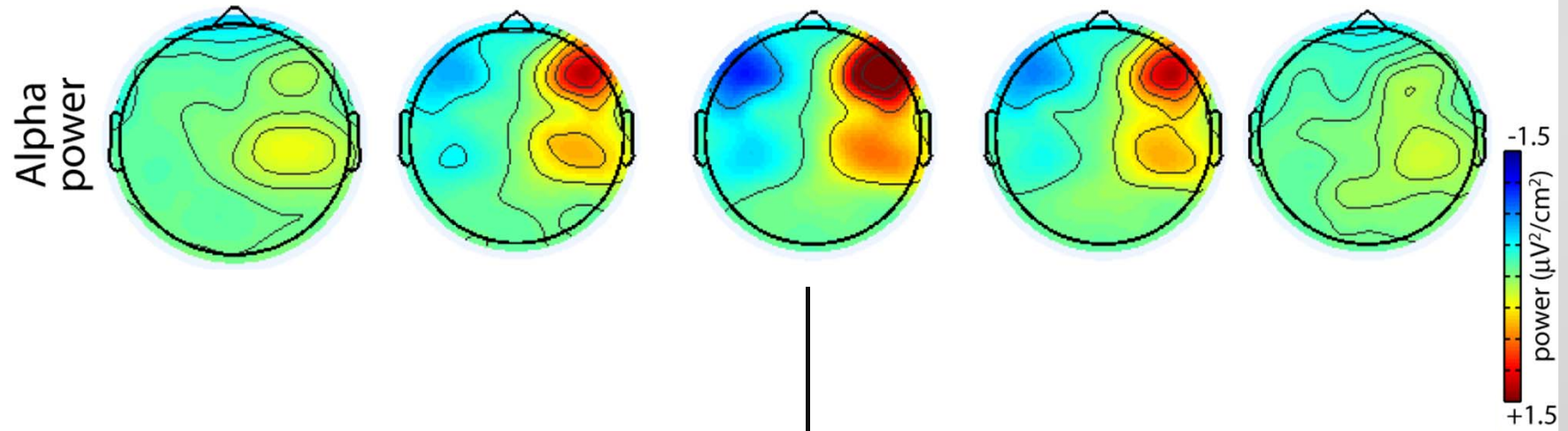
Table 3. Effect sizes (Cohen's *d*) comparing depressed groups to never depressed controls.

Diagnosis	Conventional	Peri-burst
Lifetime MDD	.43	.38
Past MDD only	.43	.27
Current MDD (with or without Past MDD)	.35	.45

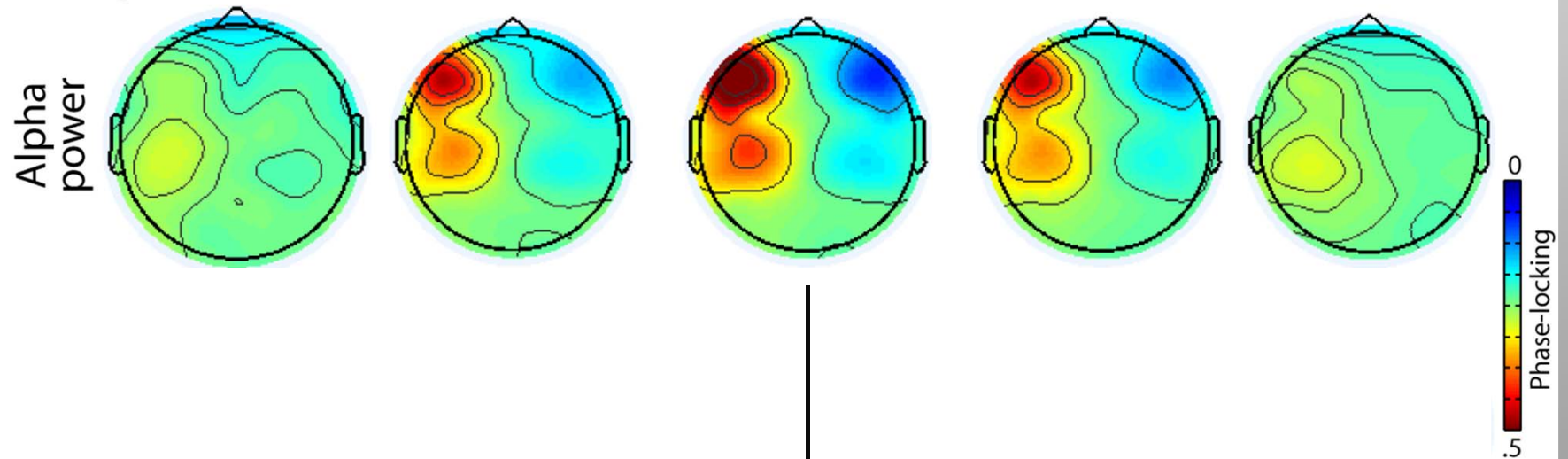
Three Central Questions

- ◆ How do the novel peri-burst metrics of dynamic asymmetry compare to the conventional FFT-based metrics?
- ◆ Do the peri-burst metrics adequately differentiate depressed and non-depressed participants
- ◆ What EEG dynamics surround the asymmetry bursts that are captured by the novel peri-burst metrics?

(A) Positive bursts



(B) Negative bursts



-150

-75

0

75

150

Peri-burst time (ms)

Allen & Cohen, 2010

So?

- ◆ Novel peri-burst metrics account for substantial variance in conventional metrics (despite being just 1%)
- ◆ Peri-burst metrics differentiate depressed and non-depressed participants, similar to conventional metrics

So?

- ◆ Bursts reflect ...
 - ◆ Transient lateralized alpha suppression that shows a highly consistent phase relationship across bursts
 - ◆ Along with concurrent contralateral transient alpha enhancement that is less tightly phase-locked across bursts
- ◆ Analogous to ERD/ERS (Pfurtscheller, 1992)?

So?

- ◆ The fact that the alpha suppression is particularly tightly phase-locked across bursts raises the possibility that the lateralized alpha suppression may drive or regulate cortical processing
- ◆ Alpha has been shown to regulate gamma power (i.e., cross-frequency coupling, Cohen et al., 2009)

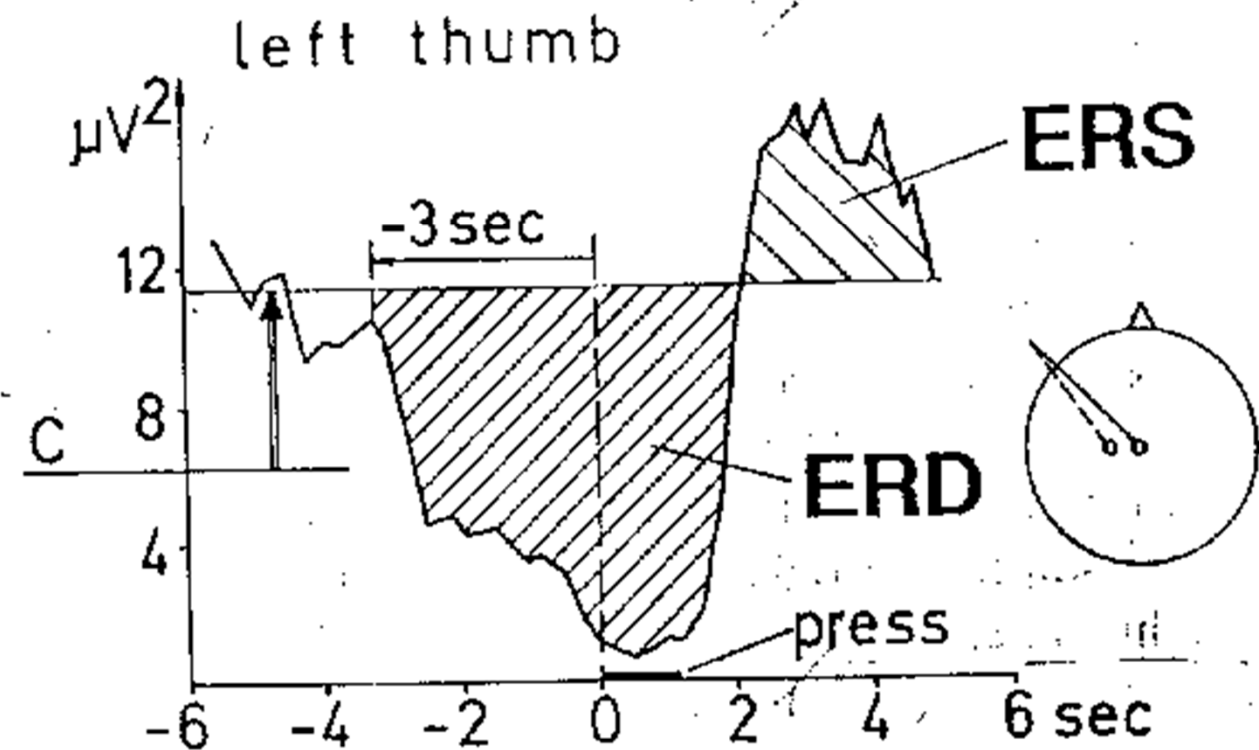
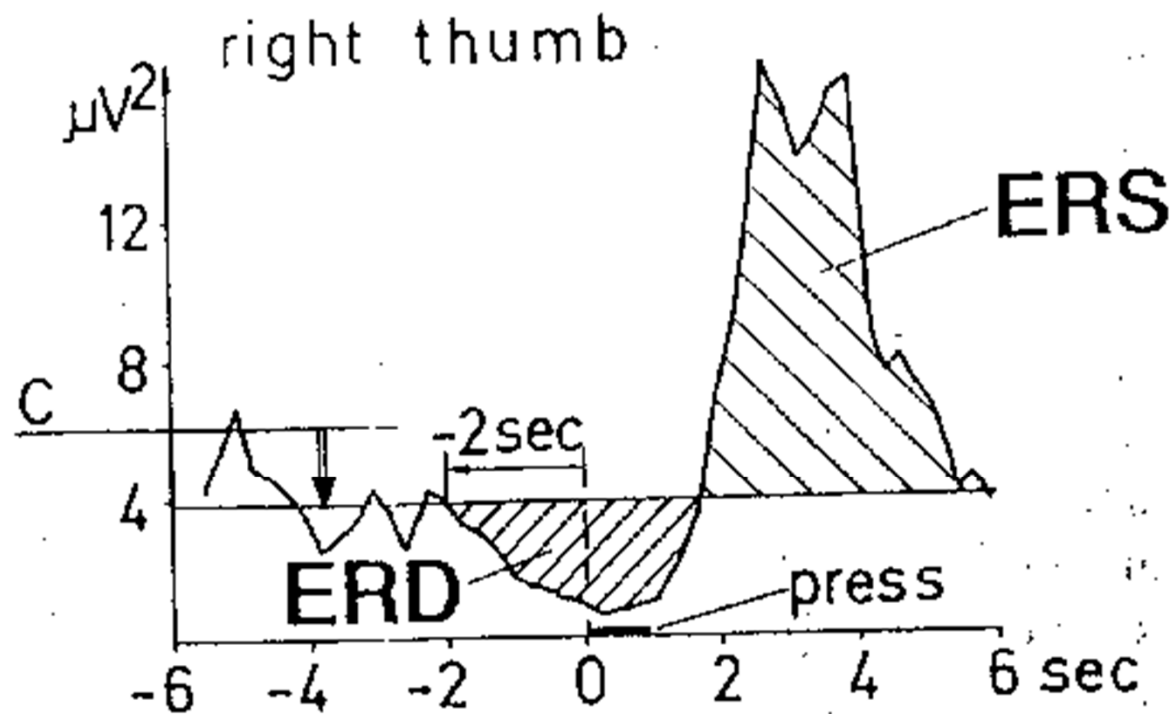


Synchronization and Desynchronization

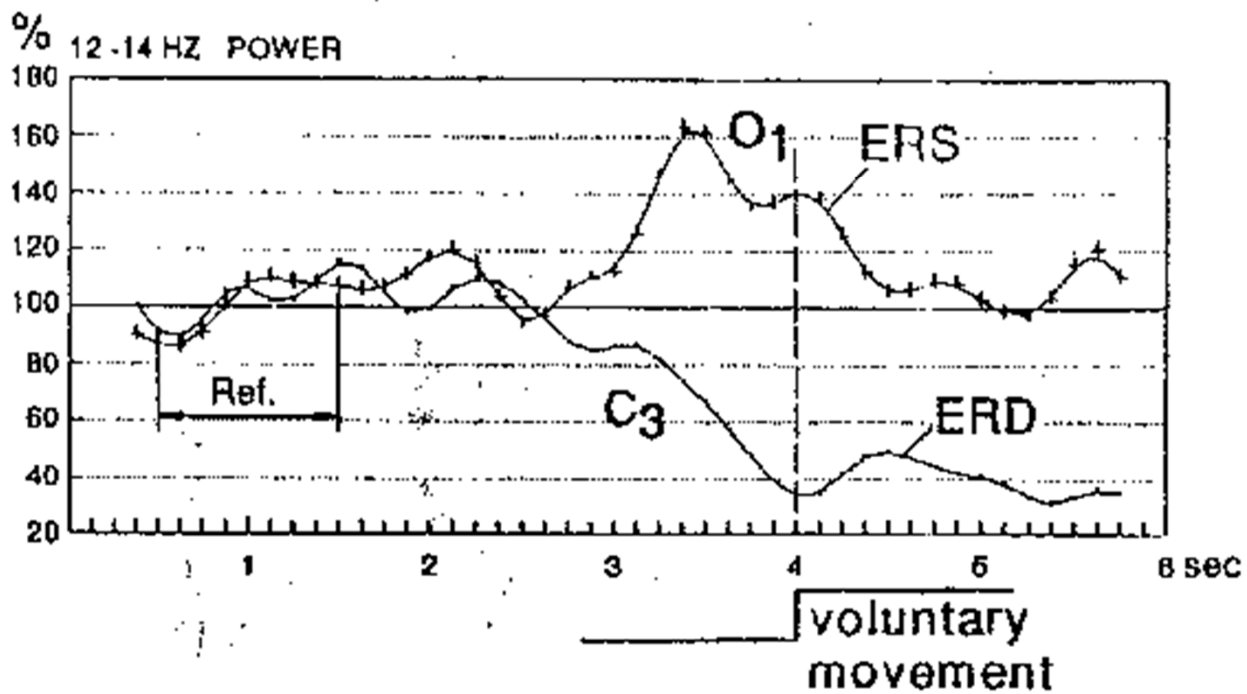
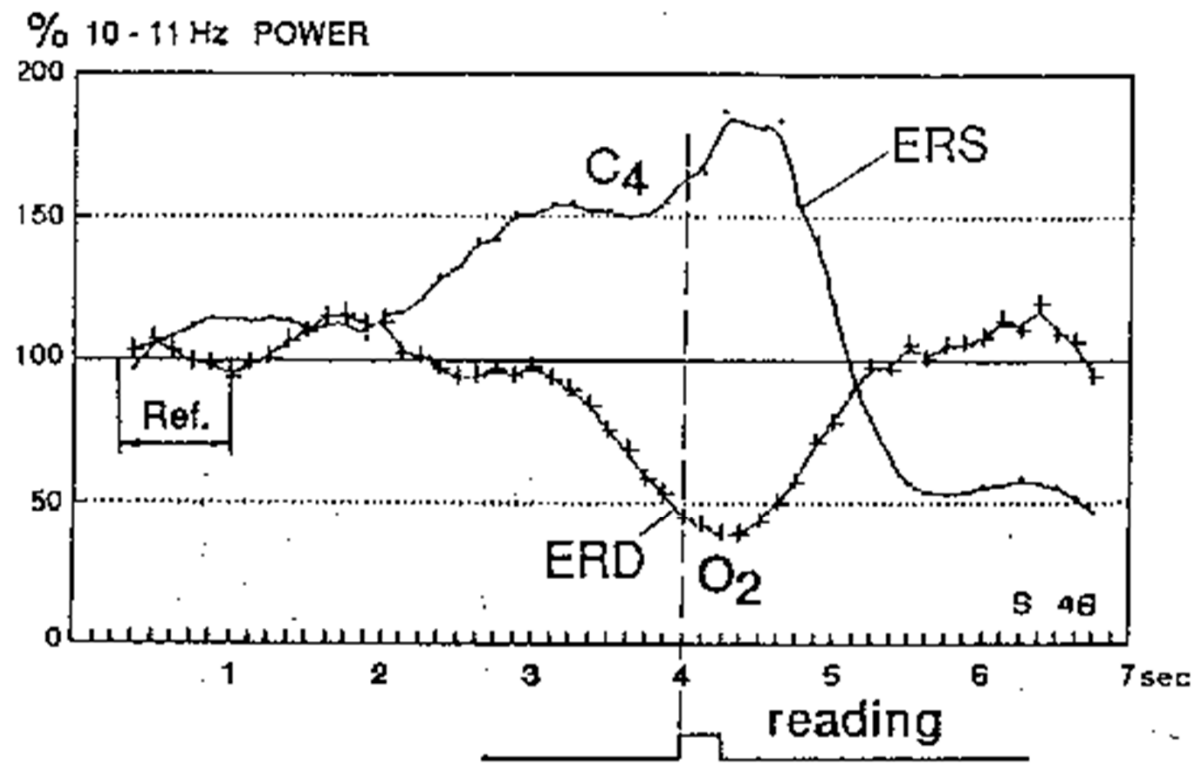
- Supposition that alpha blocking meant that the EEG had become desynchronized
 - Yet the activity is still highly synchronized -- not at 8-13 Hz
 - May involve fewer neuronal ensembles in synchrony

Event-related Synchronization and Desynchronization

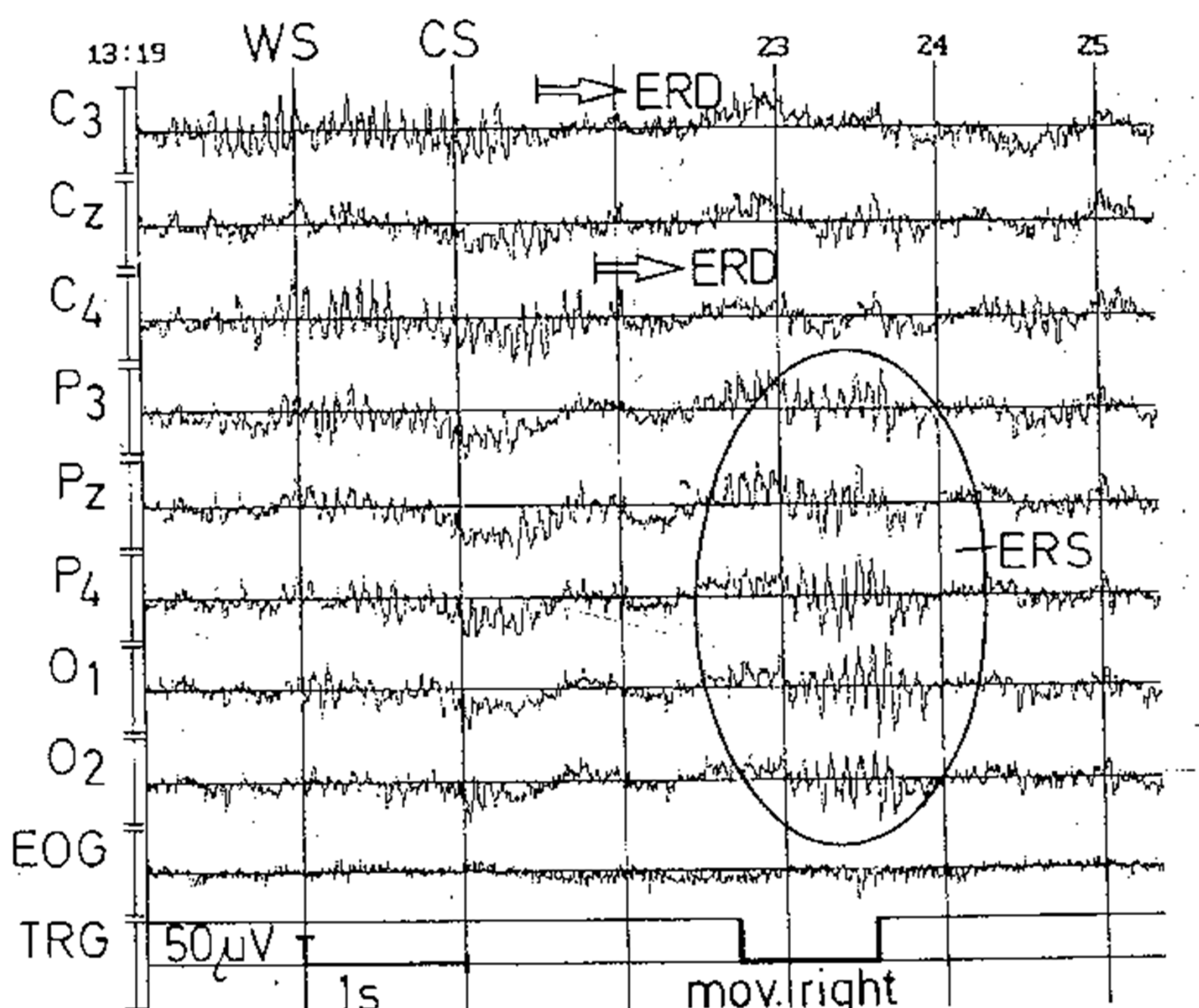
- Pfurtscheller (1992) -- Two types of ERS
 - Secondary (follows ERD)
 - Primary (Figure 3 & Figure 4)



Alpha Power time course over left central region during voluntary movements with right and left thumb



Alpha power time course during reading (upper) and voluntary finger movements (lower). Primary ERS is seen over electrodes overlying cortical areas not involved in the task.



Primary ERS seen over parietal and occipital leads during right finger movement. ERD is seen over central electrodes, with earlier onset over hemisphere contralateral to movement.

If Alpha Desynchs, what Synchs?

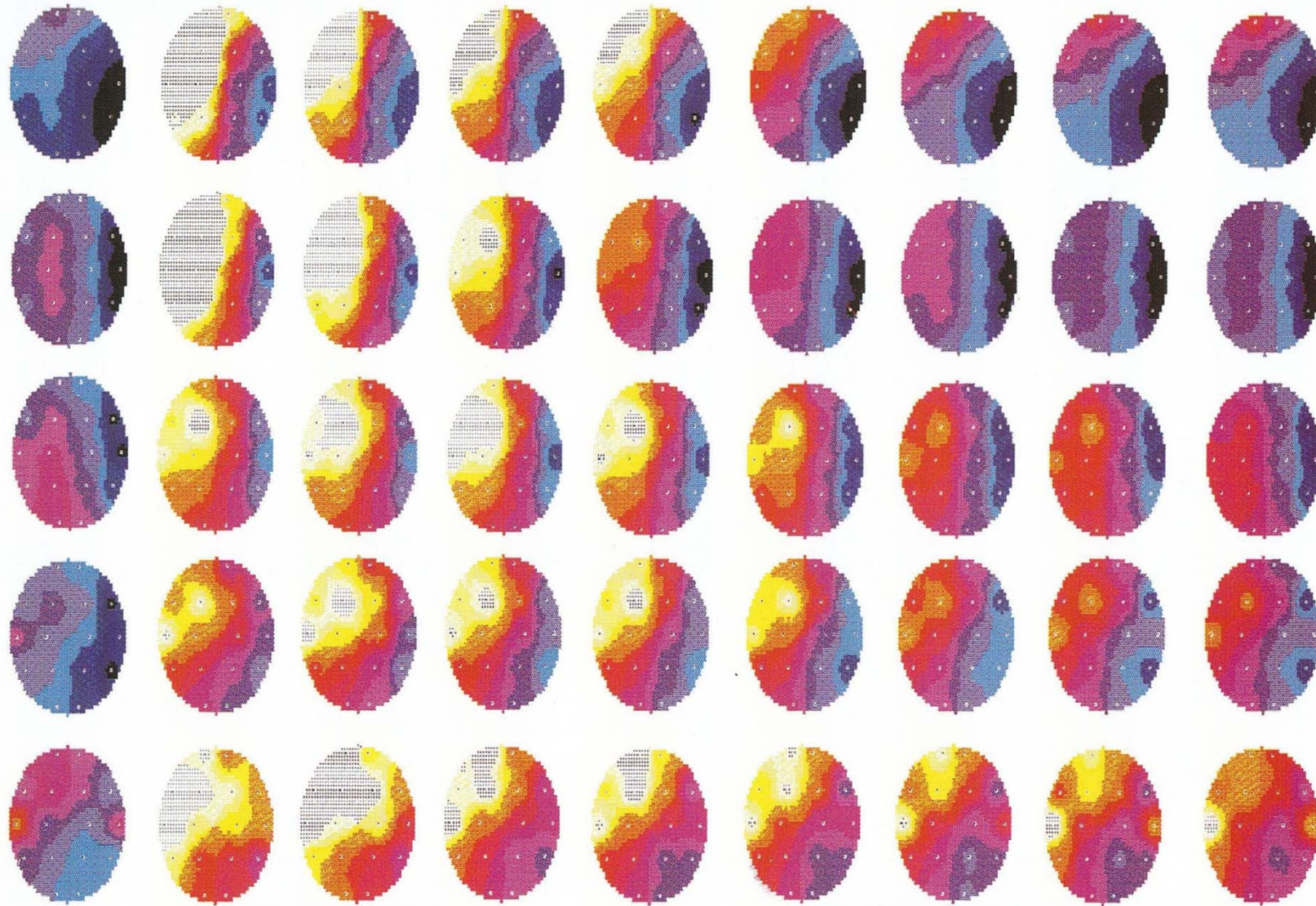
DELTA

THETA

ALPHA

BETA 1

BETA 2



Baseline

EP 1

EP 2

EP 3

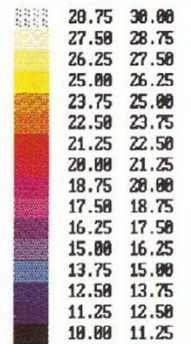
EP 4

EP 5

EP 6

EP 7

EP 8



Less drastic manipulations....

Frontal Midline Theta

(more later in advanced topics)

- Increased midline frontal theta during periods of high cognitive demand
- This is specifically under conditions in which cortical resources must be allocated for select cognitive processes
 - Attention
 - Memory
 - Error Monitoring

Saueng Hoppe Klimesch Gerloff Hummel (2007)

- Complex finger movement sequences
- Varied Task Difficulty, and Memory Load (2x2 design)
- Task-related Theta Power (4-7 Hz) computed for each condition relative to 5 min. resting baseline
- Phase coherence also examined across sites
 - Phase Locking Value (0-1)
 - Then expressed as percent increase over rest

Theta Power

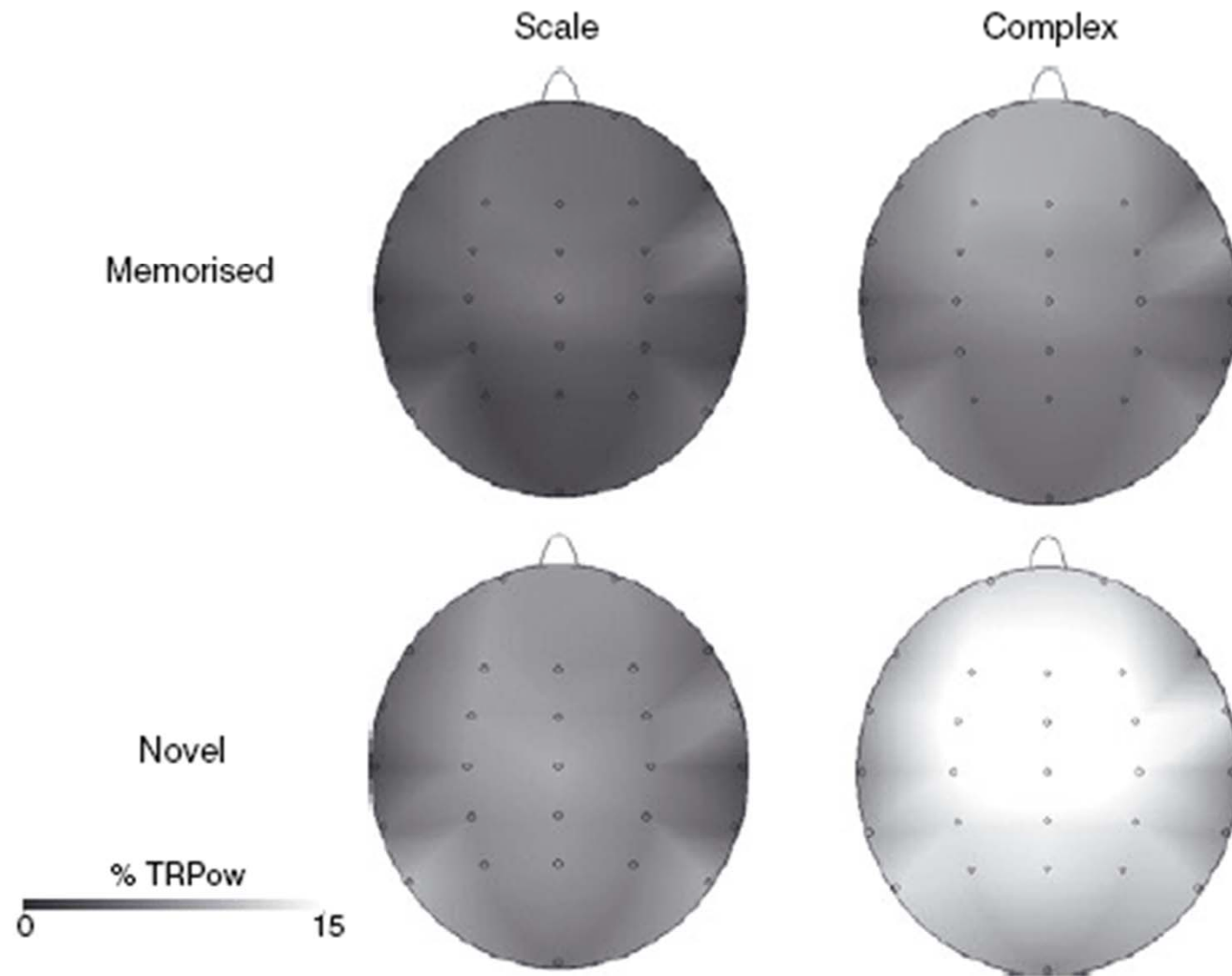
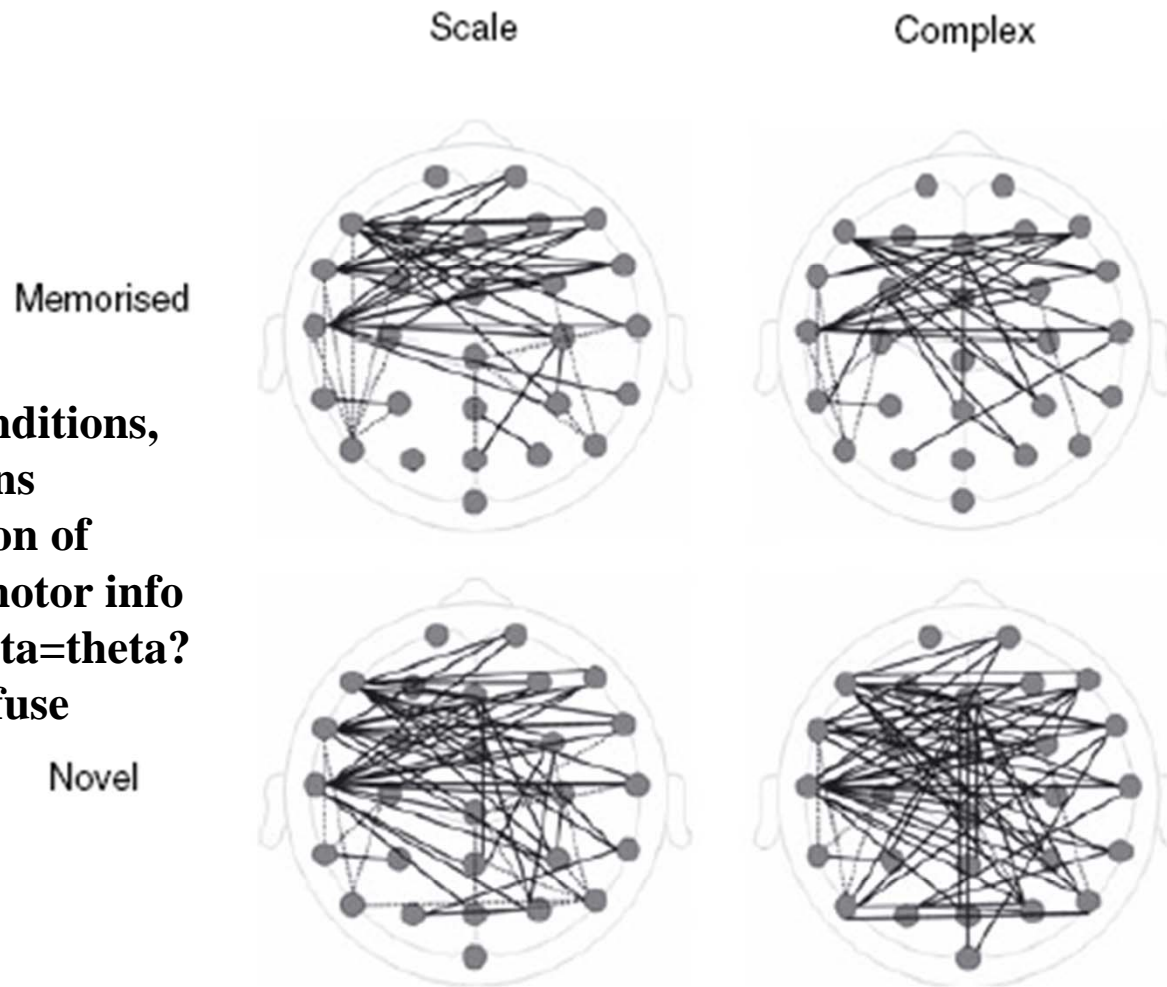


FIG. 1. Task-related theta (4–7 Hz) power increase. White indicates a strong task-related power increase compared with rest. Note that only during execution of novel and complex sequences is strong frontal-midline theta exhibited. This indicates that frontal theta activity reflects both memory load and sequence complexity.

Theta PLV



Memorised

Novel

Scale

Complex

- Higher in Novel conditions, contrary to predictions
- Speculate integration of visual with sensory-motor info
- But, does theta=theta=theta? Fronto-central vs diffuse

FIG. 3. Task-related theta phase coupling. Bold connections indicate a significant ($P < 0.005$) increase of theta phase coupling compared with rest, dotted lines indicate decrease of phase coupling. There are more significant electrode pairs during execution of novel sequences compared with performance of memorized ones. This effect is independent of task complexity. During both memorized and novel, there is no significant difference of the distributed theta network between scale and complex sequences.

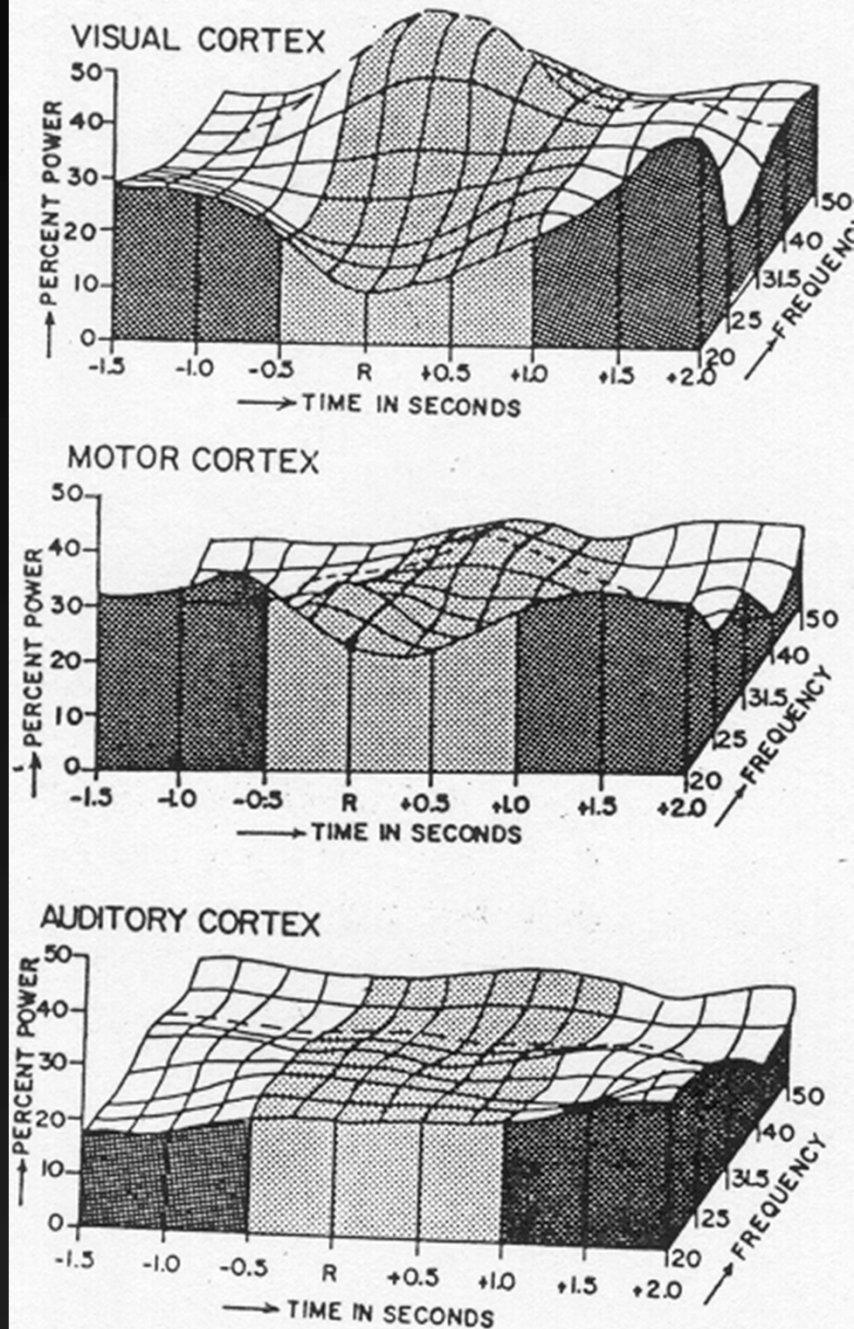
40 Hz Activity

- First reports of important 40 Hz activity
- Sheer & Grandstaff (1969) review
 - pronounced rhythmic electrical bursting
- Daniel Sheer's subsequent work until his death renewed interest in "40 Hz" phenomena

Sheer work with Cats

- Learning paradigm
- Cat must learn
 - press to S_D (7cps light flicker)
 - not S_- (3 cps light flicker)
 - the hypothesis is that the synchronized 40 Hz activity represents the focused activation of specific cortical areas necessary for performance of a task

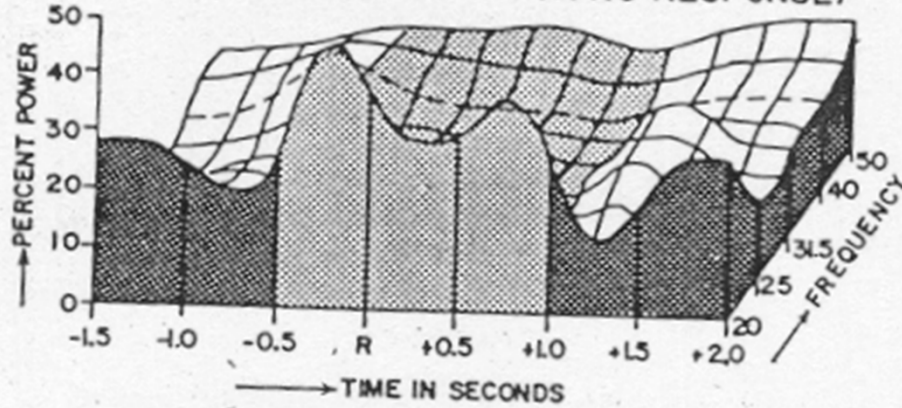
STIMULUS PERIOD 7/SEC FLICKER WITH RESPONSE



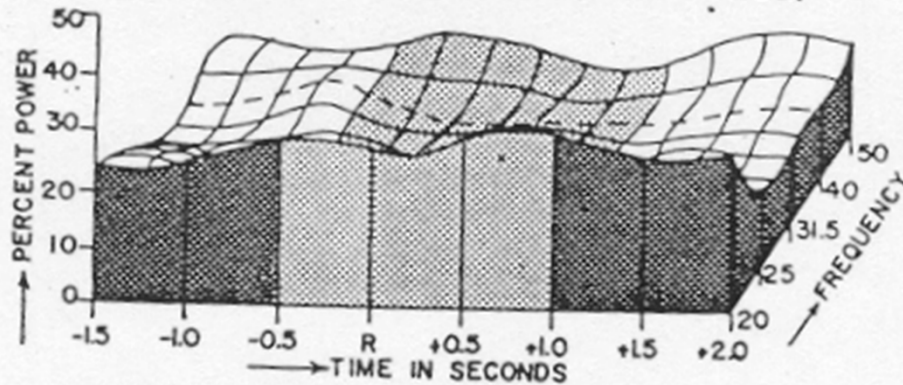
Note specificity of response to S_D , over visual cortex to discriminative stimulus, in 40-Hz range; Some hint of it later in the motor cortex. Note also decreased activity in slower bands during the same time periods.

VISUAL CORTEX

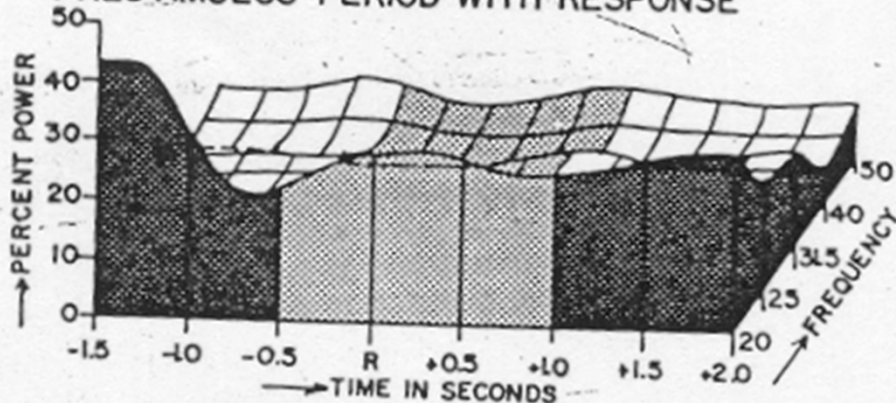
S-PERIOD (3/SEC FLICKER WITH NO RESPONSE)



S-PERIOD (3/SEC FLICKER WITH RESPONSE)



PRESTIMULUS PERIOD WITH RESPONSE



Note very different pattern to S-. No 40-Hz change in visual cortex, and marked increase in lower frequencies at same time period.

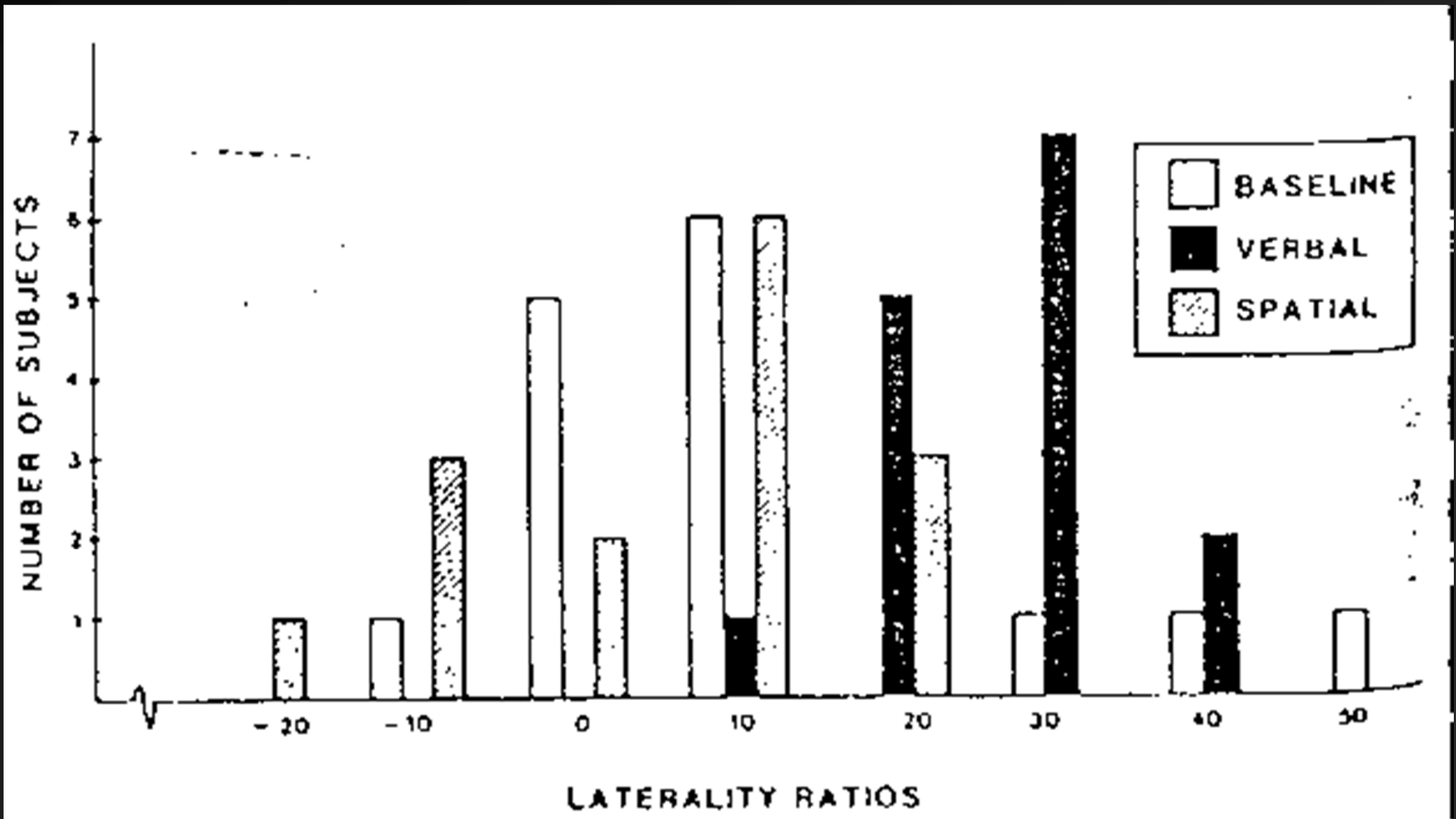
Human Studies

- Hypothesis is that 40 Hz activity correlates with the behavioral state of focused arousal (Sheer, 1976) or cortical activation
 - a "circumscribed state of cortical excitability" (Sheer, 1975)
 - Bird et al (1978)
 - biofeedback paradigm
 - increased 40 Hz activity is associated with high arousal and mental concentration
 - Ford et al., (1980)
 - subjects once trained to voluntarily suppress 40 Hz EEG are unable to maintain that suppression while simultaneously solving problems
 - concluded that problem solving and absence of 40 Hz are incompatible

Lateralized Task Effects

- Loring & Sheer (1984)
 - right-handed students
 - analogies task
 - spatial Task
- Results transformed into laterality ratios:
 - $(L-R)/(L+R)$ 40 Hz
 - higher # => greater LH activity (P3-O1-T5 triangle vs P4-O2-T6 triangle);
- Results
 - greatest variability during baseline
 - smallest variability and greatest LH activation during verbal
 - no laterality effects in the 40Hz EMG bands

Laterality of 40 Hz



Controlling for EMG contributions

- Spydell & Sheer (1982)
 - used similar tasks and found similar results
 - using conservative controls for muscle artifact

TABLE 1
Median changes in rate scores

Problems	Median Rate Score Changes									
	Alpha		Beta II		40 Hz Total		40 Hz EEG		40 Hz EMG	
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
Verbal	-36.7*	-52.4*	-20.1*	-20.2*	1.0*	0.1	1.2*	0.1	8.4*	10.6*
Rotation	-36.7*	-37.6*	-15.3*	-15.3*	0.7	1.0*	0.4	0.9*	13.9*	8.9*

* $p < .05$.

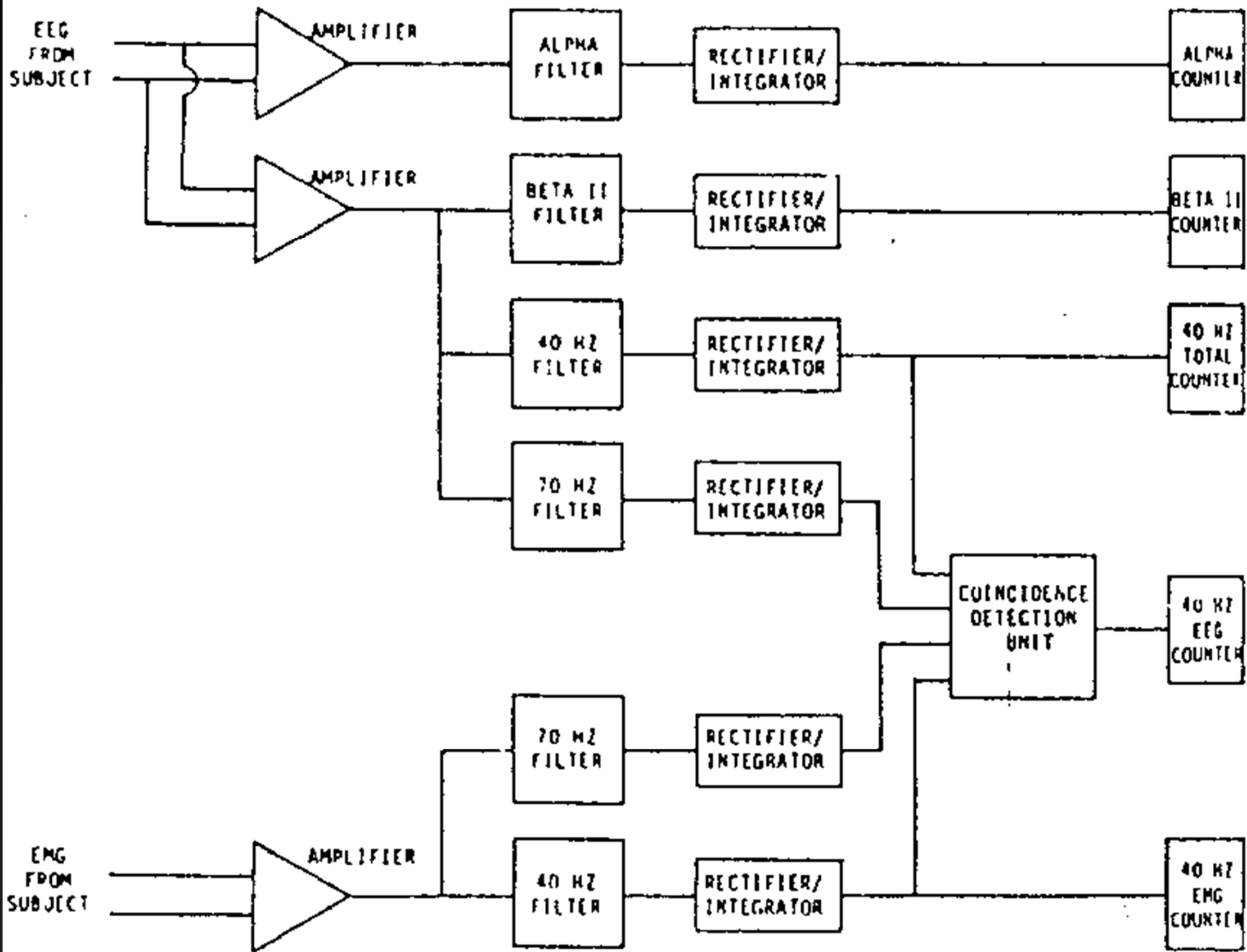
Spydell and Sheer

Vol.

TABLE 3
Spearman rank-order correlations between various 40 Hz activity measures

40 Hz Measures	Correlations							
	Verbal Left		Verbal Right		Rotations Left		Rotations Right	
	40 Total	40 EEG	40 Total	40 EEG	40 Total	40 EEG	40 Total	40 EEG
40 Hz EEG	.74*		.68*		.94*		.78*	
40 Hz EMG	.27	.28	.39	.05	.27	.35	.16	.25

* $p < .05$.

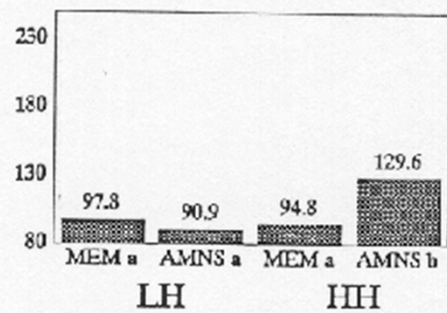


Individual Differences

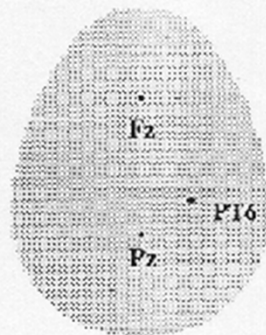
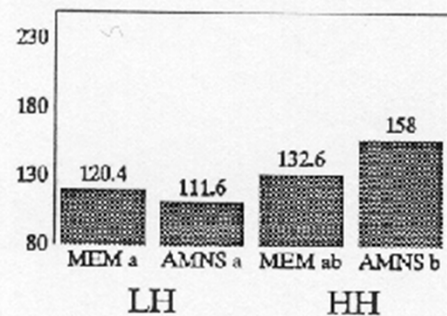
- Spydell & Sheer (1983), Alzheimers
 - controls showed task related changes in EEG with appropriate lateralization
 - Alz did not
- Schnyer & Allen (1995)
 - Most highly hypnotizable subjects showed enhanced 40 hz activity

EYES OPEN

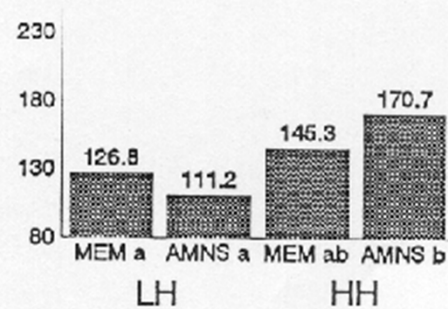
EYES CLOSED



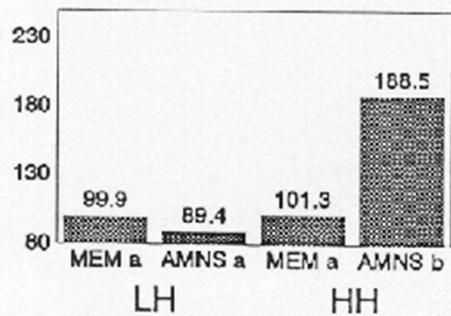
Site Fz, $F[3, 37] = 4.72, p < .01$



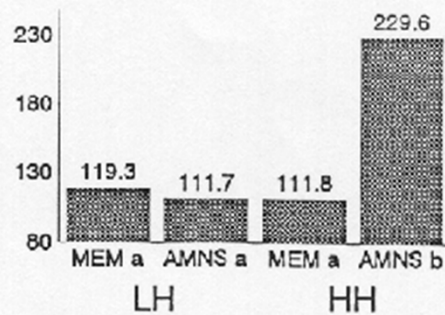
Site Pz, $F[3, 37] = 4.73, p < .01$



Site Pz, $F[3, 37] = 6.46, p < .01$



Site PT6, $F[3, 37] = 10.82, p < .001$

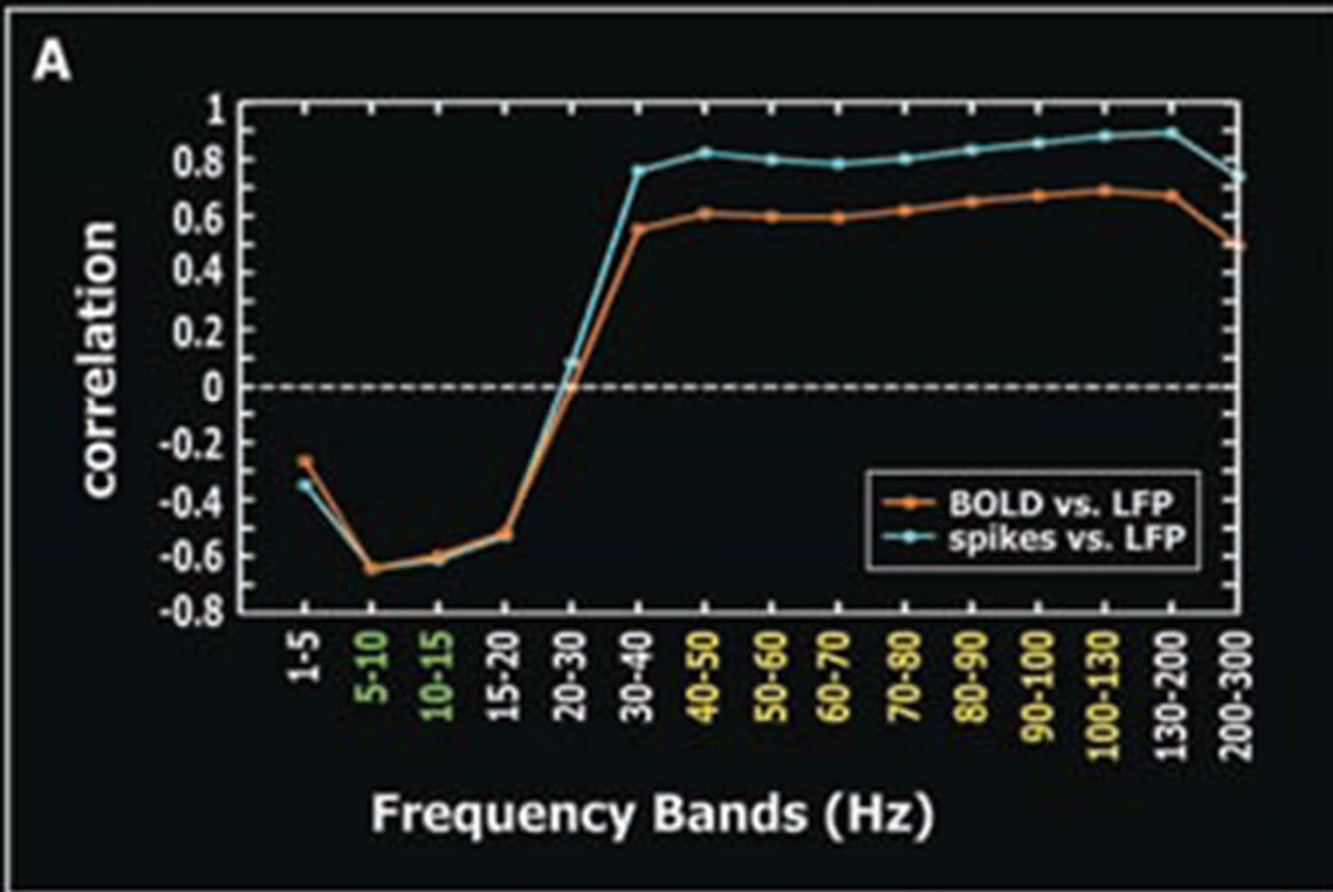


Site PT6, $F[3, 37] = 5.30, p < .001$

So this is exciting, why hasn't this work exploded?

- The EMG concern
 - The concern is likely over-rated (recall **Table 3**)
- Sheer died
- But not all is lost, as there is renewed interest...

Patient #1



Mukamel et al *Science* 2005

recorded single unit activity and local field potentials in auditory cortex of two neurosurgical patients and compared them with the fMRI signals of 11 healthy subjects during presentation of an identical movie segment. The predicted fMRI signals derived from single units and the measured fMRI signals from auditory cortex showed a highly significant correlation.

Singer (1993)

- Revitalized interest in the field

The Binding Problem

- Potentially infinite number of things and ideas that we may attempt to represent within the CNS
 - Cells code for limited sets of features,
 - These must somehow be integrated
 - -- the so-called binding problem
- If there exists a cell for a unique contribution of attributes, then convergent information from many cells could converge on such a cell
 - But there are a finite # of cells and interconnections
- And even the billions and billions of cells we have cannot conceivably handle the diversity of representations

The Functional Perspective

-- as yet merely a theory

- There is no site of integration
 - Integration is achieved through simultaneous activation of an assembly of neurons distributed across a wide variety of cortical areas
 - Neurons in such assemblies must be able to adaptively identify with other neurons within the assembly while remaining distinct from other neurons in other assemblies
 - This association with other neurons is through a temporal code of firing (Synchronicity)
 - This even allows for the possibility that a single neuron could be part of two active assemblies (via a multitasking procedure)

Implications

- Also allows for the possibility that there exists no direct neuronal connection between neurons within an assembly
 - merely the fact that they are simultaneously activated that makes the unified experience of the object possible
- This is most likely when there is an oscillatory regularity
 - If networks are tuned to a single frequency, they are easy to synchronize, but difficult to desynchronize – PROBLEM!
 - Therefore it may be adaptive to have a broader-band oscillator (centered on ~40 hz)
 - Cannot be too slow (e.g., alpha) since this would be inadequate to successfully bind percepts together efficiently
 - Cannot be much faster than gamma since the human nervous system cannot allow synchronization at frequencies much beyond gamma

Implications

- This view is a dynamic view
 - depends on experience
 - can change with experience
- Synchronously activated units more likely to become enhanced and part of an assembly that will subsequently become synchronously activated
- Singer concludes:
 - Points out the problem of looking for synchronous activation on the micro level, suggesting that a return to the EEG literature looking for task-dependent synchronization in the gamma (aka 40 Hz) band!
- Forty-Hz may indeed make a comeback!
 - “Forty” = $40 \pm$ some range
 - Gamma! (Stay tuned during advanced topics)