Synchrony and the attentional state

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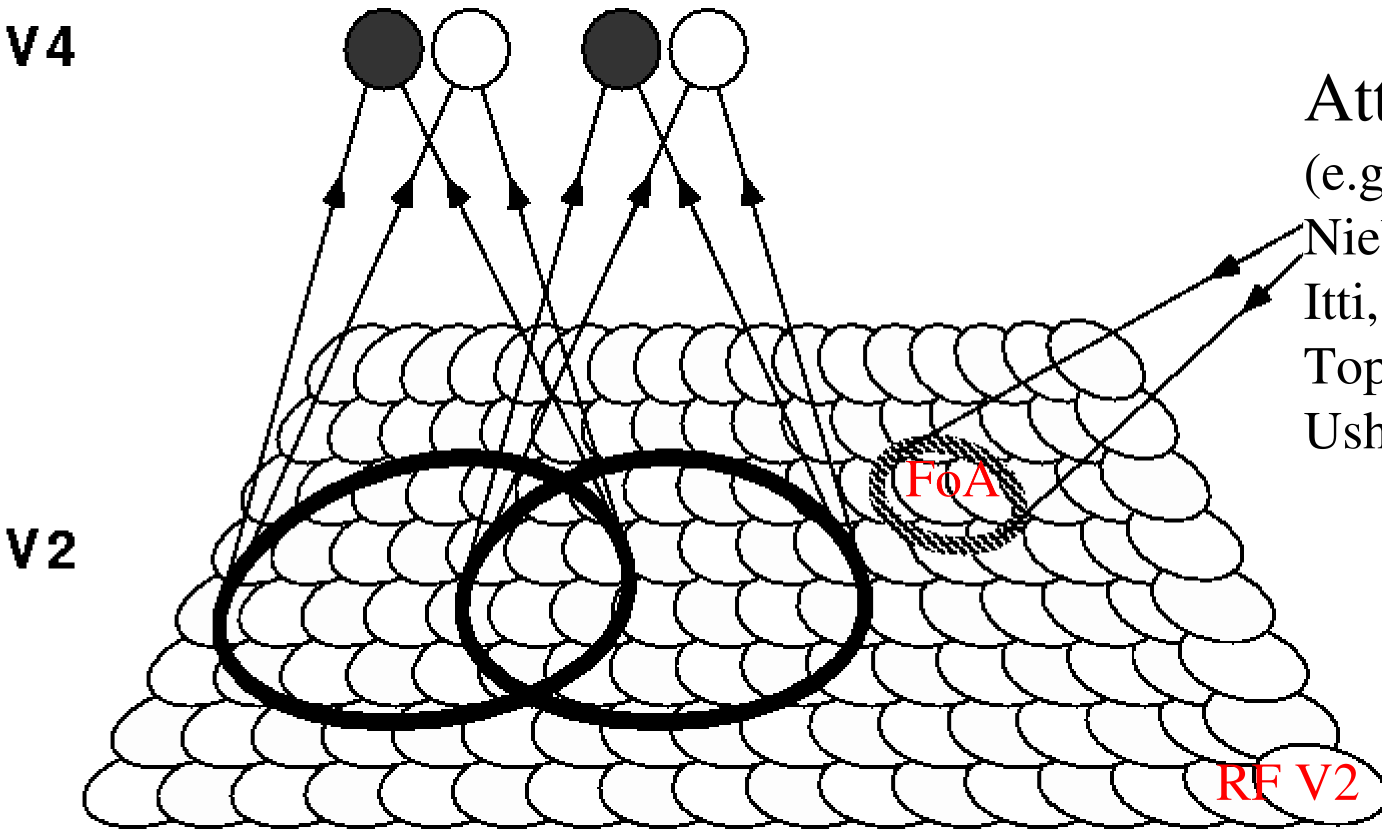
Collaborators

- *monkey* Arup Roy
- *monkey* Peter Steinmetz (now Arizona State U)
- *monkey* Steven Hsiao
- *monkey* Ken Johnson †
- *human* Supratim Ray (now Harvard U)
- *human* Nathan Crone

Modeling the *What* Pathway

- Assume attentional selection has been made in *Where* pathway: How to *tell* the What pathway? ("What is the representation of attention?")
- Physical properties and attentional state are 'quasi-orthogonal' -- difficult to represent *both* by firing rate
- Hypothesis: Attentional state is represented by synchrony structure of spike trains (quasi-orthogonal to rate)
- *"Temporal Tagging"*
- A hybrid (temporal code --> rate code) representation

Temporal Tagging

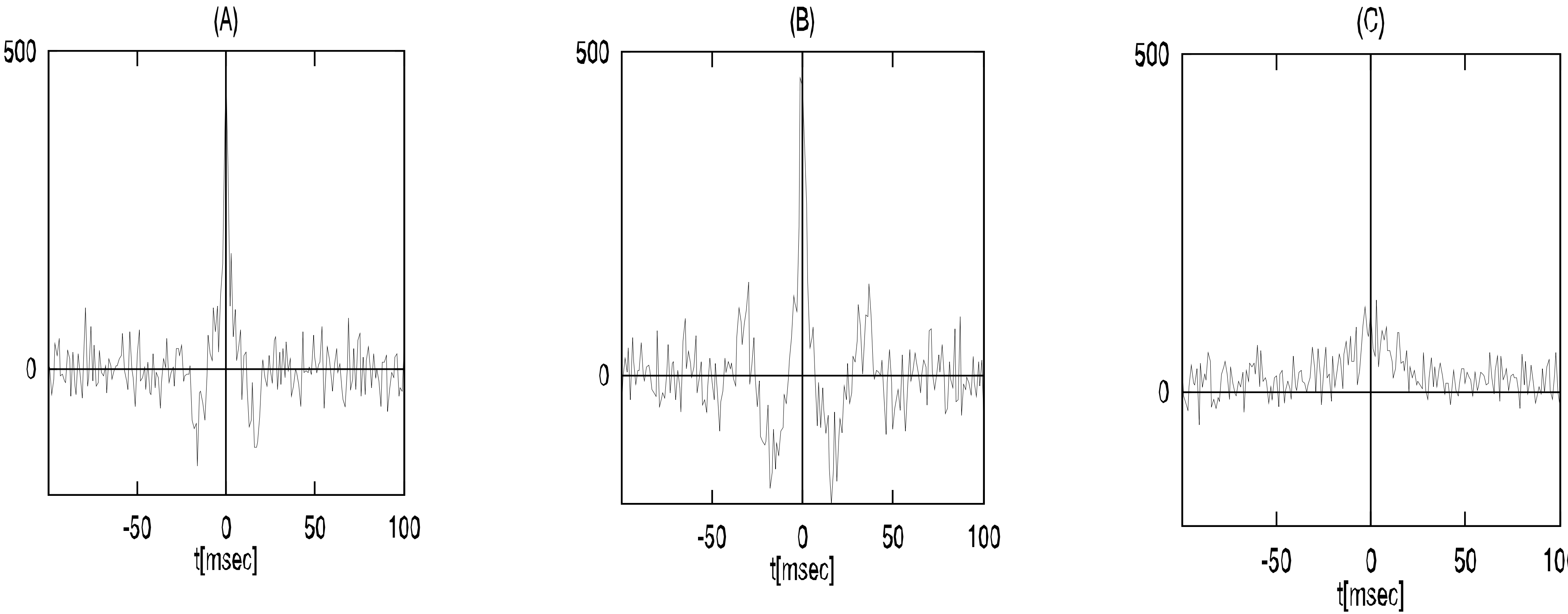


Attentional Control
(e.g by bottom-up Saliency Map:
Niebur & Koch, 1996;
Itti, Koch, Niebur 1998;
Top-down control:
Usher & Niebur 1995)

V2: Modulation of temporal structure
V4: Coincidence detection/Integration

Predictions

- Peak in crosscorrelation between attended stimuli
- No peaks between unattended stimuli
- Rate dependence at higher levels



V2 Attended | V4 Attended | V4 Unattended

Niebur & Koch, 1994

Experimental Test: Somatosensory attention in awake behaving monkey

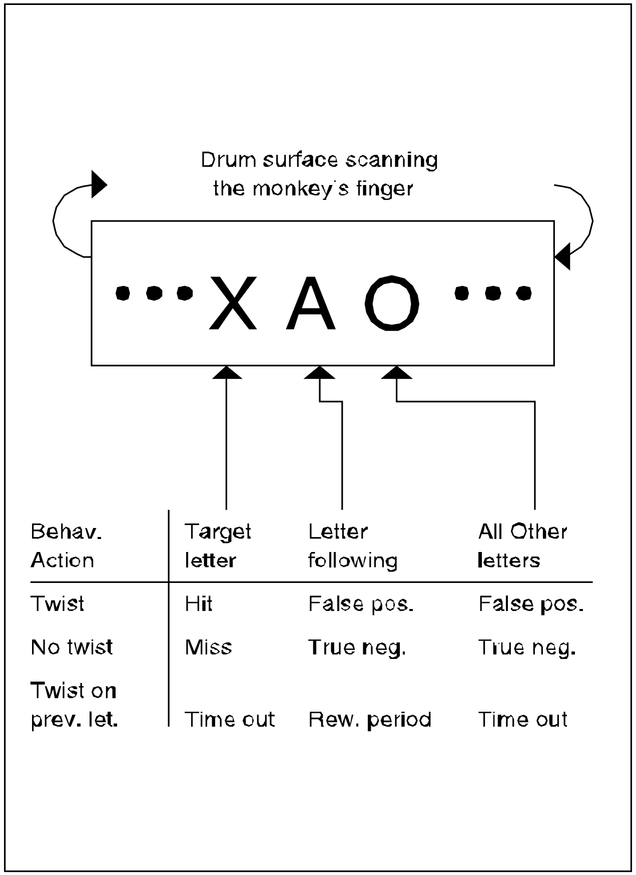
Experimental Paradigm:

•Macaque receives simultaneous visual and tactile stimulation
•Attention switched between visual and tactile task
•Performance approx. 90% correct
•Tactile input identical during both tasks
•Record in SII cortex
•Analyze temporal structure and correlation with attentional state

Task Monkeys 1&2

- Complex patterns (letters) scanned across finger pad
- Twist lever when target pattern appears
- Blocked with visual task (dimming detection)

TACTILE TASK



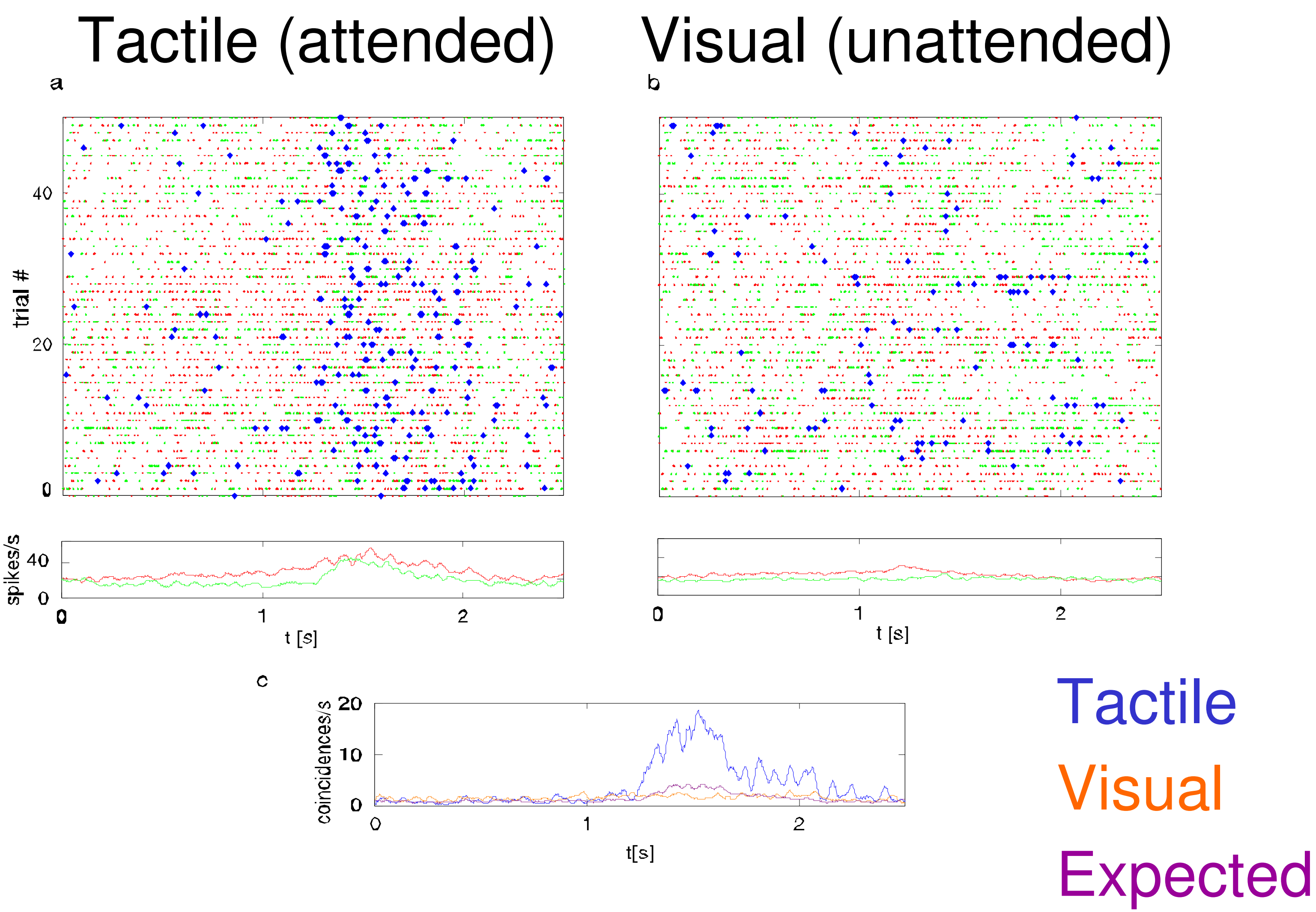
Task Monkey 3

- Tactile task: Delayed match to sample of orientation
- Visual task: Detect dimming (as for M1 & M2)

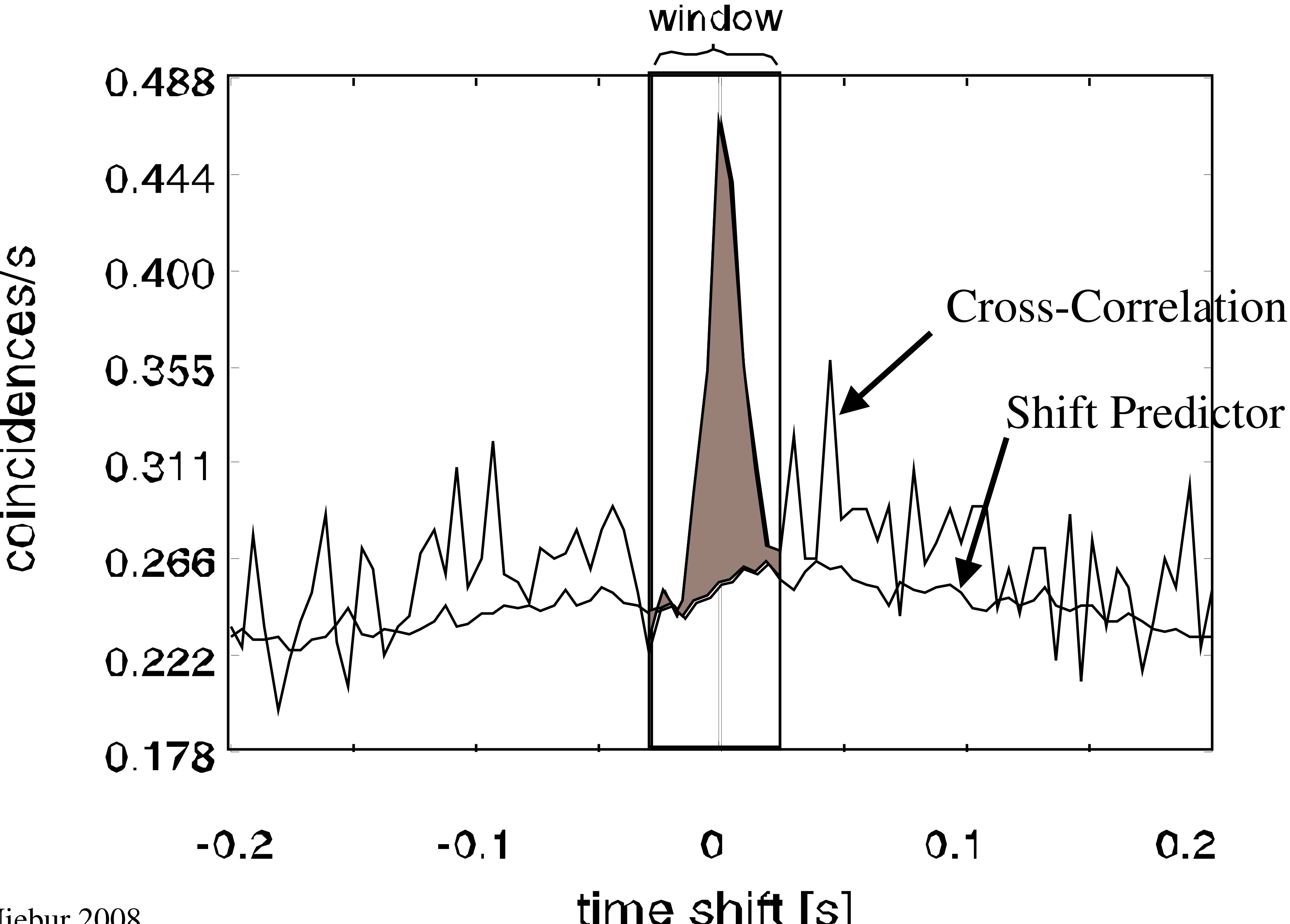
Data Set

- Up to 7 electrodes
- 436 SII cells in 4 hemispheres of 3 monkeys.
- 648 cell pairs analyzed.
- Cells in pair had overlapping fields on the hands.
- Cells in pair recorded on separate electrodes, average distance 1 mm, minimum 400 μm.

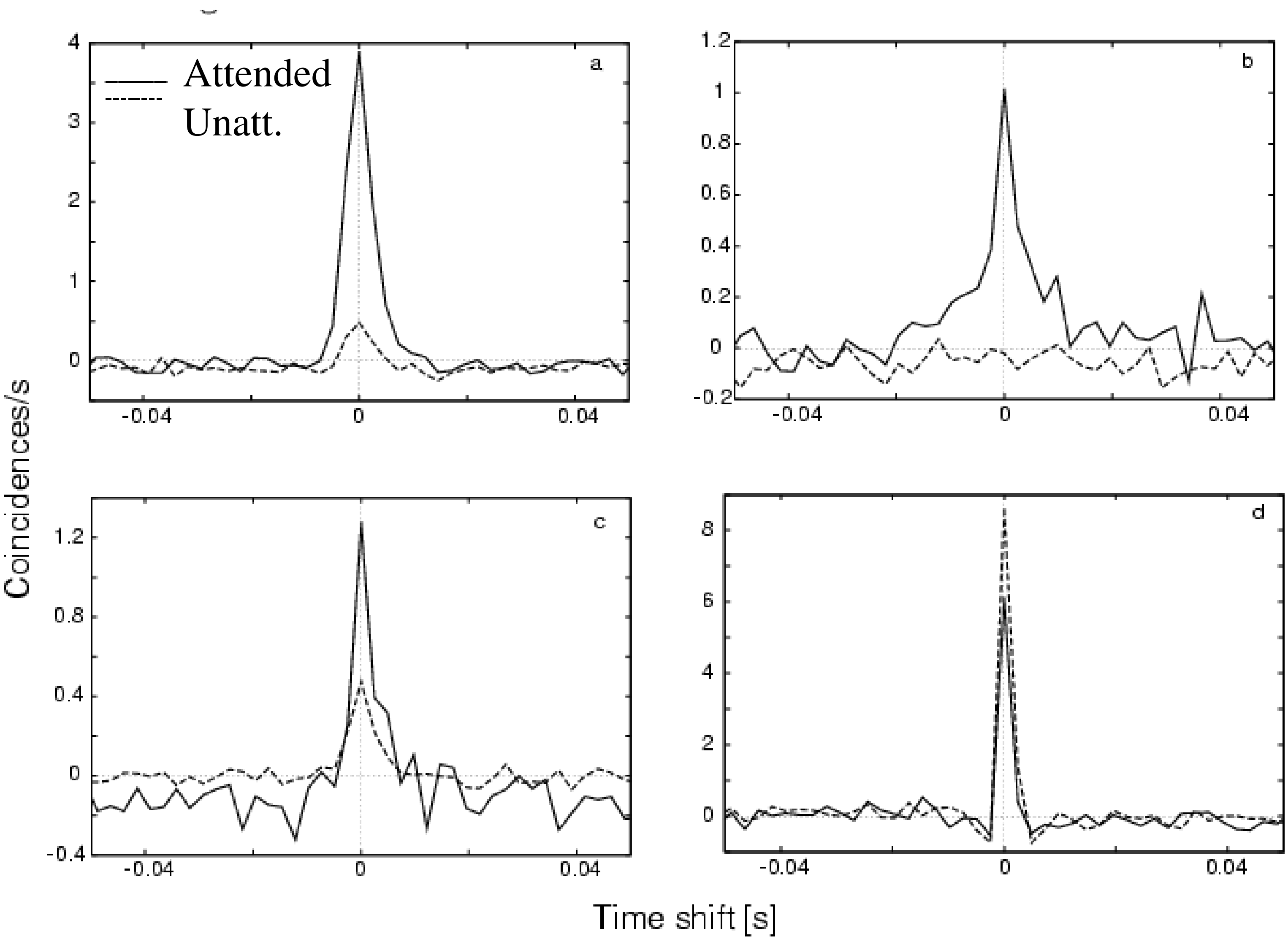
Responses of a neural pair



Quantify deviation of correlation function from shiftpredictor

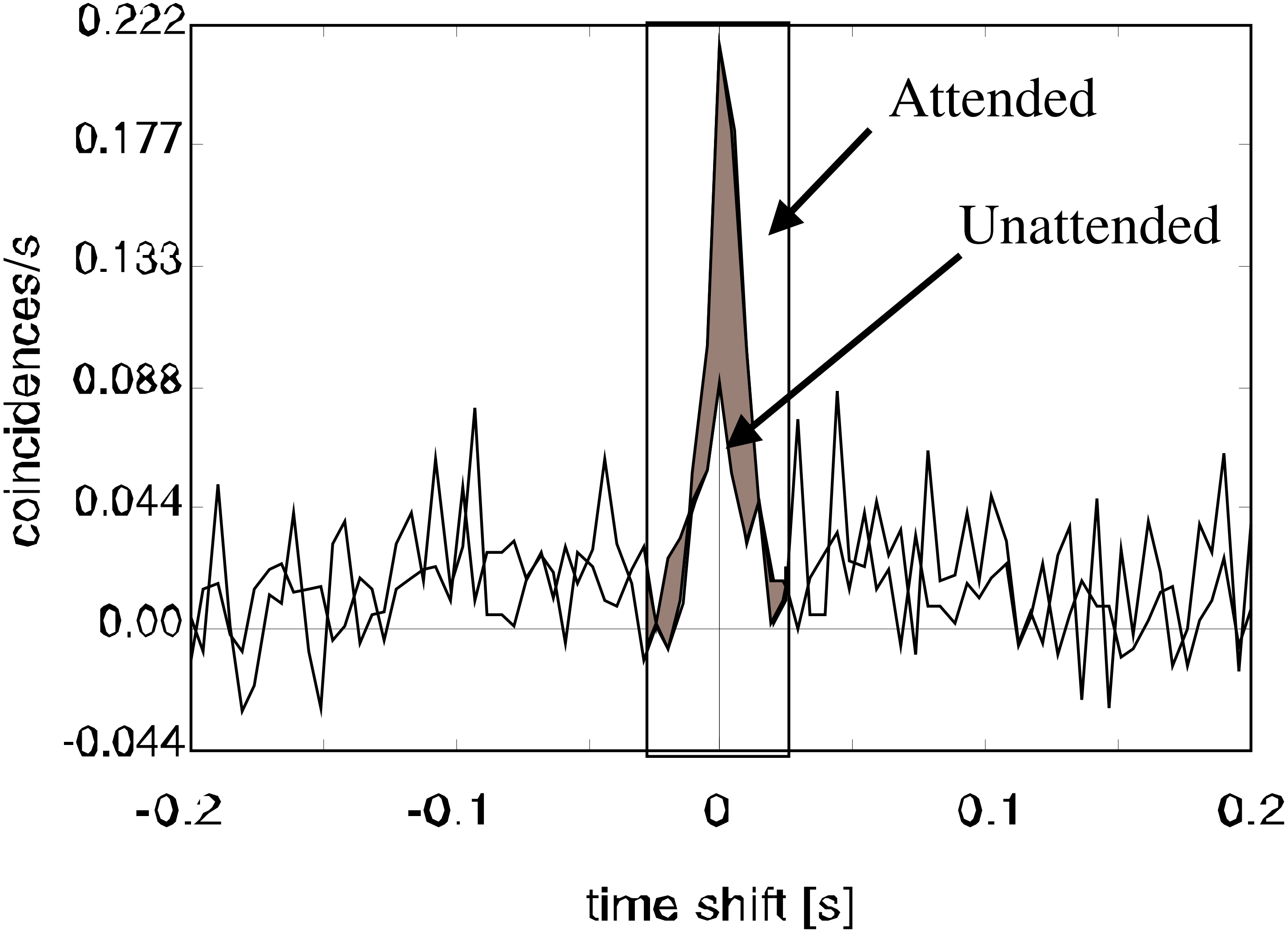


Synchrony changes with attentional state



(remember the predictions...)

Quantification of difference between shift-predictor corrected corr. Functions

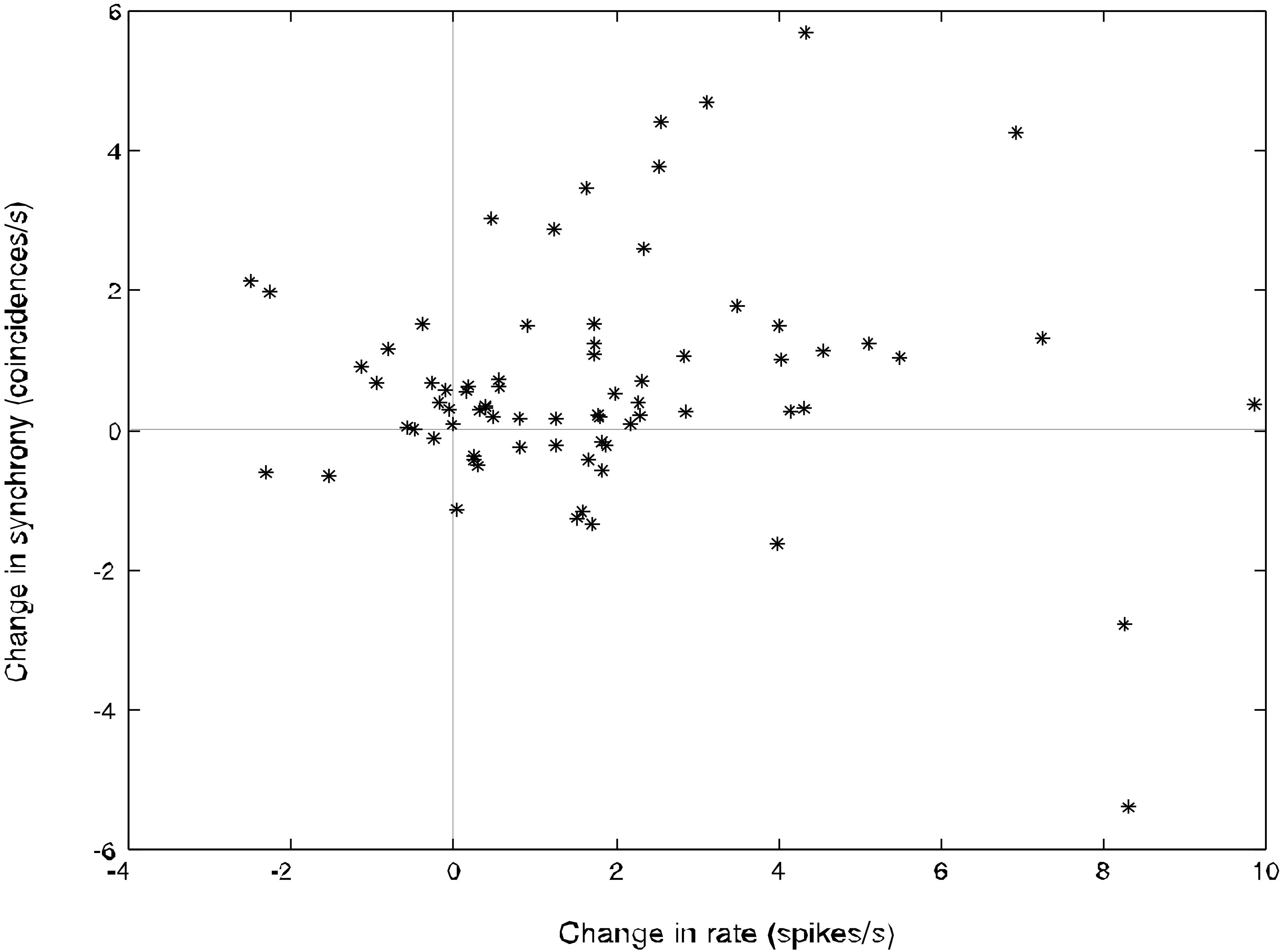


Significance testing by bootstrap

Pairs with synchrony

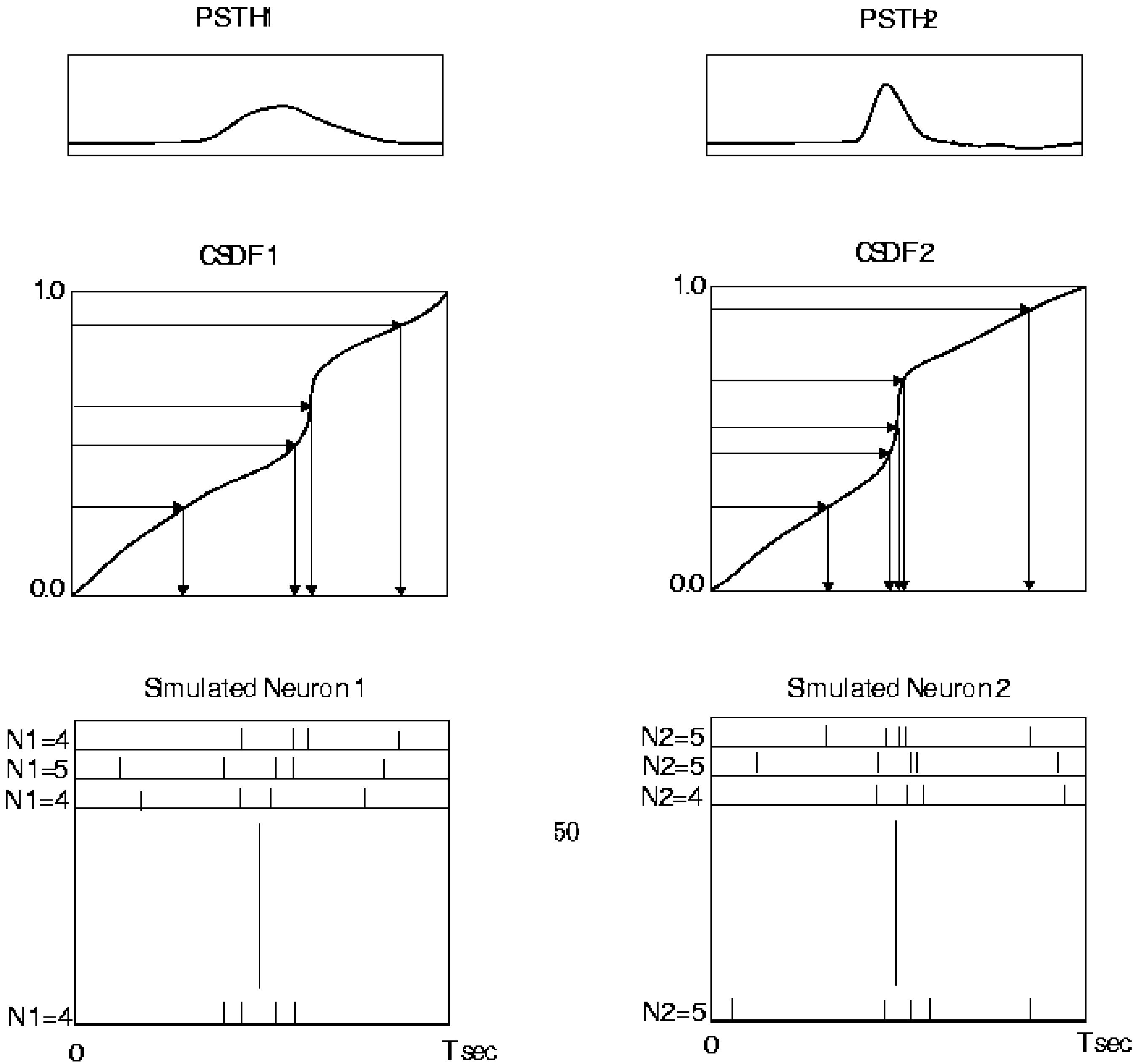
Monkey	Synchronous pairs	Change with attention	Increase with attention
M: constant target letter	50/95 (53%)	8/50 (16%)	7/8 (87%)
M2: varying target letter	113/145 (78%)	41/116 (35%)	35/41/ (85%)
M3: orientation same-different	264/408 (65%)	24/264 (9%)	17/24/(68%)

Synchrony *vs.* firing rate

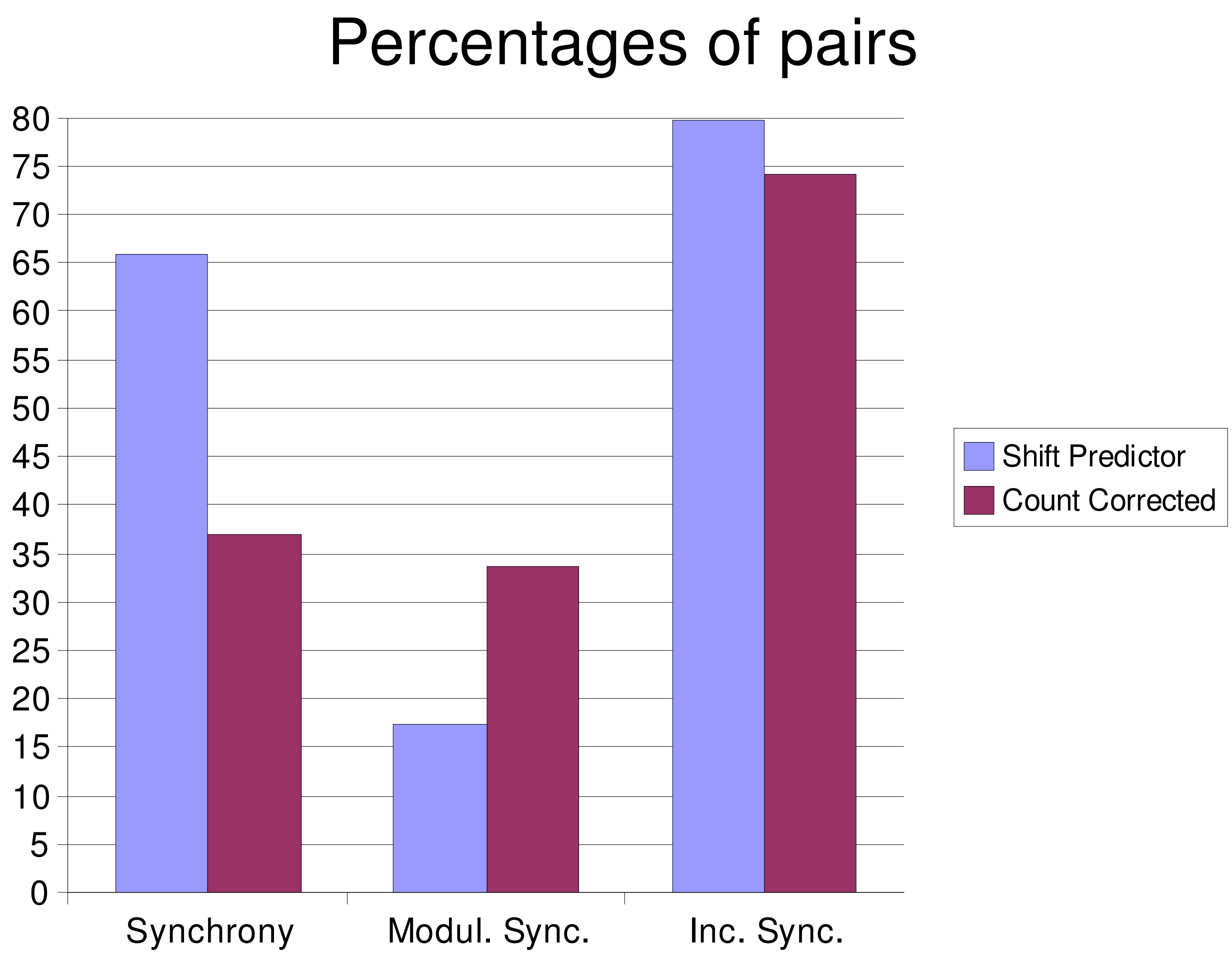


Correction for spike counts

Oram, Wiener, Lestienne, Richmond, *J. Neurophysiol.* 1999. Also Brody, *ibid*. 1998.



Shiftpredictor Correction *vs*. Count Correction



- Count correction reduces total number of sync. pairs
- Essentially no change in *number* of sync. pairs modulated by attention
- Therefore: relative proportion of modulated pairs increases (to 34%)
- Fraction of pairs with increased synchrony nearly unchanged

Control for Movement Effects

- Observation: increased firing at time of response (mainly M2)
- Remedy: remove 100ms after response

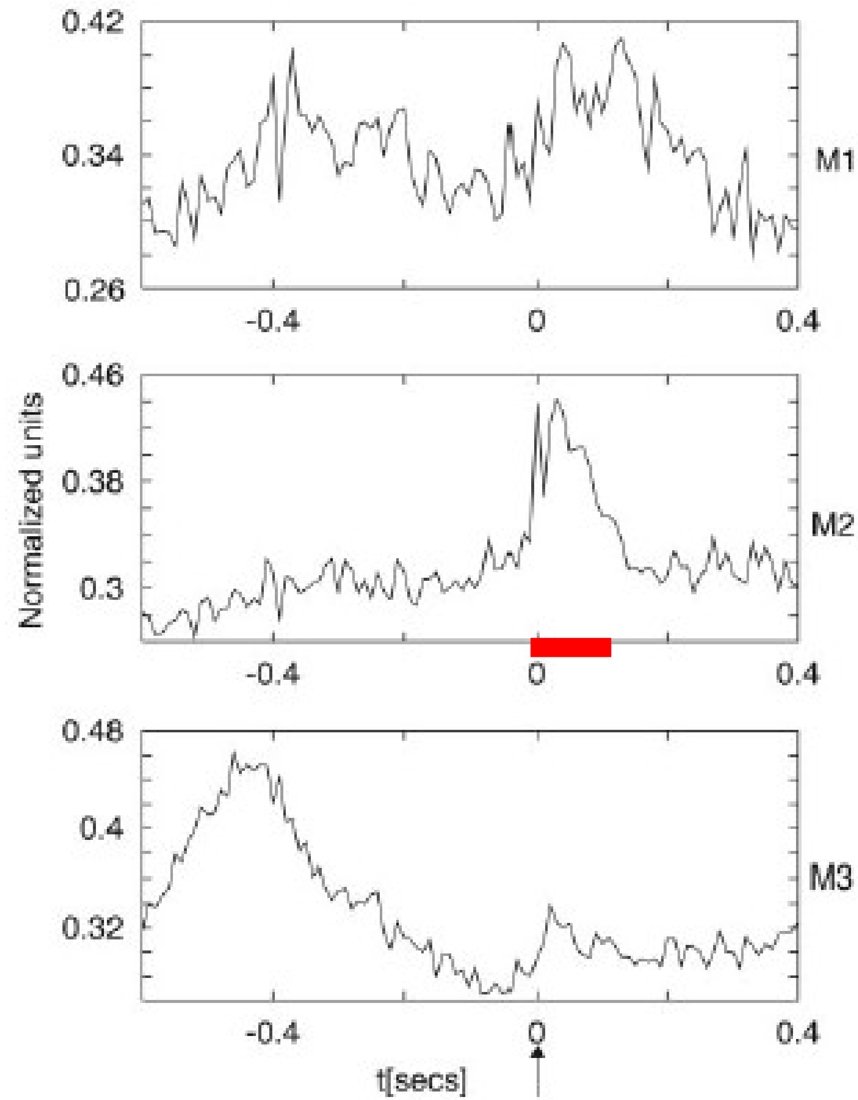


FIG. 3. Averaged peristimulus time histograms (PSTHs, over all neurons) shown for each monkey, of spike times relative to the throwing of the switch on each trial (*time point 0*, shown by black arrow). Spike rates have been normalized to correct for neurons with widely varying rates. Notice the abrupt change in rate in monkey M2 locked to the throwing of the switch.

Pairs with synchrony

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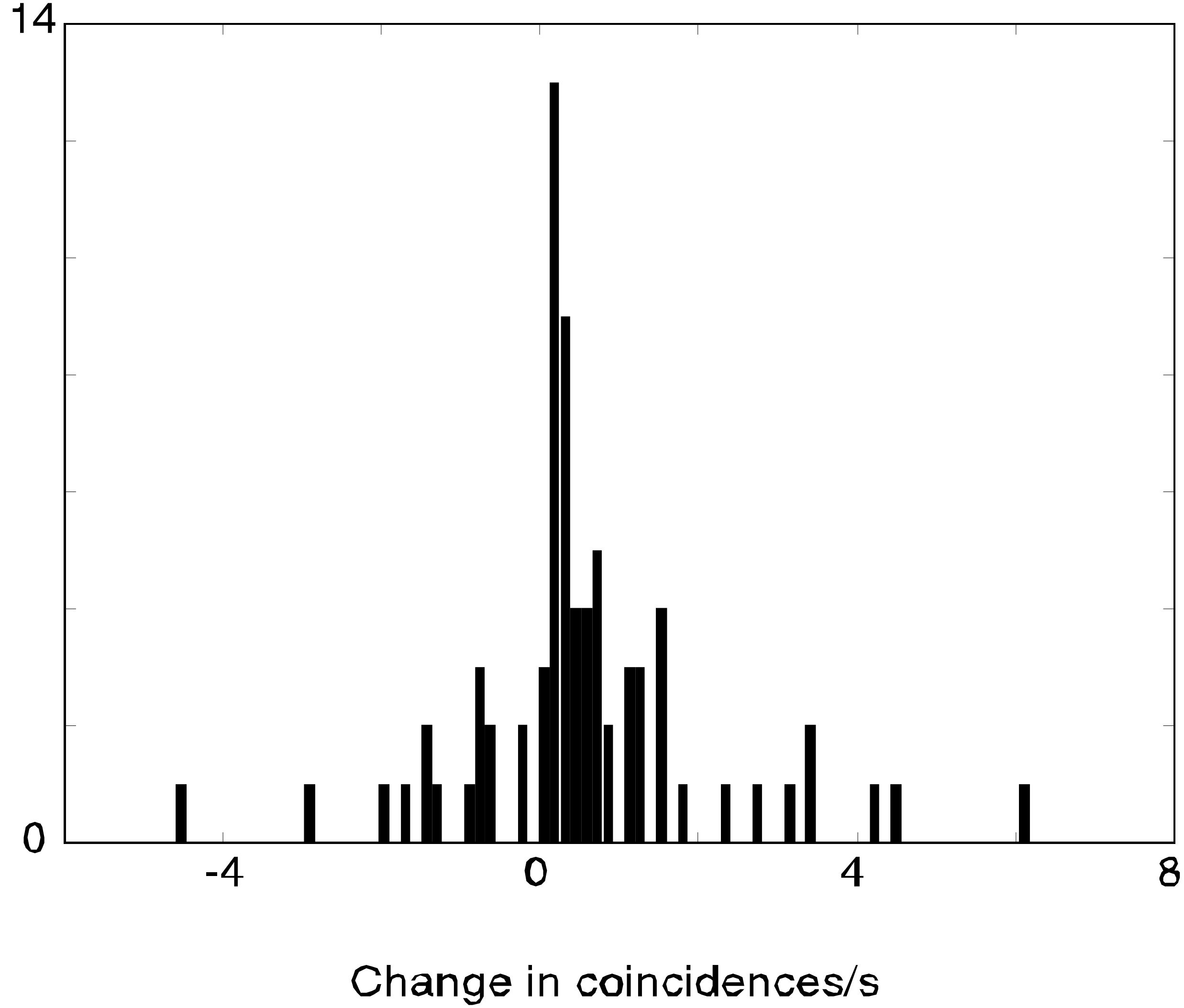
Pairs with synchrony

Monkey	Synchronous pairs	Change with attention	Increase with attention
M: constant target letter	50/95 (53%)	8/50 (16%)	7/8 (87%)
M2: varying target letter Deletion around response	113/145 (78%) 40/145 (28%)	41/116 (35%) 29/40 (73%)	35/41/ (85%) 23/29 (79%)
M3: orientation same-different	264/408 (65%)	24/264 (9%)	17/24/(68%)

Pairs with synchrony

Monkey	Synchronous pairs	Change with attention	Increase with attention
M: constant target letter	50/95 (53%)	8/50 (16%)	7/8 (87%)
M2: varying target letter Deletion around response True Negatives	113/145 (78%) 40/145 (28%) 49/145 (31%)	41/116 (35%) 29/40 (73%) 27/45 (60%)	35/41/ (85%) 23/29 (79%) 16/27 (60%)
M3: orientation same-different	264/408 (65%)	24/264 (9%)	17/24/(68%)

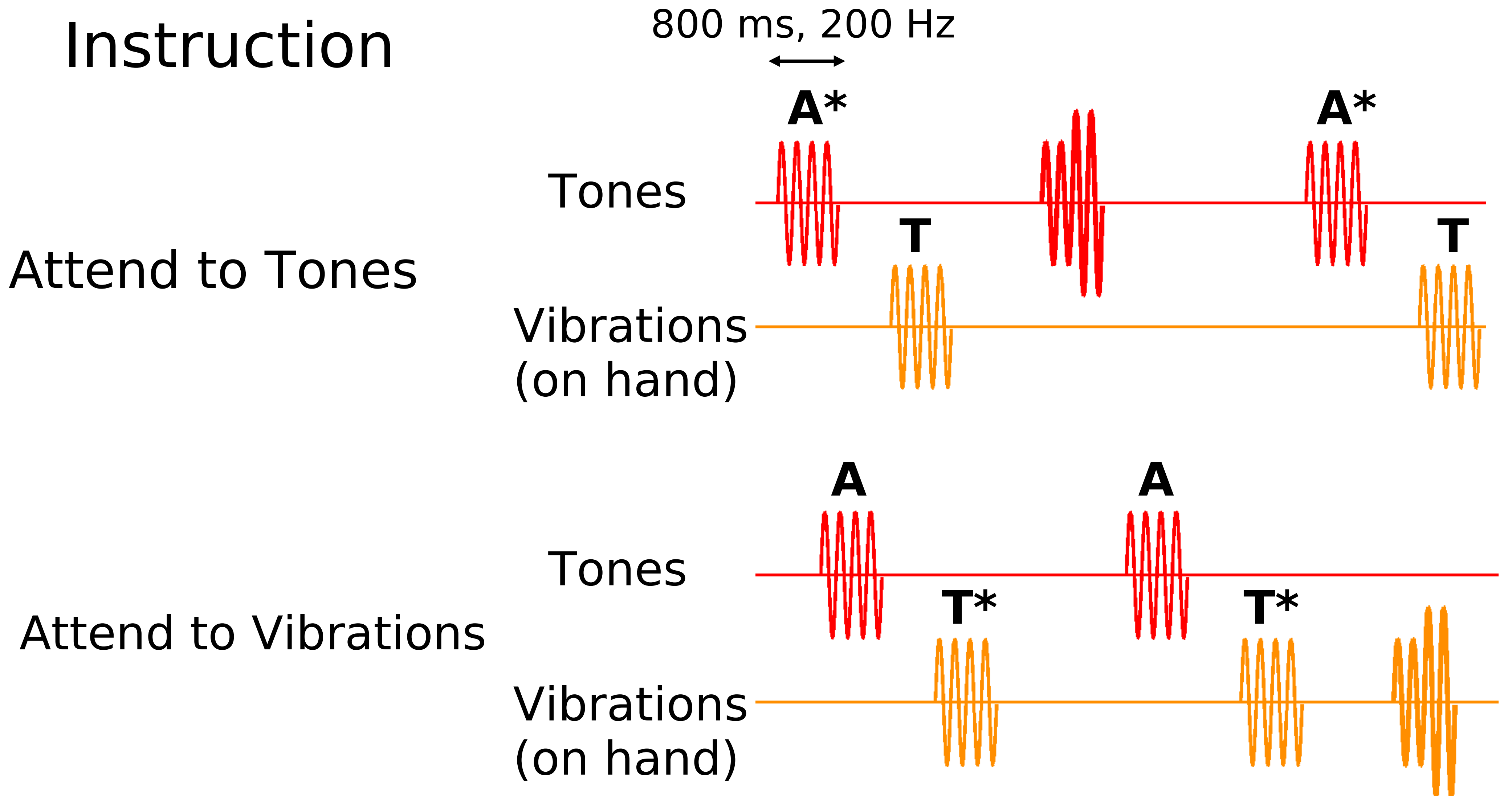
Overall Changes in Synchrony



Summary of monkey data

- Synchrony present in 66% of neuron pairs in SII (37% with count correction)
- Synchrony changes with attentional state in 17% of those pairs (34% with count correction)
- Synchrony increases with attention in most pairs (80% with shift predictor, 74% with count correction)
- Evidence for mixed rate/temporal code, in agreement with model predictions

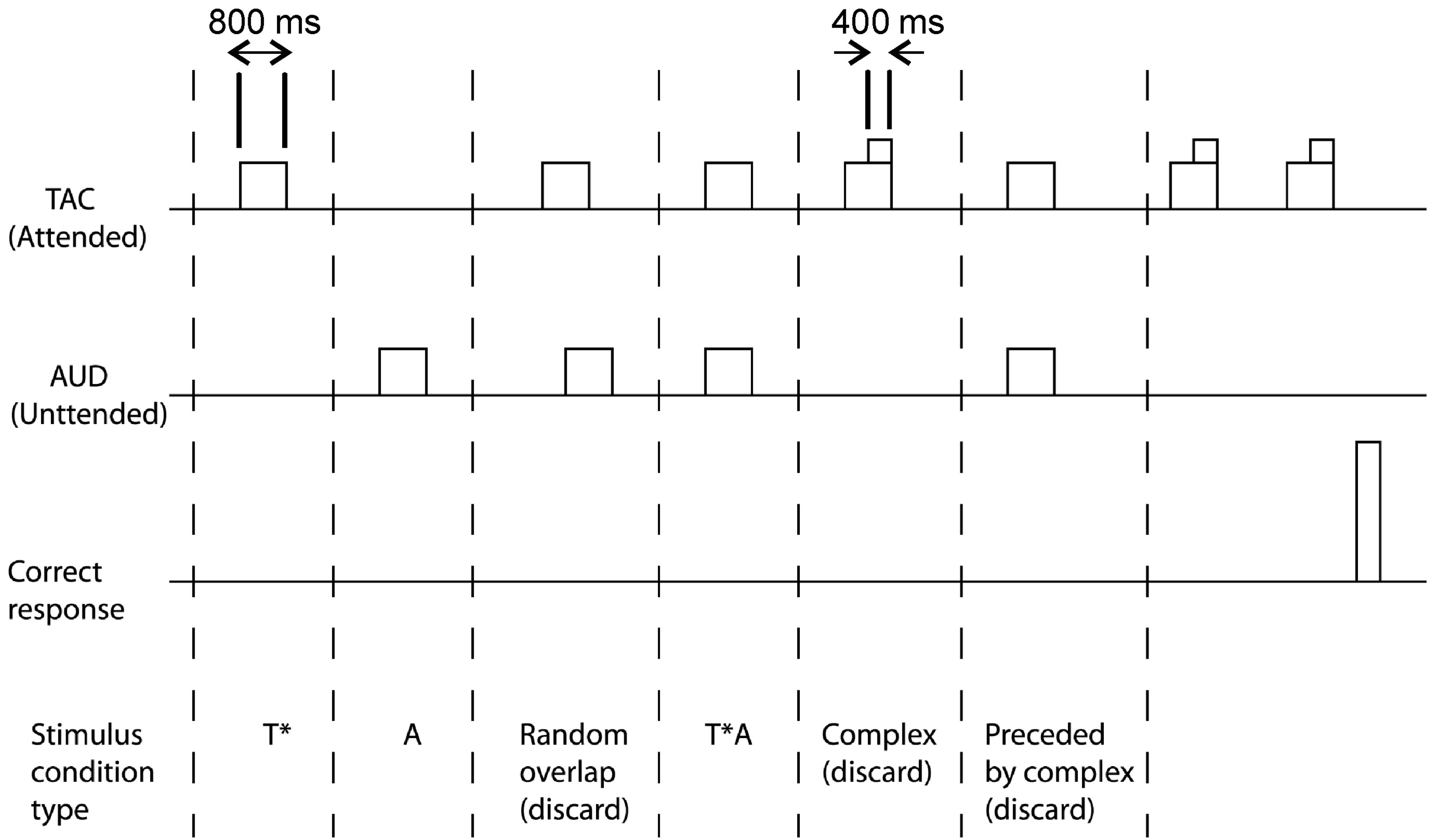
The Other Primate



Basic experimental parameters

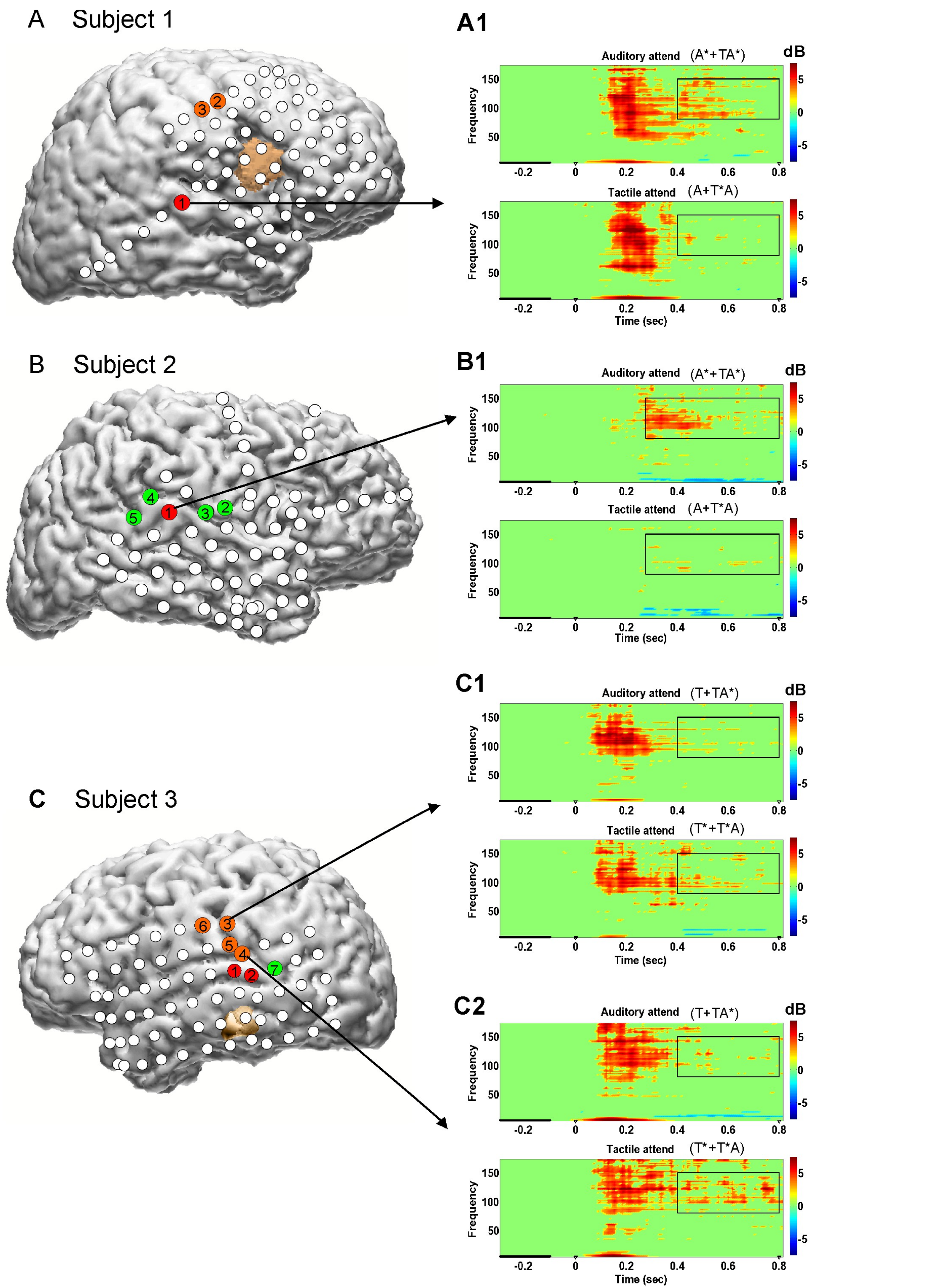
- Three patients with intractable epilepsy
- Record electrocorticogram;
  grids of (~80) subdural electrodes
- Switch attention between tactile and auditory stimuli
- Matching Pursuit analysis for non-stationary responses

Experimental Protocol

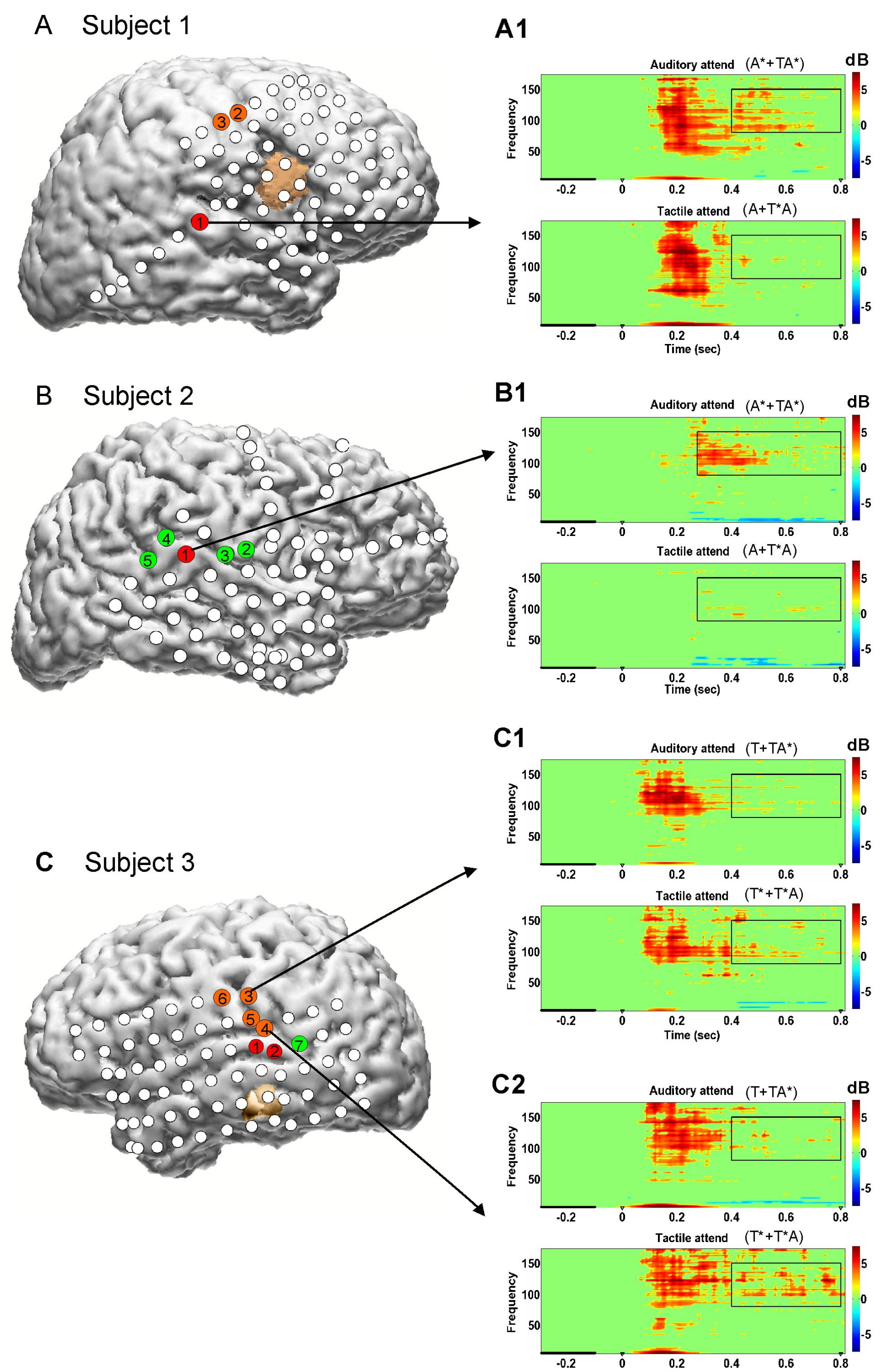


(attention to AUD analogous)

Examples from 3 subjects



Examples from 3 subjects

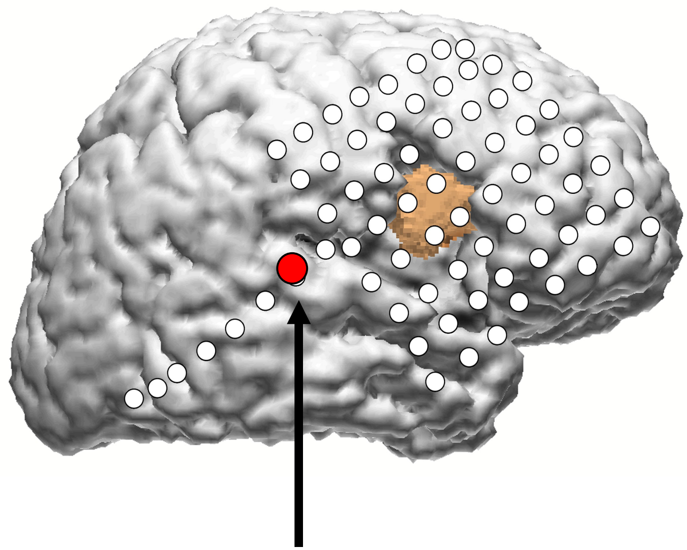


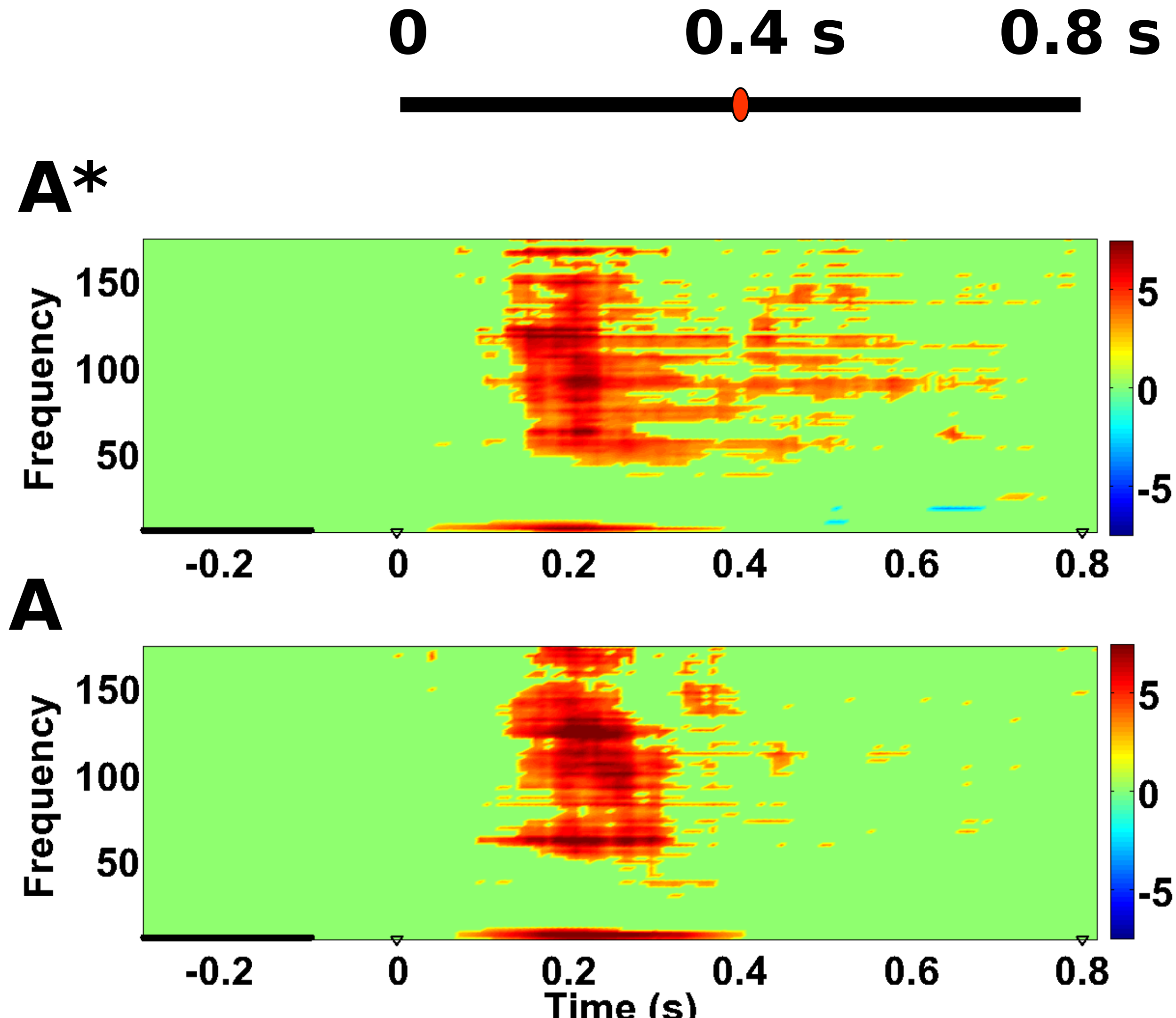
Findings:

--stimulus-related response independent of attentional state

--attentional response at time of expected relevant stimulus (400ms)

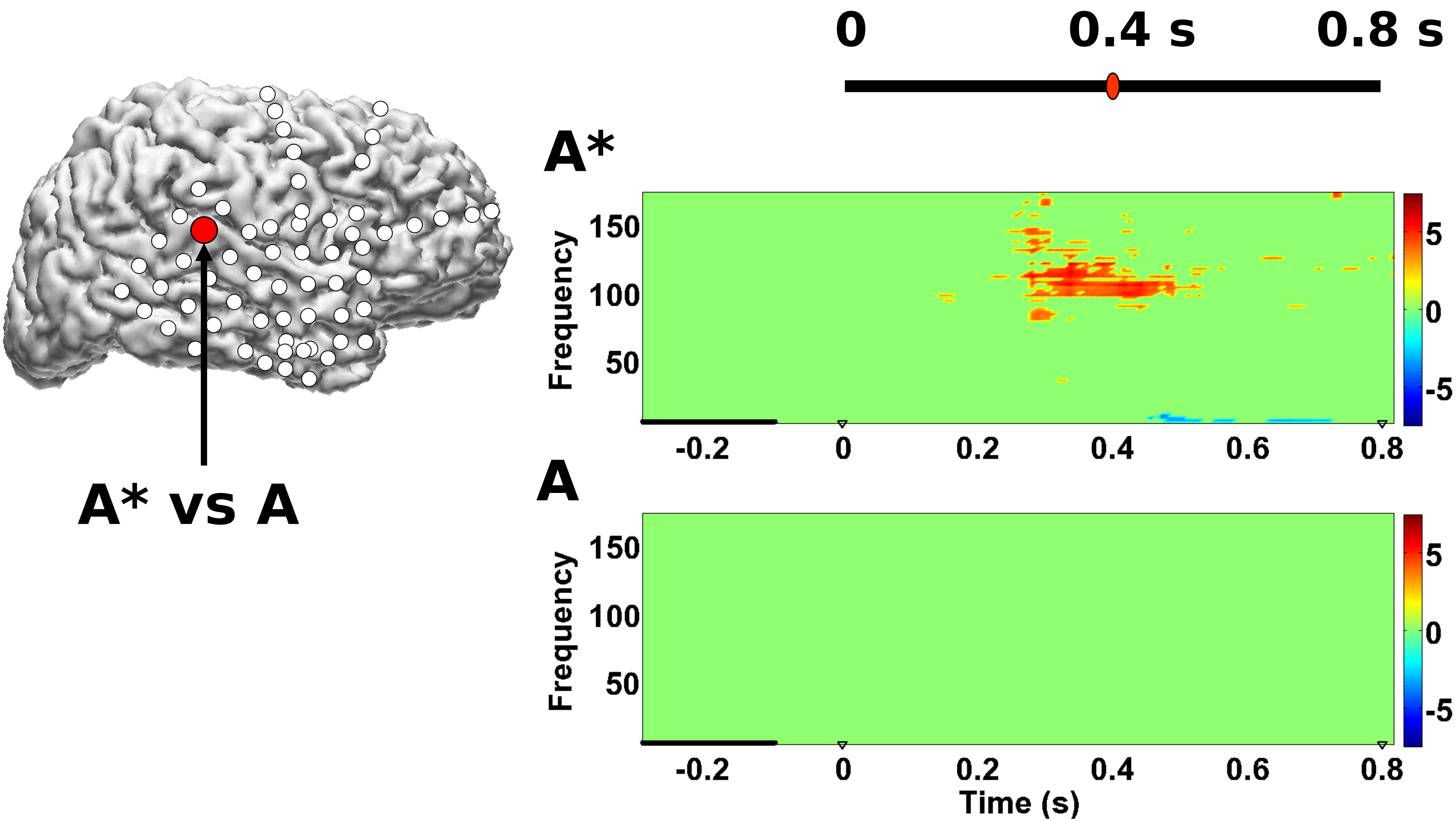
Results: Auditory cortex



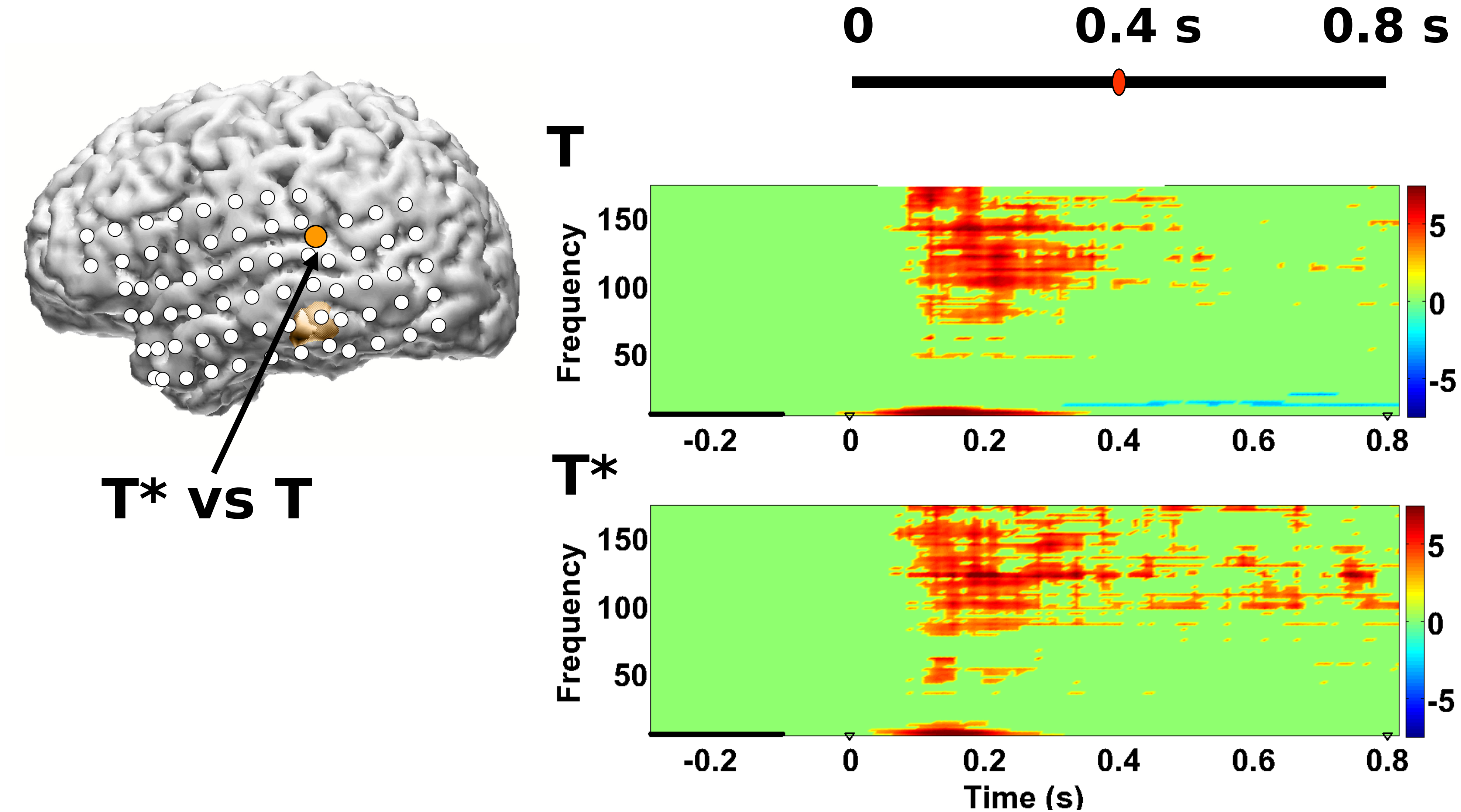


Ray et al, 2008

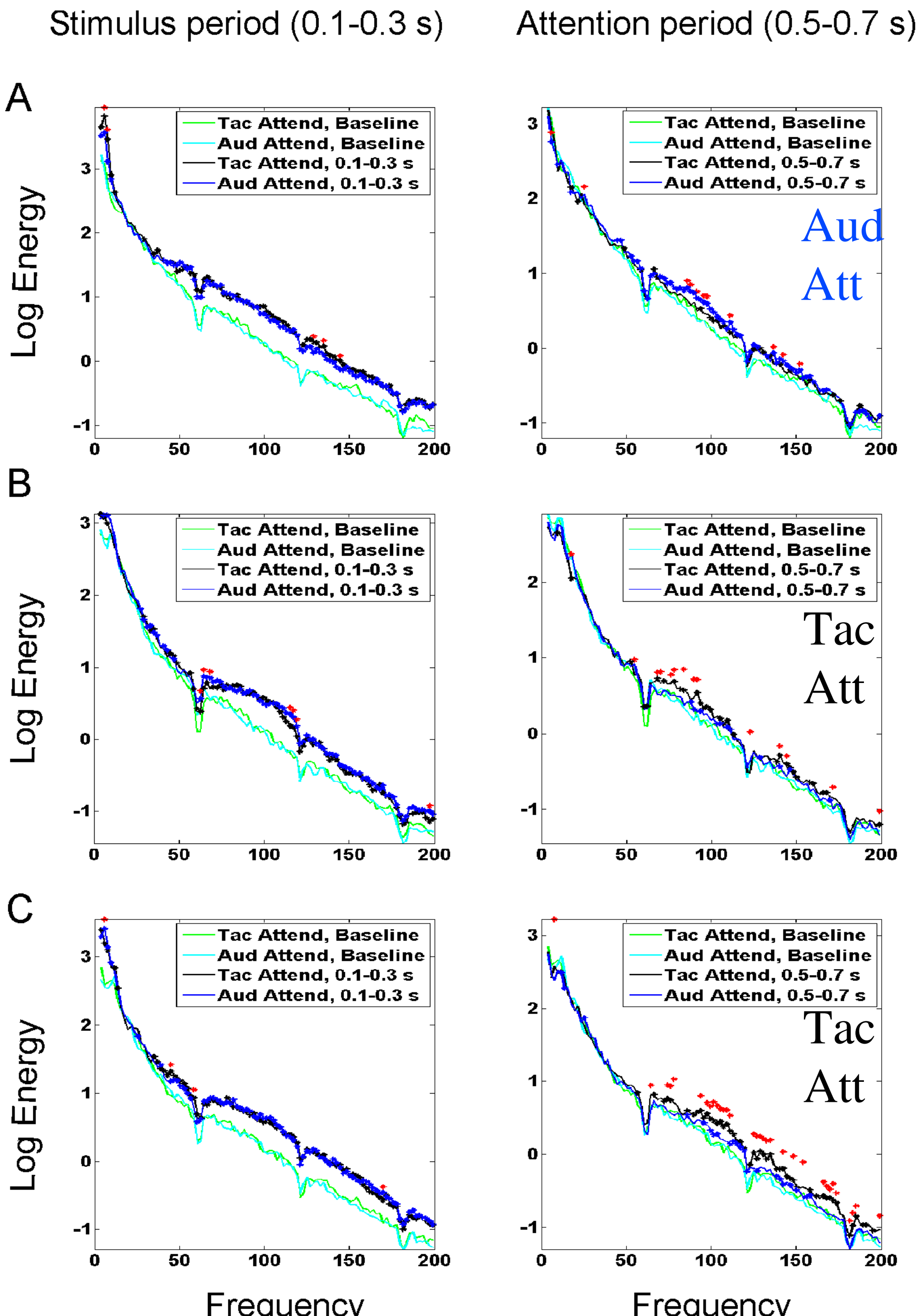
Results: Auditory cortex



Results: Somatosensory cortex



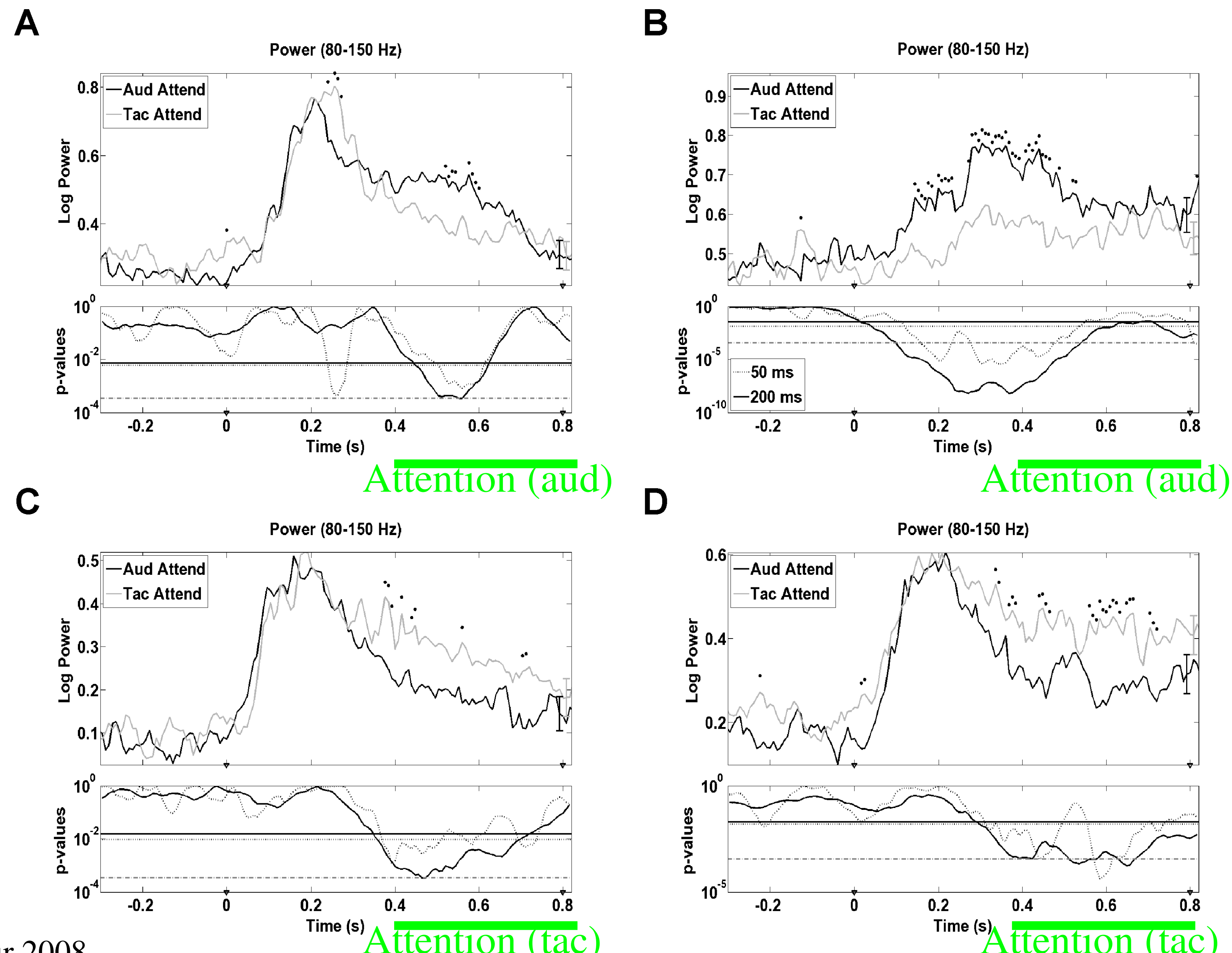
Frequency range



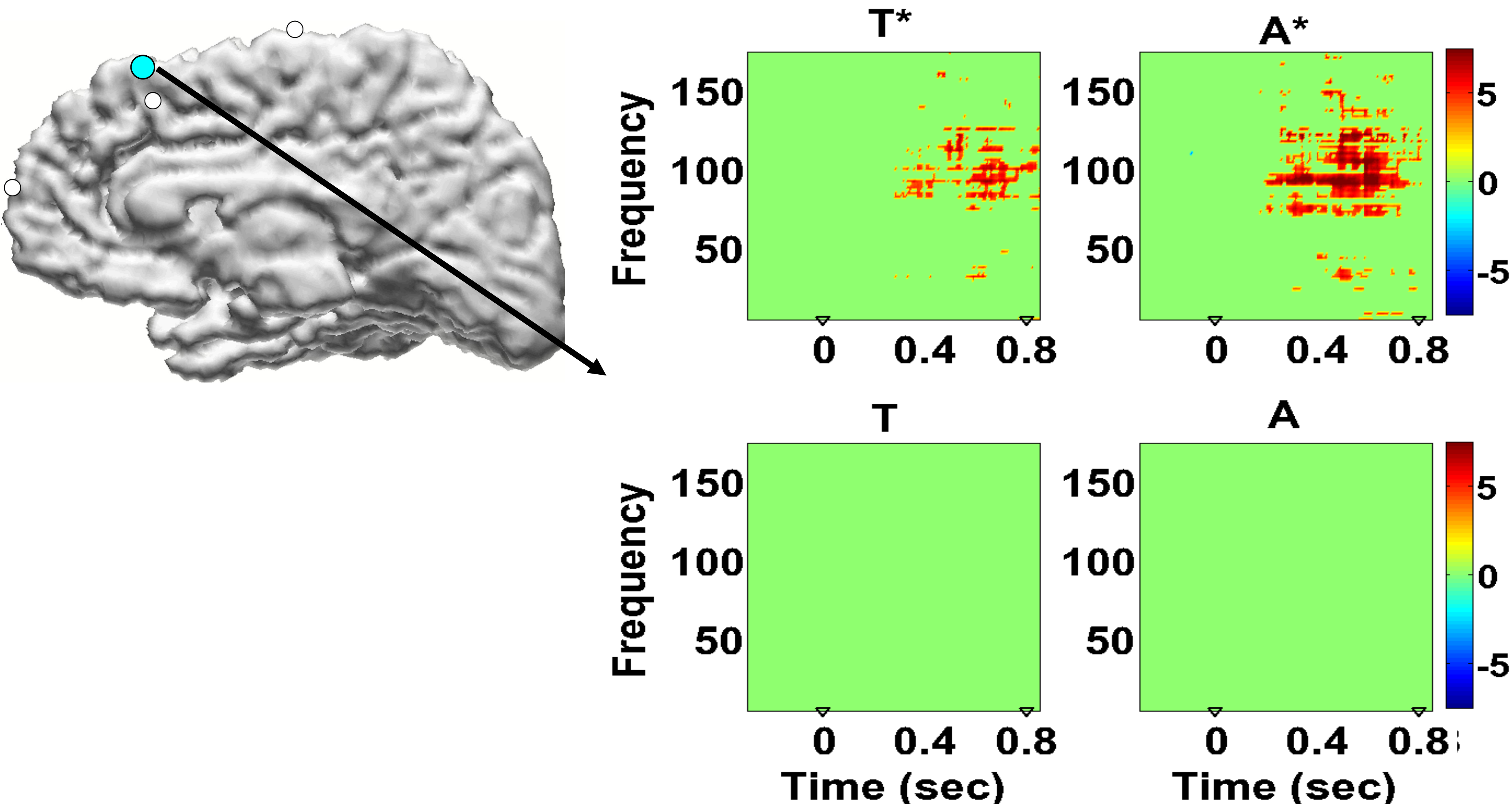
Stimulus-related response: Broadband (gamma) range (>40Hz)

Attention-related response (difference between attended and unattended; *, p=0.05): High-gamma range (60-150Hz)

Attention-dependent differences appear at time of expected relevant stimulus



Frontal cortex



More frontal results

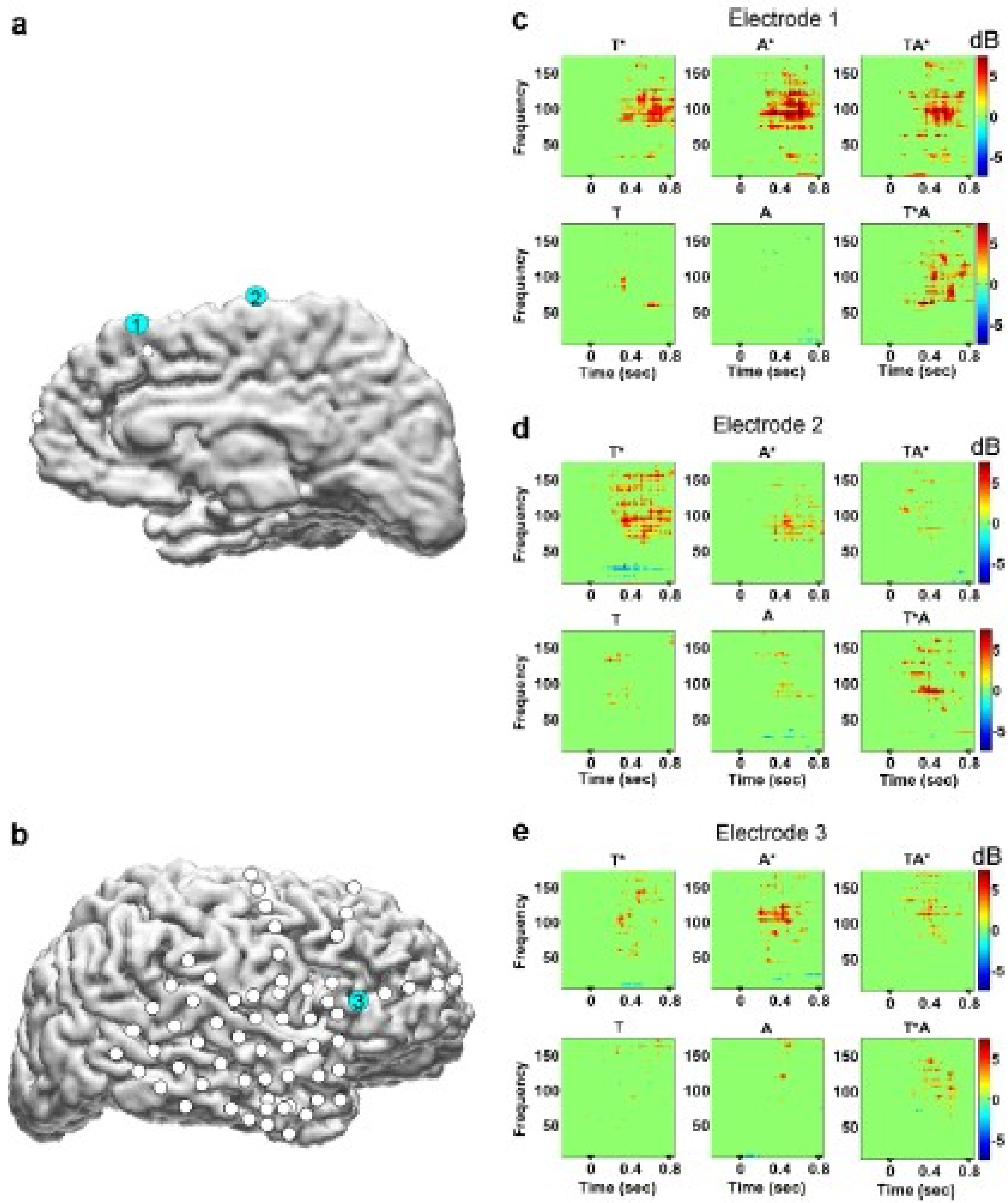


Fig. 5. Time-frequency plots of the six experimental conditions for electrodes over frontal regions in Subject 2. (a) (Medial view of the right hemisphere) and (b) (lateral view of the right hemisphere) show the electrode positions. The spectra shown in (c–e) correspond to the electrodes marked 1, 2 and 3, respectively, in (a) and (b).

Conclusions

- Activity in high-gamma range (80-150Hz) is strongly correlated with selective attention
- Over sensory and frontal cortex
- Speculation: due to underlying synchronous activity
- Consistent with temporal tagging models