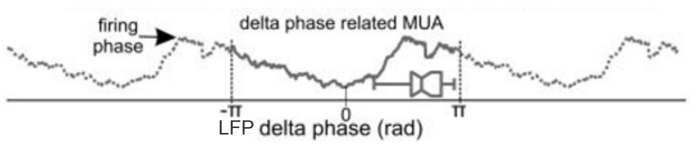
Entrainment of neuronal oscillations as a mechanism of attentional selection: intracranial human recordings

J. Besle, P. Lakatos, C.A. Schevon, R.R. Goodman, G.M. McKhann, A. Mehta, R.G. Emerson, C.E. Schroeder

Oscillations and excitability

- Oscillations correspond to fluctuations in neuronal excitability (e.g. Shu et al. 2003; Lakatos et al, 2005.)



Lakatos et al, J. Neurophysiol. 2005.

- Can delta oscillations be used as a tool for attentional selection?

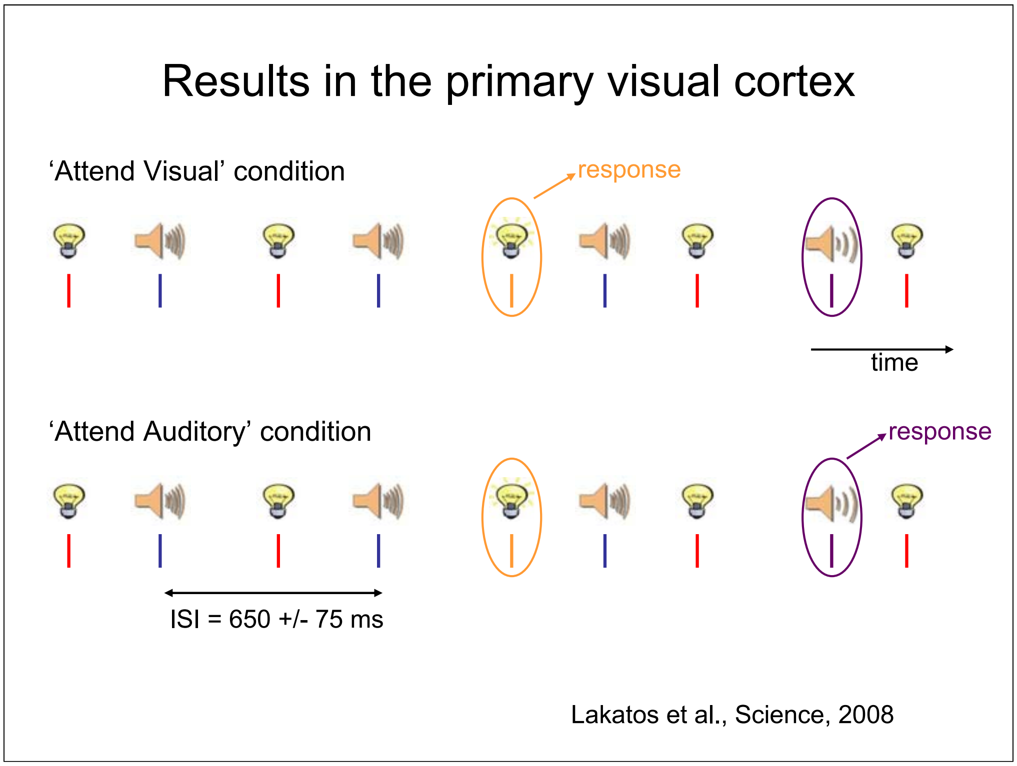
Oscillations and in particular slow oscillations correspond to fluctuations in neuronal excitabilty

For example, Lakatos and colleagues have shown that, in spontaneous eeg in the monkey auditory cortex, there is a phase of the oscillation where neurons are more susceptible to fire (the ideal phase) and a phase where they are less susceptible (the worst phase)

And if one presents an stimulus during the ideal phase, the evoked response is significantly larger than if one presents the same stimulus during the worst phase

They have thus proposed that fluctuations in excitability could be used as a tool for attentional selection.

The idea is that if the brain is able to shift delta oscillations in time so that the ideal phase coincide with the presentation of a stimulus, then the processing of this stimulus could be enhanced



A recent study recording LFP and MUA in the primary visual cortex of the monkey have show that this is indeed possible.

In this study, the authors presented the monkey with 2 alternating streams of auditory and visual standard stimuli.

Among those standards, some auditory and visual targets were presented

In the Attend Visual condition, monkeys had to respond to visual targets and ignore auditory targets

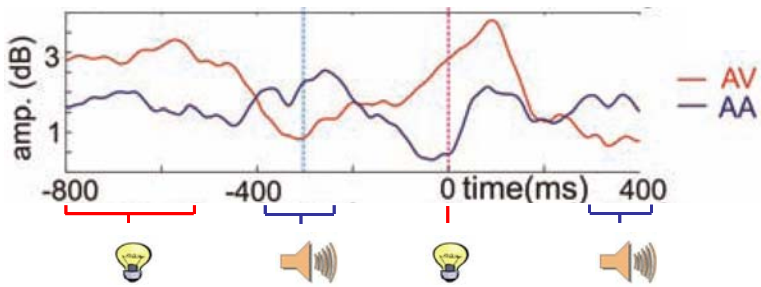
And in the 'Attend Auditory' condition, monkeys had to respond to auditory targets and to ignore visual targets

An important aspect of this paradigm is that, although the InterStimulus Interval was randomly jittered, the distribution of ISI was normally distributed so that there was a certain rhythmicity to the streams

The time between two successive stimuli of the same modality was on average 650 ms.

Thus, although stimuli were exactly the same in both conditions, monkeys had to pay attention to two different interdigitated streams of stimuli at 1.5Hz

Results in the primary visual cortex



Lakatos et al., Science, 2008

- Thus attention can shift the phase of entrained delta rhythms to modulate the sensory response through excitability

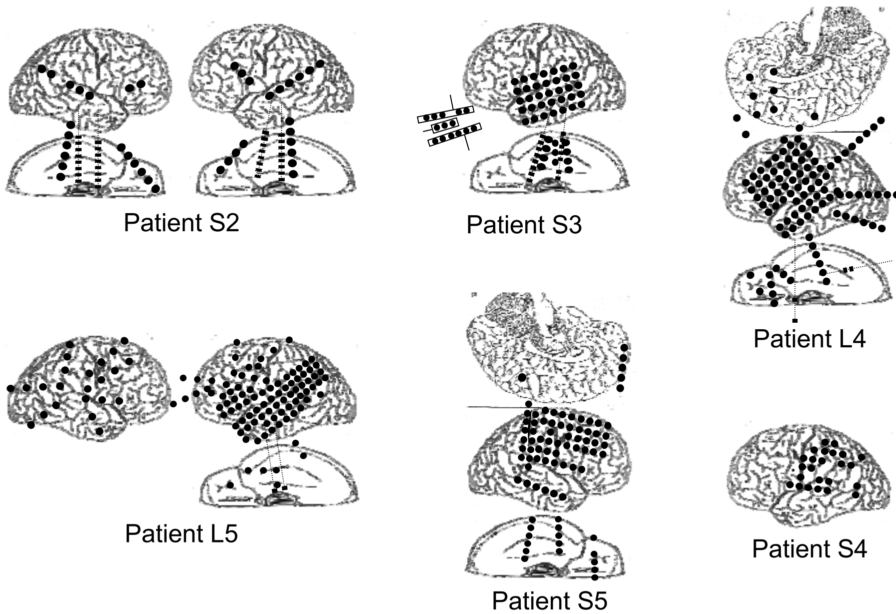
These are the LFPs they recorded from the supra-granular layer of the primary visual cortex

there is a delta rhythm at the rate of stimulation that is shifted 180 degrees when the monkey pays attention to the auditory or the visual stream

So when the attention is on the visual stream, the delta rhythm is such that visual stimuli will be presented in a good phase and when attention is on the auditory stream, the delta rhythm is such that visual stimuli will occur during a worst phase of the oscillation

Thus it seems that attention can shift the phase of entrained delta rhythms to modulate the sensory reponses through excitability

Study in human subdural cortical recordings

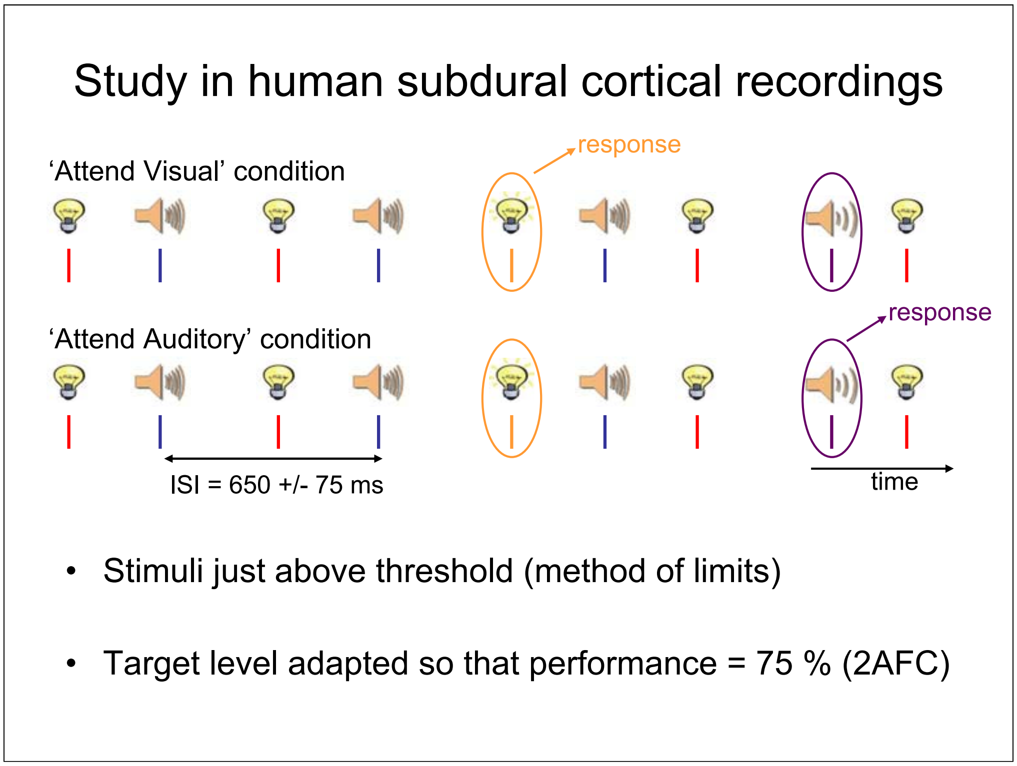


In the present study, we wanted to se how this results generalize to the human brain and outside the primary visual cortex / to other cortical areas

we thus conducted a similar paradigm with epileptic patients undergoing evaluation for brain surgery

These are the implantations of the 6 patients we recorded

As you can see, we had large coverage of the temporal, posterior frontal and anterior parietal lobes, in particular areas surrouding the sylvian fissure



We used the the same paradigm as was used for the monkey experiments

'Attend Auditory' and 'Attend Visual' were presented in blocks of about 1 minutes including 8 targets of each modality

The most important difference with the paradigm used for monkeys is that we presented stimuli just above threshold

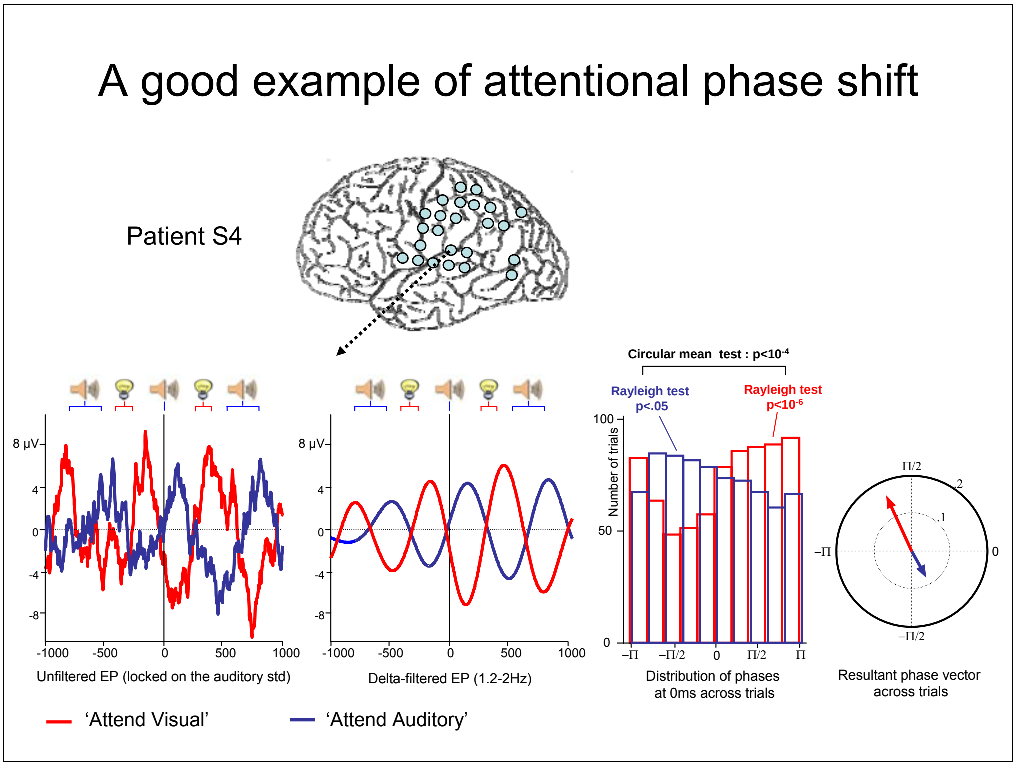
Visual stimuli were grey circles against a black background.

Auditory stimuli were pure tones at 440 Hz

The contrast of the presentation screen and the intensity of the sound were adjusted using the method of limits so that stimuli could barely be detected.

Visual targets were intensity deviants and Auditory targets were frequency deviants

The target deviance was adjusted in both modalities so that performance equals 75%, using a 2 alternative forced-choice paradigm.



This is an good example of the attentional phase shift . This patient had a 8 by 6 grid of electrodes. 24 electrodes were excluded because they showed persistend interictal activity.

In the remaining electrodes, we excluded trials with interictal spikes.

I'm gonna show detailed results for this electrode over the sylvian fissure

The blue curve is the averaged response for the auditory standard in the Attend auditory condition

It is evident here that there is a rhythm here that corresponds to the rate of presentation of the one of the stimulus streams (most probably the auditory stimulus)

And the red is for the Attend visual condition: there is also a 1.5Hz rhythm but it is in phase opposition

It is even more evident in the averaged response filtered in the low delta range

But this is the reponse averaged over all the trials, it doesn't show that the phase was consistent across single trials

We thus looked at the distribution of the phases across trials at the time of presentation of the auditory stimulus

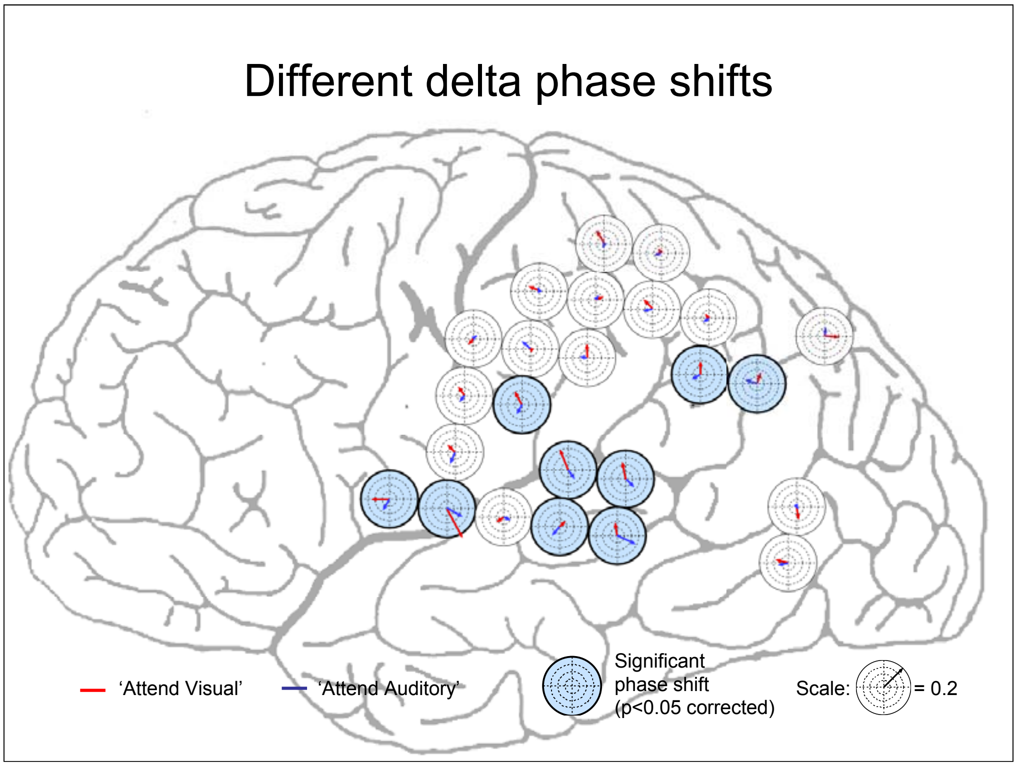
For both attentional condition, there was a significantly non-uniform distribution of phase across trials, as assessed by the rayleigh test.

But their mean was different and this difference was significant, showing that there was a consistent phase difference across trials between the two attention conditions

Another way of plotting the result is to plot the resultant phase vector

The direction of the arrow indicate the mean phase and the length (which correspond to the phase-locking factor) indicates how the phases across trials are concentrated around the mean value)

On this plot, you can clearly see the 180 degree phase difference between attentional conditions



We can plot those resultant vectors for all the electrodes in this patient

In this patient, 9 electrodes, highlighted here, showed both non-uniform distribution of phases across trials and a significant attentional phase shift

however there was a large range of phases shifts

This is the electrode I just showed you on which the delta phases are 180degrees apart in the 'attend auditory' and 'attend visual'

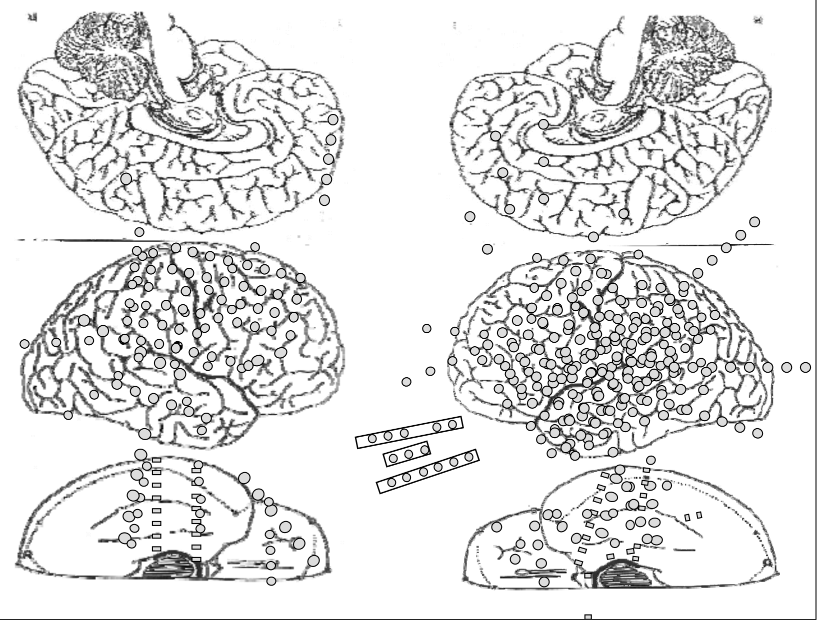
Neighboring electrodes show the same kind of phase differences

But other electrodes further away show smaller, but still significant, effects of attention on the delta phase.

This is not in line with our hypothesis that delta oscillations will be in phase opposition when paying attention to the two alternated stimulus streams

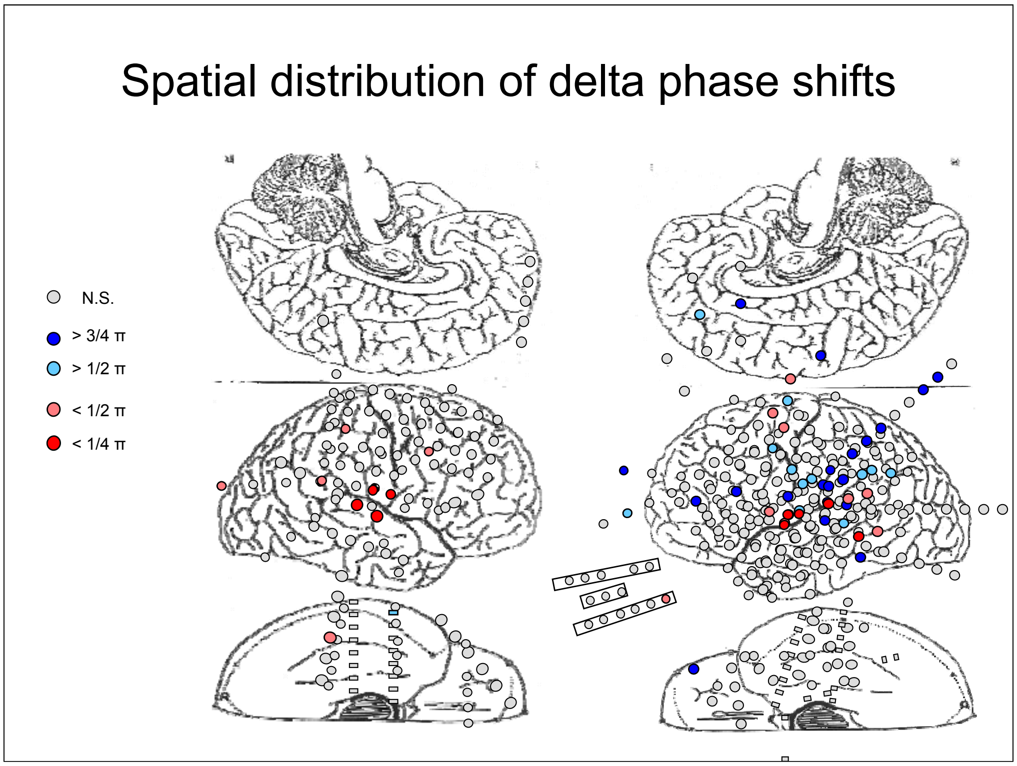
How can we explained this wide variation in phase shifts ?

Spatial distribution of delta phase shifts



To help answer this question, let's look at the spatial distribution of significant phase shifts for all patients.

On this figure, I overlayed the implantations of all patients



All colored circles are for significant differences. Significant effect of attention on the phase of delta rhythms were found in many different areas and it's difficult to make sense of it

Different colors correspond to different phase shift values

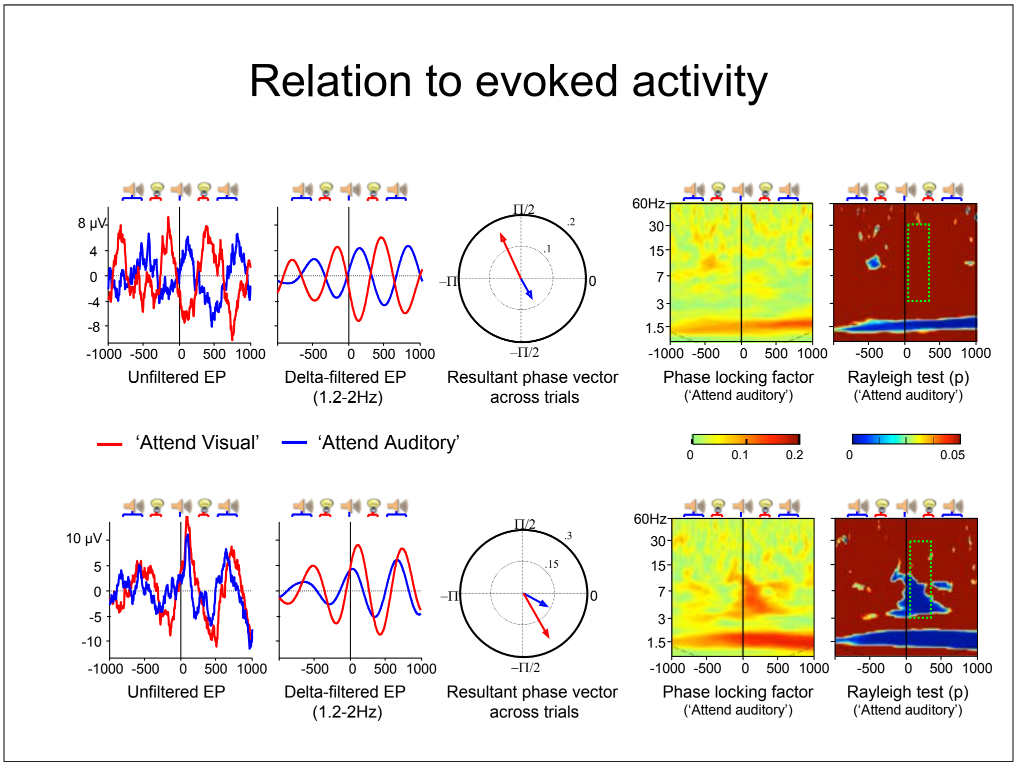
Dark blue are for phase differences that are close to a phase opposition

And red are for phase differences that are less that 45 degrees.

What is striking to me is that small phase differences were consistently found over the sylvian fissure, at a location compatible with the auditory cortex

It is not apparent on this slide, but we observed this for each of the patients.

So that made us think that one possible explanation for the small phase difference: maybe the phase shift is small at these electrodes because it is hidden by a sensory evoked potential at the rate of stimulation



Let's explore this idea

This is the data from the electrode I showed earlier with 180 degree phase opposition. Clearly there is no detectable sensory evoked potential on this electrode

We computed the phase-locking factor, which is an index of evoked activity in the broad sense with wavelet decomposition, along with is statistical significance.

only the low-delta frequency shows a significant phase-locking factor, with suggests that the spontaneous delta rhythm was entrained to the stimulation stream

Let's now look at a case where the phase shift was significant but small: in this case there was an auditory evoked potential. Since auditory stimuli were presented at a delta rhythm and were the same in both attentional conditions, the evoked response creates a delta rhythm with a similar phase in both attentional conditions, as you can see on the delta-filtered curves

However, there was still a significant delta phase shift, which suggests that the effect was there, but obscured by the evoked activity

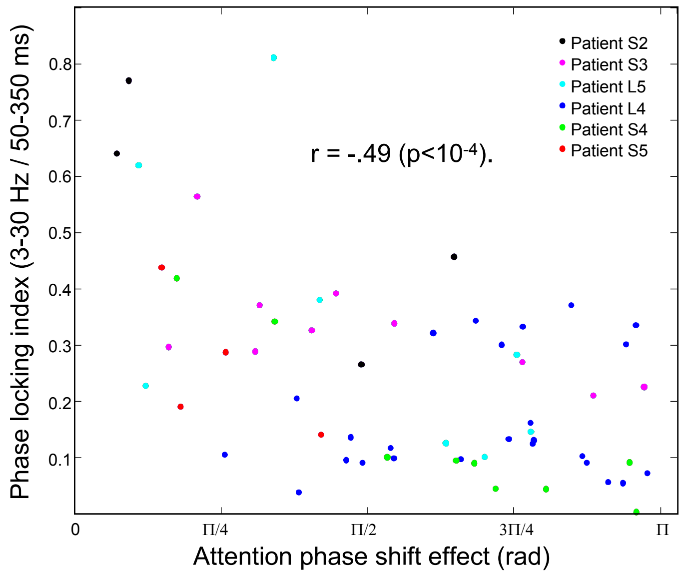
When computing the pahse-locking factor, there was a significant increase frequencies higher than delta

So it seems that the presence of a sensory evoked component can obscure the attentional phase shift

To see if this can explain the wide range of phase differences observed across electrodes and patients, we used the phase locking factor at frequencies higher than delta as an index of the presence of evoked activity

And we computed the correlation between the attentional delta phase shift and the phase-locking index across all electrode showing a significant effect of attention

Correlation between evoked activity and phase difference

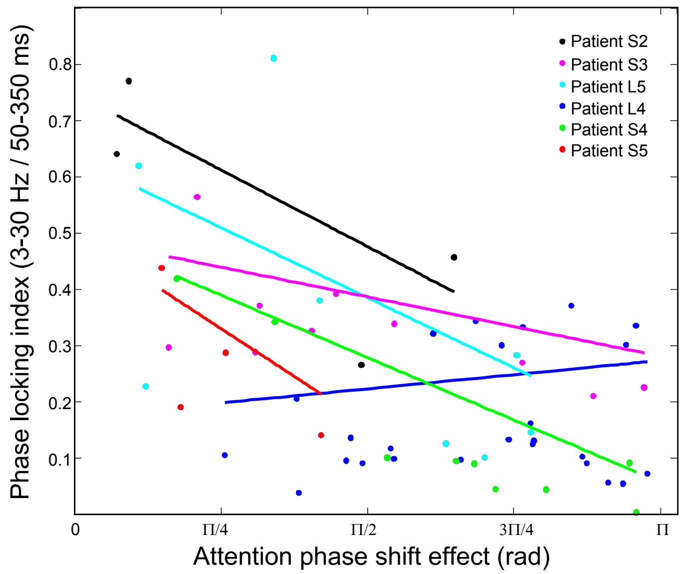


As you can see, overall there is a inverse relationship between the attentional phase shift and the phase locking: the more evoked activity, the less the attentional phase shift

Although it is more evident for phase shift less than 45 degrees.

The correlation was very significant

Correlation between evoked activity and phase difference



if we plot the linear regressions for each patient, this relationship was true for all patients except one.

So it seems that the presence of a sensory evoked component can explain in part the differences in phase shift.

Discussion

- Phase opposition of the entrained delta rhythm when patients attended either of two alternated stimulus streams

  → Attention can control the entrainment of oscillations to different event streams

- The presence of an evoked sensory response can obscure the effect and might explain the variability of observed phase shifts

At some electrodes, we observed a phase opposition in the entrained delta rhythm when patients attended either of two alternated stimulus streams

Thus Effects observed in the primary visual cortex of the monkey generalize to the human brain and to other cortical areas: attention can control the entrainment of oscillations to event streams

However at this stage it is difficult to say in which areas this mechanism operates because there was limited spatial agreement of the results from patient to patient.

There was also a large variability in the value of the observed phase shift and we showed that this variability could be explained in part by the presence of evoked potentials over sensory areas that could obscure phase differences.

Thank you for your attention