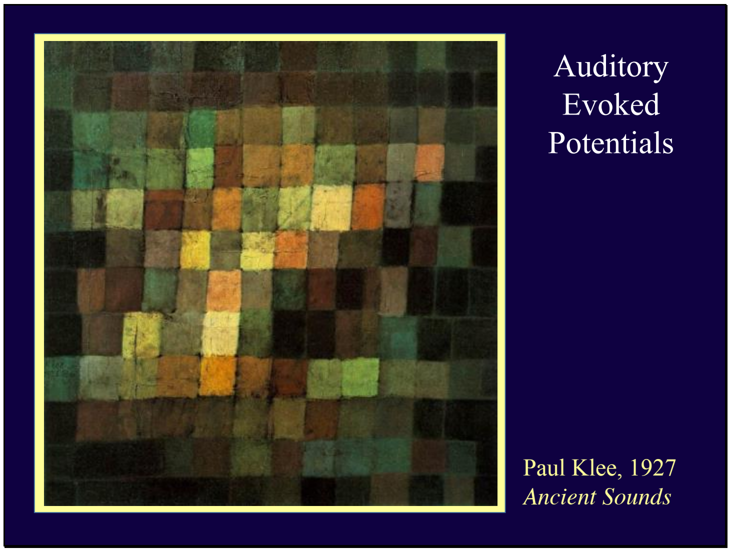
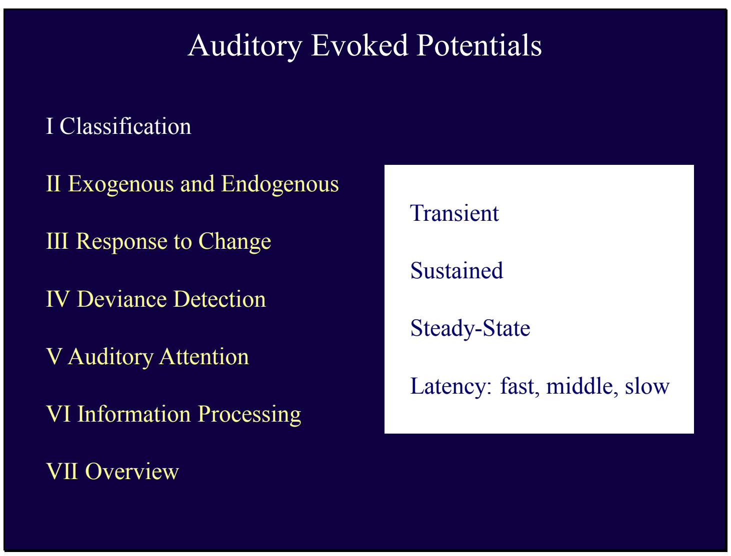
Slide 1



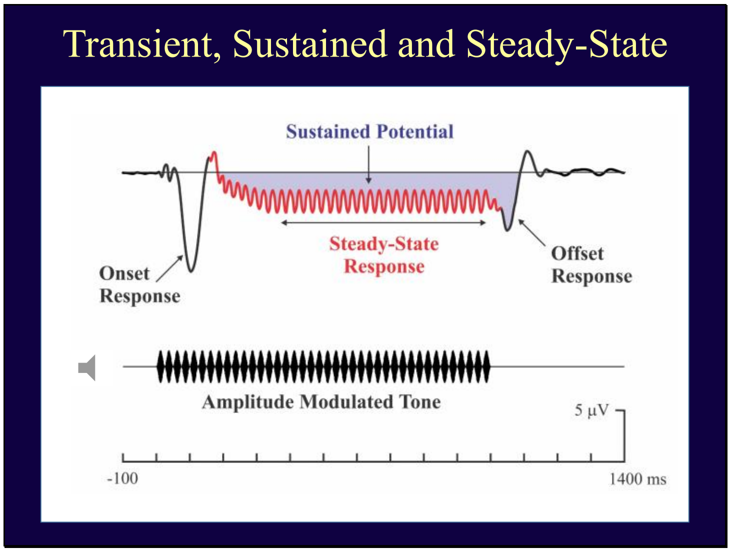
This is one of Paul Klee's pictures from his years at the Bauhaus. He is attempting to portray sounds by means of colors. Perhaps you can see or hear the bright sounds of a flute, the darker notes of a cello. My talk will consider the auditory evoked potentials - how the brain processes the sounds that Klee tried to represent in colors.

Slide 2



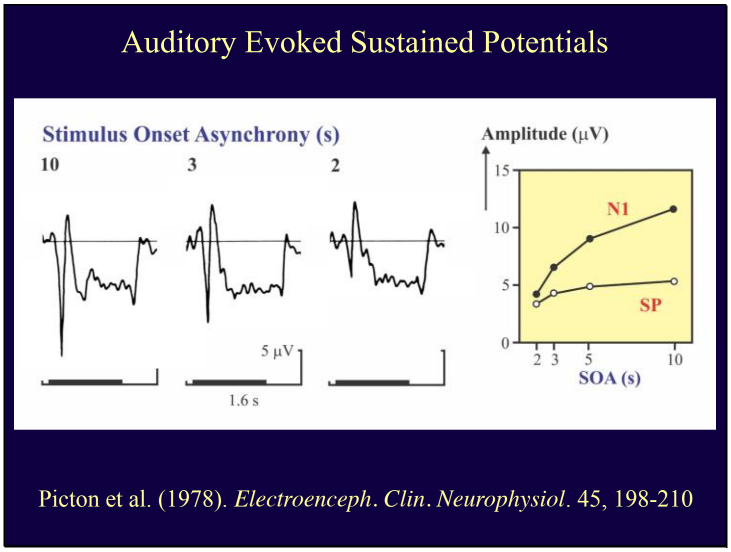
Many different auditory EPs can be recorded from the human scalp. They derive from all the different regions of the auditory system, and mean many different things in relation to how sounds are processed. Some sort of classification is helpful in keeping our bearings. I shall present three: one based on the relation of the EP to the time-course of the sound – transient, sustained and steady state, one based on latency – fast, middle and slow, and one based on what determines the waveforms – exogenous and endogenous.

Slide 3



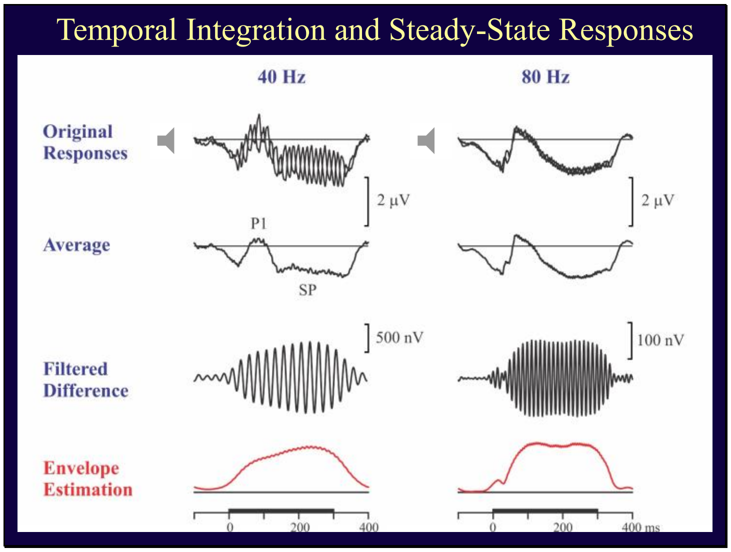
This diagrams shows the response to an amplitude-modulated tone. There are transient responses to the onset and the offset of the tone, a sustained potential during the tone and a steady-state response that follows the amplitude modulation.

Slide 4



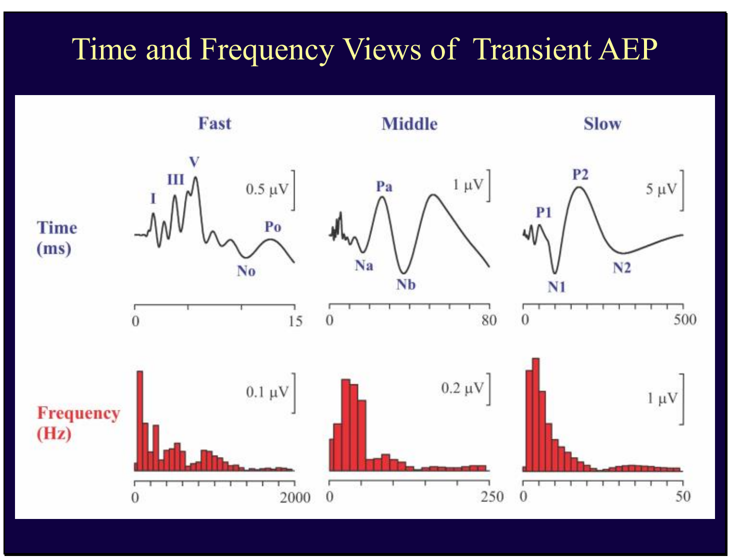
Sustained potentials last during the continuation of a stimulus. Increasing the presentation rate decreases the onset response but has much less effect on the sustained potential.

Slide 5



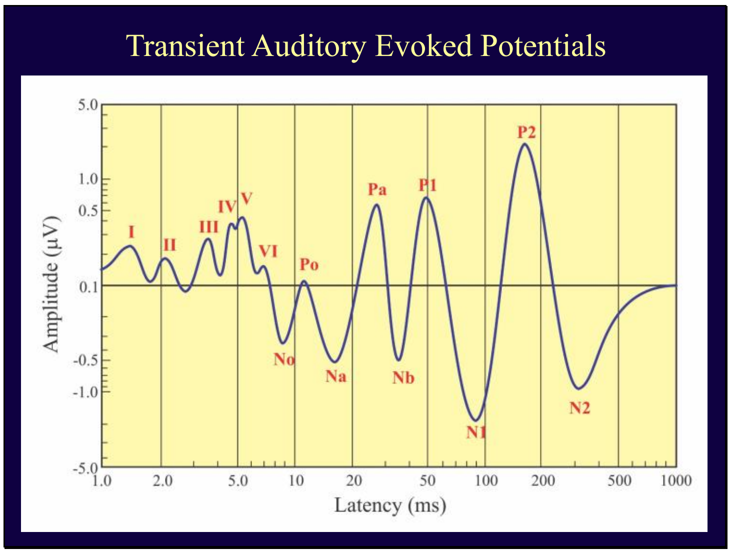
This slide shows the responses to the intermittent amplitude modulation of a continuous tone – at 40 Hz and at 80 Hz. The modulations alternate in their phase. So averaging the responses to the different modulations together cancels out the steady-state response and leaves the transient and sustained potentials. The onset of the modulation evokes an onset response that consists mainly of a P1 wave. Since the stimuli are presented rapidly, the N1 is very small. A sustained potential lasts through the duration of the modulation. If we take the difference between the responses to the out-of-phase stimuli, we cancel the transient and sustained potentials and are left with the steady-state response – which can be filtered and amplified. These recordings show the build-up of the steady-state response over time. The 80 Hz response originating in the brainstem builds up quickly – the cortical 40 Hz response takes about 200 ms to reach steady state.

Slide 6



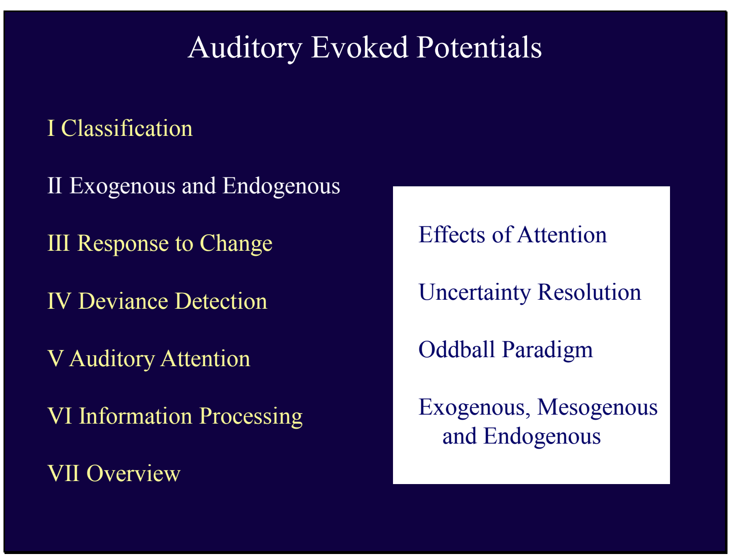
Most psychophysiological research with the auditory evoked potentials uses the transient evoked potentials. These follow the auditory processing from the cochlea through the brainstem up to the auditory cortex and then to the association areas of the cerebral cortex. The nomenclature follows the discovery of the waves. First, the slow waves which are large and can occasionally be seen in the single trial EEG. Looking at the earlier portion of the slow response and increasing the band-pass of the amplifiers shows the middle latency response. Looking at the early part of this waveform shows the brainstem response.

Slide 7



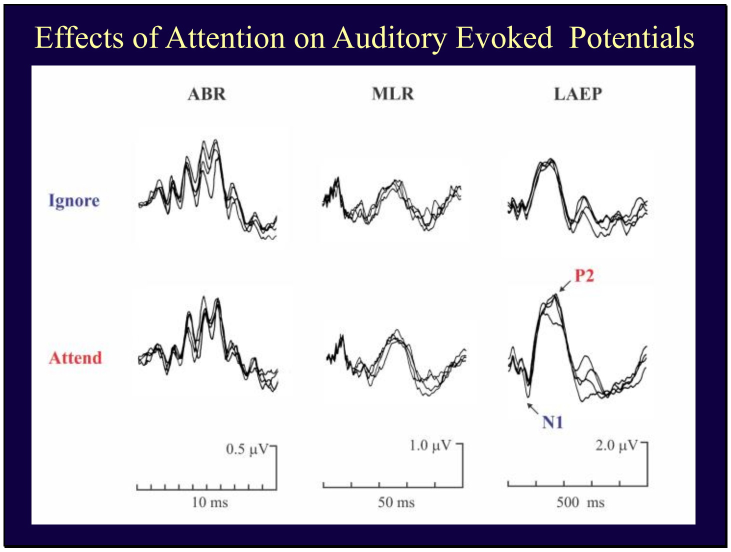
Bob Galambos and I found that all the transient auditory evoked potentials can be plotted on a log-log plot so that makes the earlier and smaller potentials more readily detected.

Slide 8



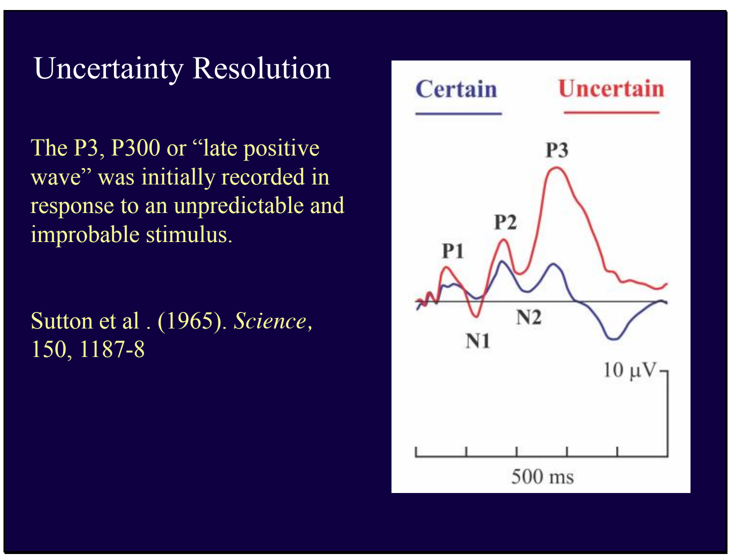
We have considered the different auditory evoked potentials, classifying them on the basis of their latency and on how they respond to the time-course of the stimulus. From the point of view of psychophysiology, another system of classification may by helpful, based on how the response change with attention.

Slide 9



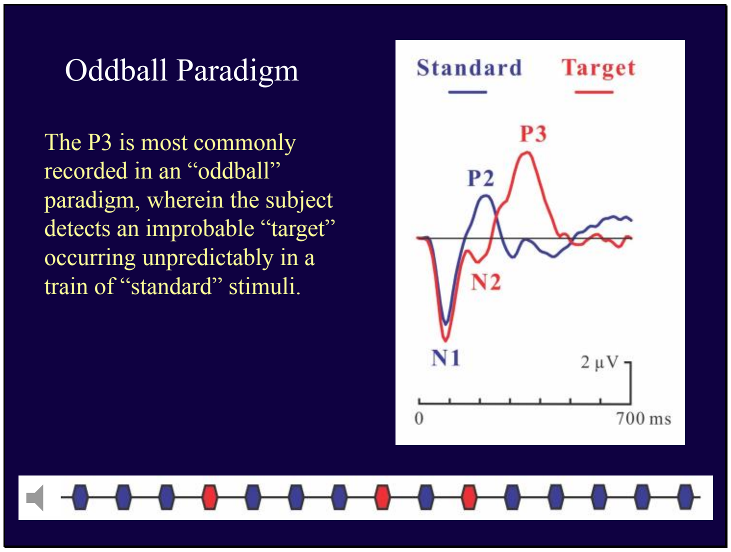
The transient evoked potentials to a click change when the subject pays close attention to the click in order to detect an occasional change in its intensity. The changes involve the slow responses – the late auditory evoked potentials. The earlier responses are remarkably resilient to manipulations of attention. It is as though the brain analyzes all sounds but attends to only some of them.

Slide 10



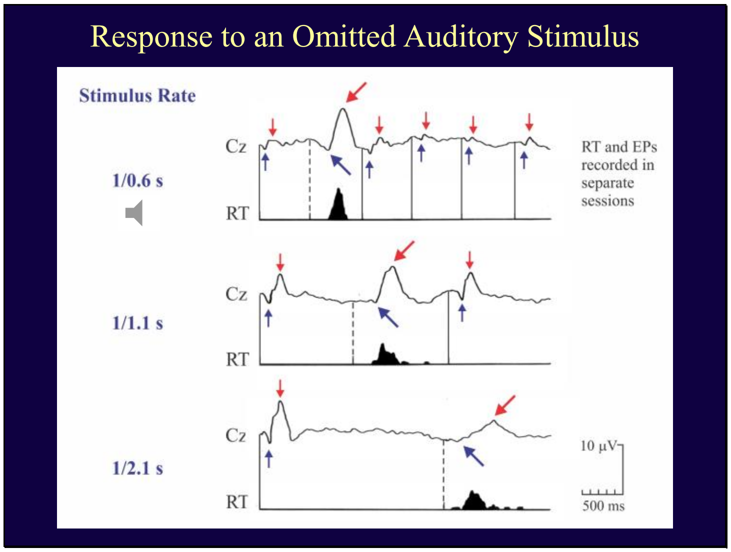
Some components of the event-related potential appear to reflect the psychological meaning of a stimulus rather than its physical parameters. Sutton and his colleagues discovered a late positive wave in the event-related potential when the stimulus (auditory or visual) resolved uncertainty but not when it was predictable. Sutton considered the wave endogenous – related to inner world of perception – as compared to the earlier exogenous waves – determined by the outer physical world.

Slide 11



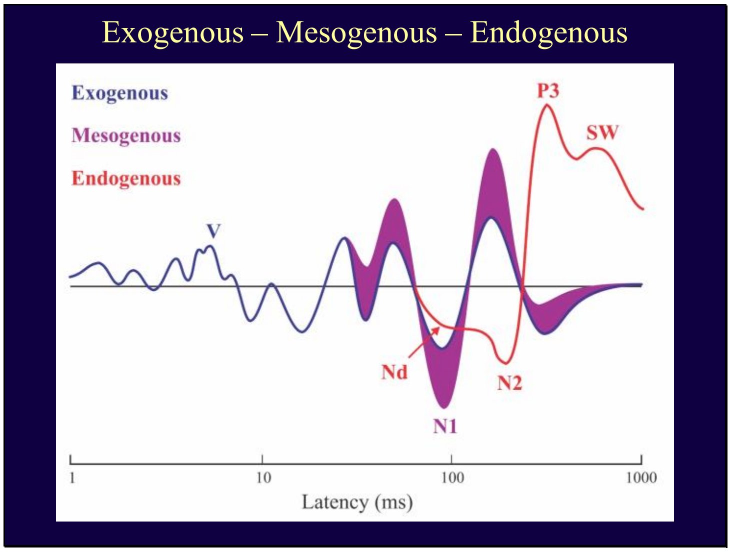
Nowadays the P3 …. The sample sounds are unpredictable and do not exactly follow the illustration. In this paradigm the target elicits a complex containing N2 and P3 waves that is not present in the response to the standard.

Slide 12



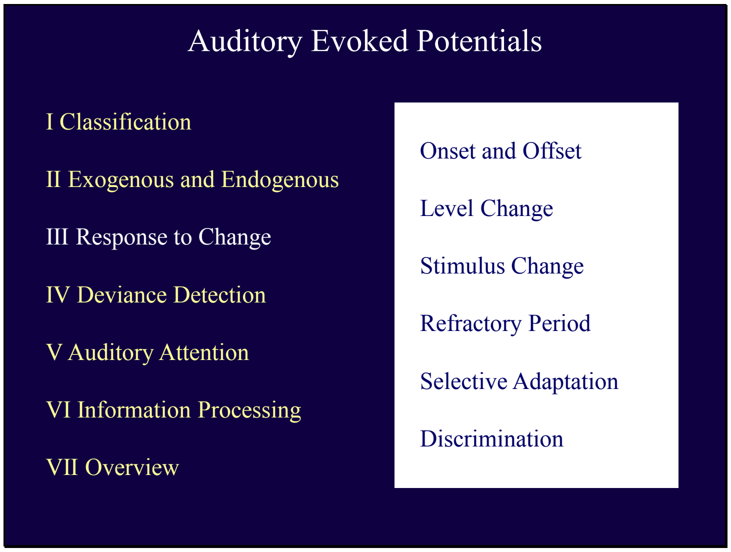
If we omit an occasional stimulus in a regular train and ask the subject the count the number of omissions, the N2-P3 complex occurs in response to the omission. This thus represents a completely endogenous process. The clicks are faint – so listen carefully. When the clicks occur at a slower rate, the response is smaller and more spread out. If on separate trials we record the reaction time to the omission, we see that this becomes more variable as the interval between the stimuli increases. The broad waveform at slow rates is the result of latency jitter in the perceptual decision. Exactly what the P300 represents is not clear – it is not the decision process itself since it can follow after the RT. It likely represents an updating of working memory.

Slide 13



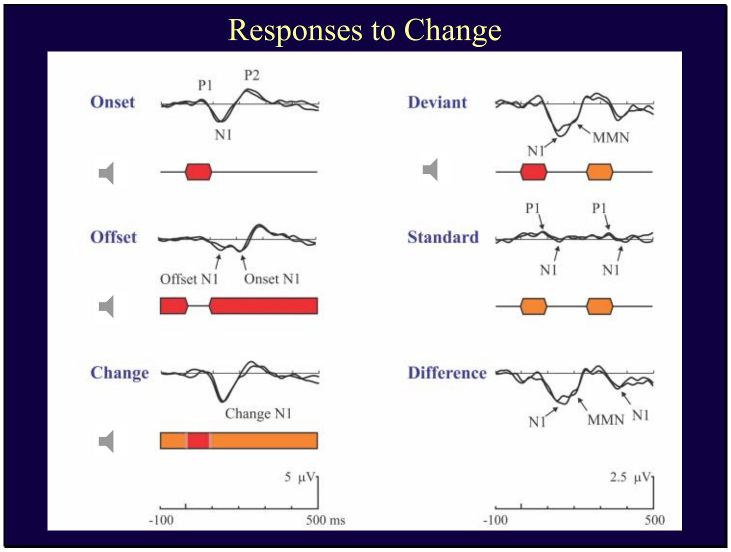
Many years ago Steve Hillyard and I proposed that the event-related potentials could be classified as exogenous – controlled by the physical world, endogenous – related to psychological meaning, and mesogenous – affected by both the outer world and the inner mind. The classification quickly passed away. This slide is an attempt at resuscitation. The early evoked auditory evoked potentials are exogenous, and the later potentials are mesogenous. Superimposed on these waves are a variety of endogenous components as attended stimuli are evaluated, decisions made and memories updated.

Slide 14



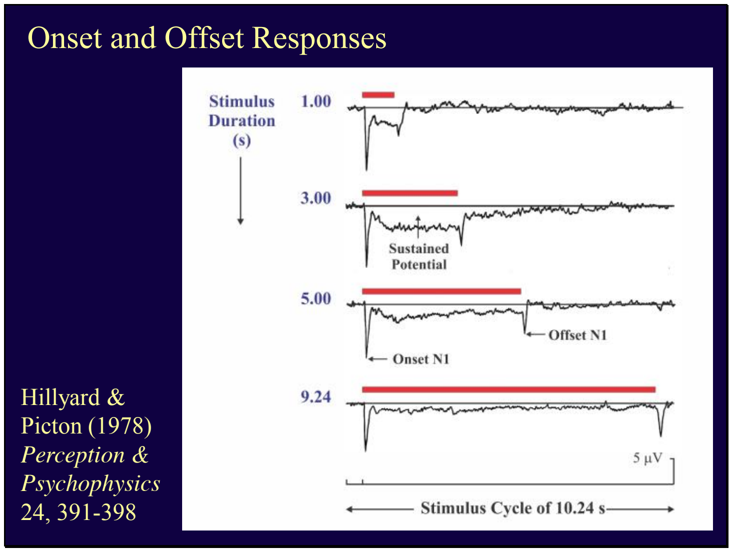
We have considered the exogenous and endogenous components of the response and postulated that there may also be mesogenous components. This section will deal with these mesogenous components, and how they respond to changes in the world. We will consider in particular how these change-responses are affected by the timing of the stimuli.

Slide 15



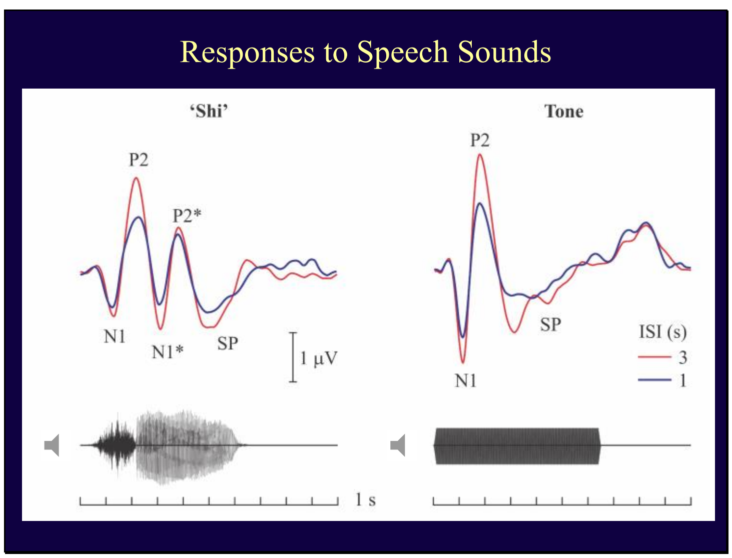
This slide shows the response to an auditory stimulus in different contexts. The occasional stimulus evokes a P1-N1-P2 complex. The occasional pause in an ongoing tone evokes a response to both the offset of the tone and its re-onset. A brief change in the frequency of a continuous tone evokes a similar response to the onset of a brief tone. These are simple responses to simple changes. Things get more complicated when multiple stimuli are involved. If the occasional tone differs from the preceding tones, we record both an onset response and a later negative wave in response to the stimulus deviance – the mismatch negativity. The difference between this response and the response to an ongoing standard stimulus shows both the N1 of the onset-response and the MMN to the change. Also visible in these results is the fact that at rapid rates the N1 response to the standard is small whereas the P1 persists. As well as the N1 response to a standard being smaller than the response to the deviant, and the response to the standard that follows the deviant is larger than to a standard that follows another standard. We shall consider this selective adaptation later.

Slide 16



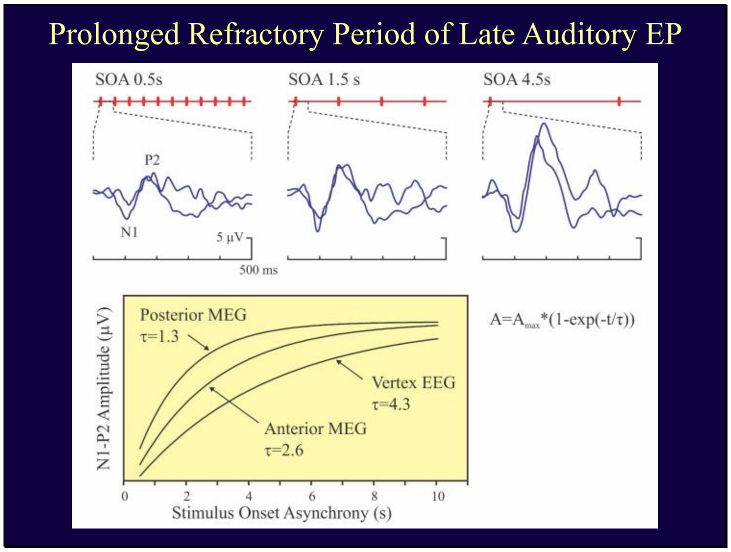
But first the onset and offset responses. Ancient findings of Steve and Terry. Given the same on-off duty cycle, the offset response is about half the size of the onset response. Both are smaller when more closely preceded by the other. The offset response can be difficult to measure because it occurs at the same time as the return to baseline of the negative sustained potential.

Slide 17



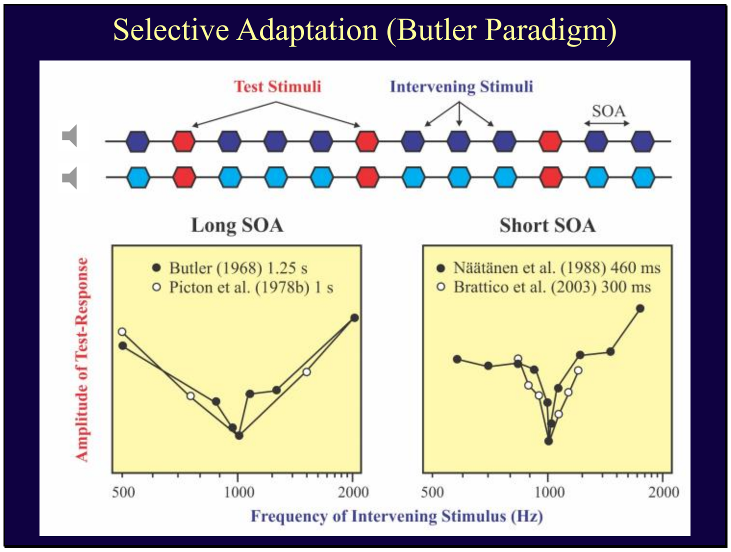
Why is the response to the onset and offset of a sound so important? One reason is that it allows us to parse the different components of a speech sound. The response to the sound 'shi' contains an onset response to the beginning of the sibilant and another onset response to the beginning of the vowel. The onsets mark the changes in the speech envelope. Indeed the response to the speech envelope obtained through deconvolution is similar to the N1-P2 response. Among other things the N1-P2 may also be a phoneme parser. Another aspect of the response is its sensitivity to the interval from the preceding stimulus. The longer the interval the larger the response.

Slide 18



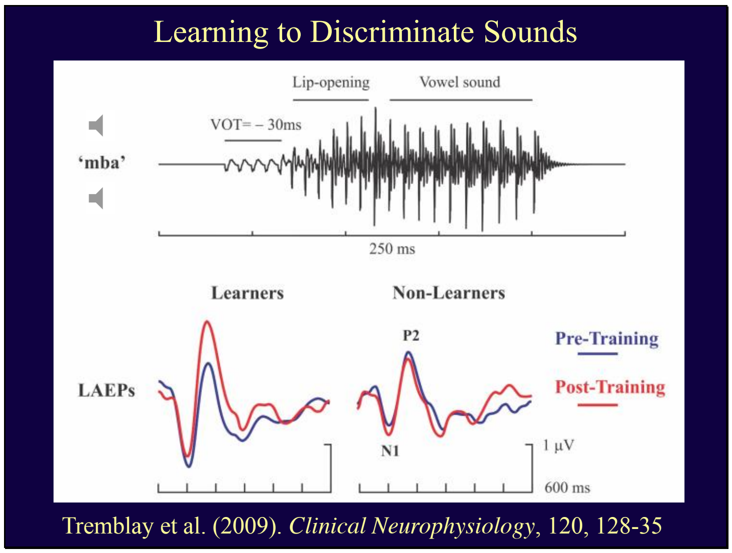
This slide shows some of my first recordings of the auditory evoked potential – they are forty-five years old. They show that the N1-P2 response gets larger as the stimulus onset asynchrony increases. The response keeps getting bigger even beyond ten seconds. This is an intriguing effect. Some people have related it to the duration of echoic memory – perhaps information is maintained and if the stimulus repeats the response only has to boost the residual activity rather than initiate a whole new memory. Studies of the cortical response using the MEG show different time courses. The posterior response quickly returns to normal; the anterior response takes longer but still not as long as the EEG response (which might reflect activity in both temporal and frontal lobes).

Slide 19



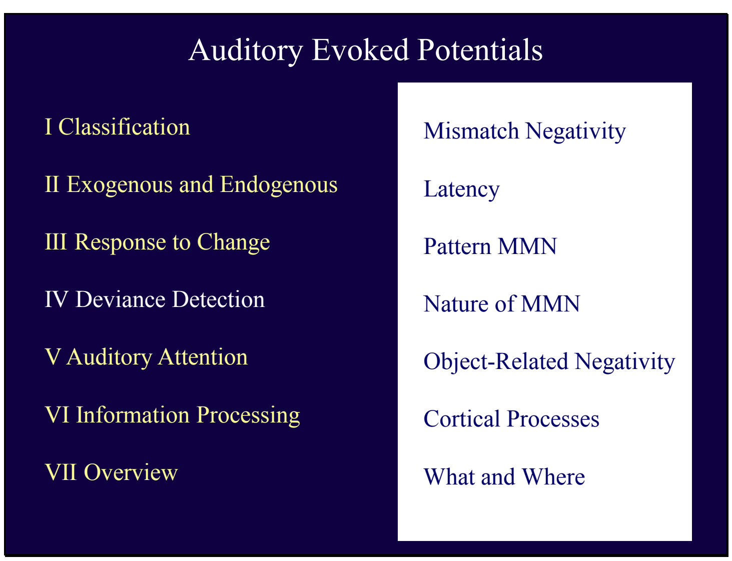
This prolonged refractory effect is selective. If a test stimulus is preceded by intervening stimuli of a different tonal frequency, the response to the test is larger the more different the frequencies. You can hear the difference. This effect varies with the stimulus onset asynchrony. One suggestion is that the posterior auditory system responds quickly to all stimuli whereas the more anterior system responds over a longer period and is more frequency specific. Perhaps the specificity of the refractory period is related to our ability to discriminate sounds.

Slide 20



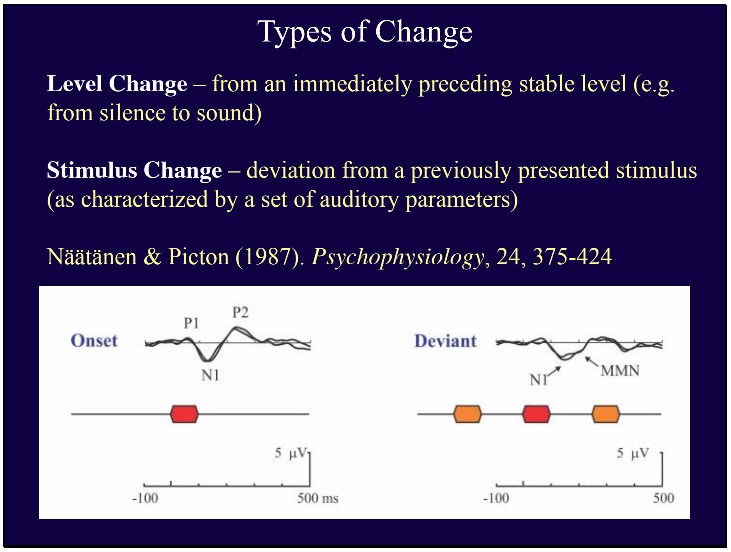
Together with Kelly Tremblay and others we have looked at what happens when we learn to discriminate sounds we are originally unable to tell apart. English differentiates between voiced and unvoiced stop consonants – 'ba' and 'pa.' Some languages such as Thai also differentiate a consonant wherein the voicing begins before the onset of the stop consonant but this is very difficult to recognize for an English speaker. As we learn to tell the difference the P2 wave in the response gets bigger. In addition those who are ultimately able to learn are characterized by a larger N1 wave. N1 provides the ability and P2 the discrimination.

Slide 21



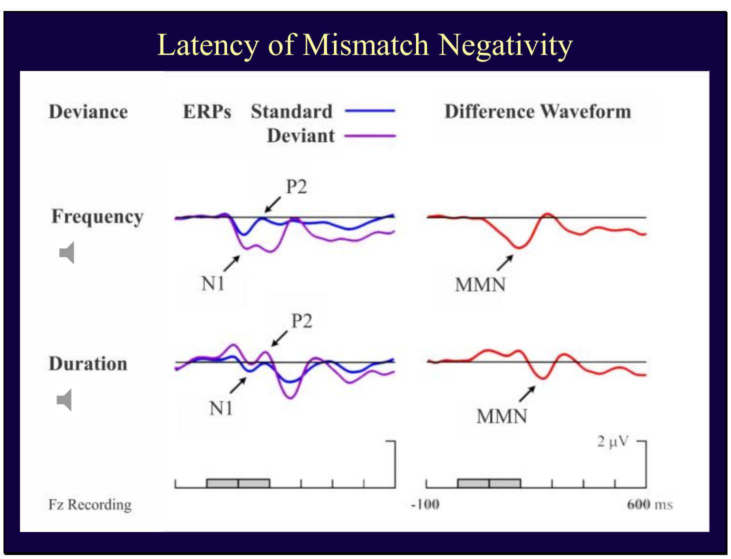
We have so far considered the response of the brain to simple auditory changes – the onset or offset of a sound or a change in its frequency content. A different response to change occurs when a changes occur between stimuli rather than within stimuli. From the California change response we move to the Helsinki deviance detector – the mismatch negativity.

Slide 22



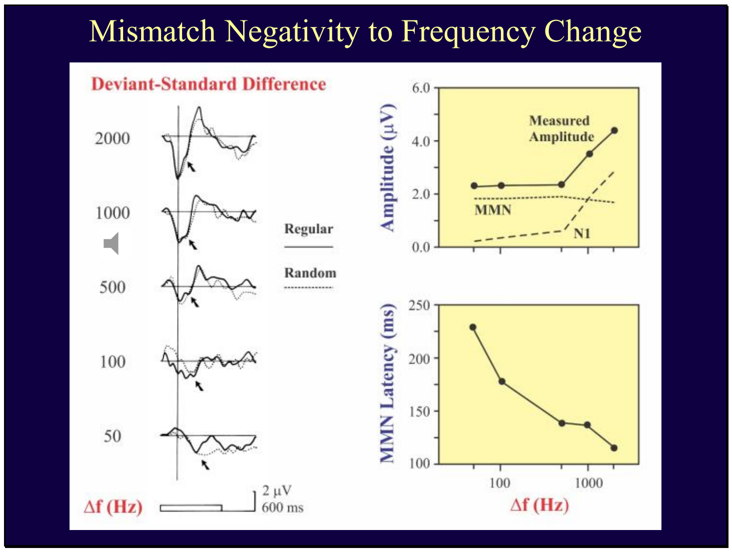
Risto Naatanen from Helsinki and I distinguished two kinds of auditory change: level change … and the stimulus change …The response to an occasional deviant stimulus in a train of standards contains both an onset response to the change in intensity level from nothing and a mismatch negativity to the stimulus change from the preceding stimulus.

Slide 23



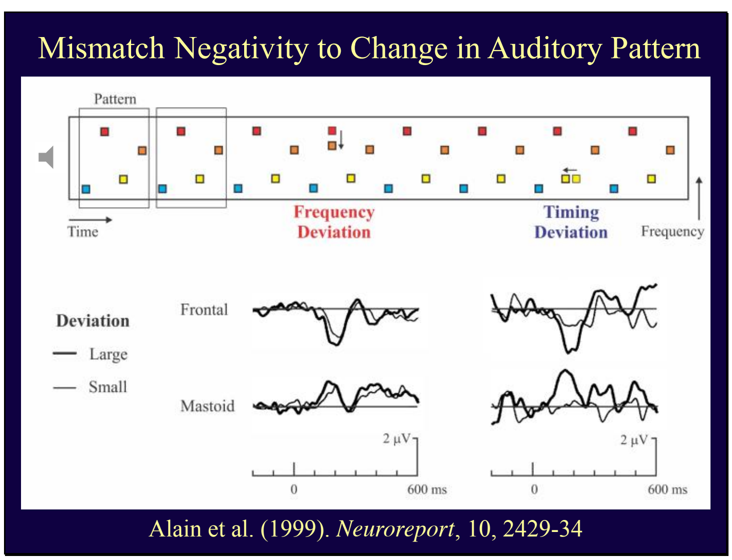
The MMN is a small negative wave that is most easily demonstrated by subtracting the response to the standard from the response to the deviant. The latency depends on how long it takes to process that the deviant differs from the preceding stimuli. For a duration deviant, the discrimination is not possible until the duration of the shorter stimulus is passed. The sounds you heard have a long-duration deviant. The same result would occur (with the same latency) if the deviant were short and the standard long. This is perhaps more elegant since the deviant then sounds less loud than the standard.

Slide 24



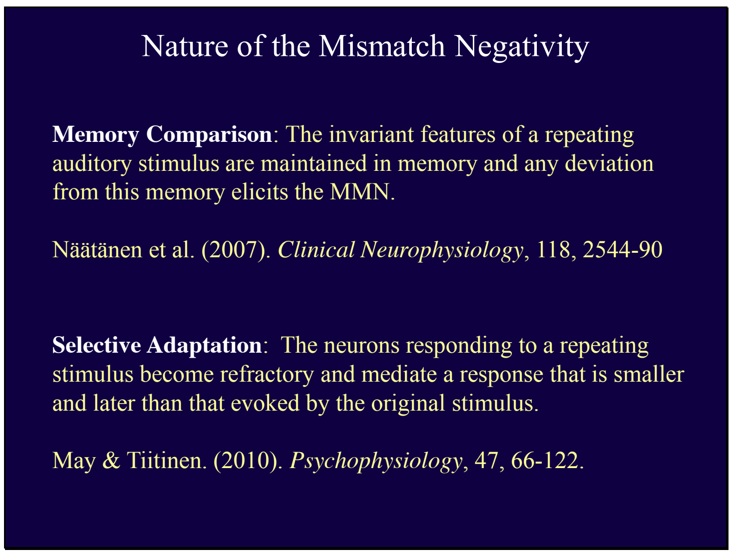
The latency of the MMN to a frequency deviant varies with the difference in frequency between the standard and the deviant. For a larger difference the MMN rides on a change in the N1 due to selective adaptation. For a small difference there is little if any change in the N1 due to selective adaptation and the later MMN is more easily seen.

Slide 25



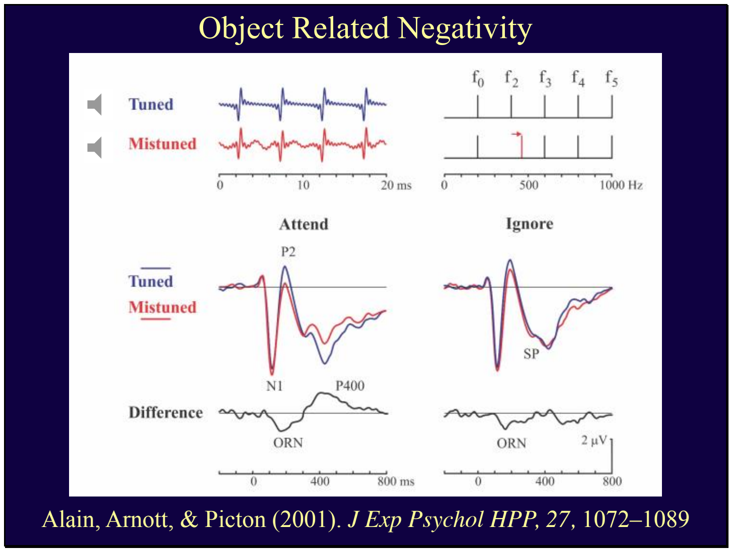
The MMN can be elicited in response to changes in complex stimulus parameters such as a repeating pattern of frequencies. Claude Alain and I studied the responses of the brain to changes in a repeating four-note pattern. The stimuli changed either their expected frequency or their timing. In the sounds (which do not follow the figure) you will hear one example of each. In the actual experiment there were both small and large deviations. Both deviances elicited a MMN – negative over the frontal regions and positive over the mastoids. The experiment is important since the changes cannot be explained by the selective adaptation of the refractory period – the frequency-change makes the deviant closer to the preceding frequency, and the timing-change brings the deviant closer to the preceding standard.

Slide 26



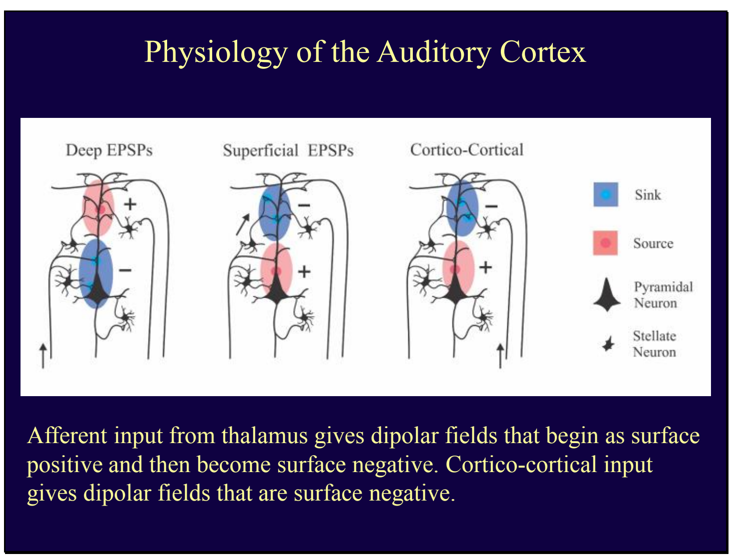
The nature of the MMN is a matter of some disagreement. One theory is that the MMN represents the activity of memory comparison. The incoming stimulus is compared to what is registered in a simple auditory memory. Deviance then serves to alert the higher regions of the brain to the change. The other theory is that the MMN is a variant of selective adaptation, with the MMN being a delayed and attenuated N1 response. Peacekeepers have suggested that selective adaptation is a simple form of memory.

Slide 27



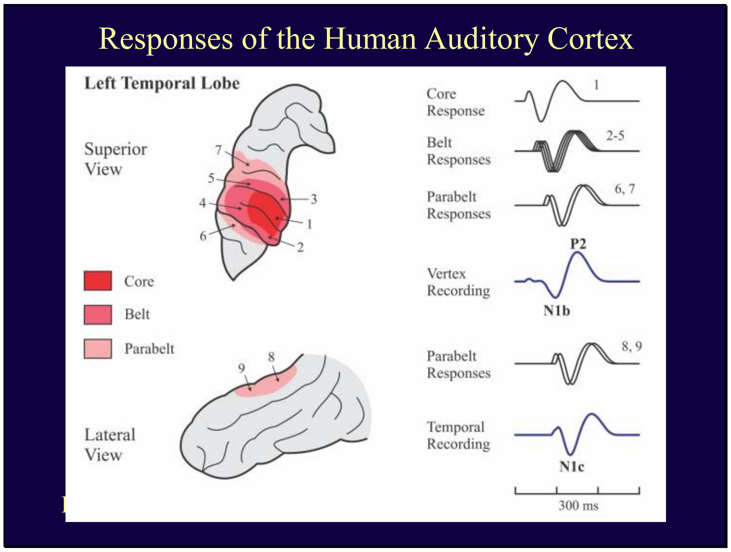
Other negative waves are also generated on the surface of the temporal lobe. A sound that has multiple harmonics will be heard with a pitch equal to that of the fundamental. This sounds like a buzz at 200 Hz. If one of the harmonics is mistuned, it can no longer be reconciled as part of the same sound. It is heard as a separate pure tone superimposed on the buzz – a separate auditory object – the boop in the buzz. This elicits an object-related negativity, a negative wave that is similar in morphology to the MMN but unaffected by whether the mistuned stimulus is standard or deviant. If the stimuli are attended the object-related negativity is followed by a late positive wave.

Slide 28



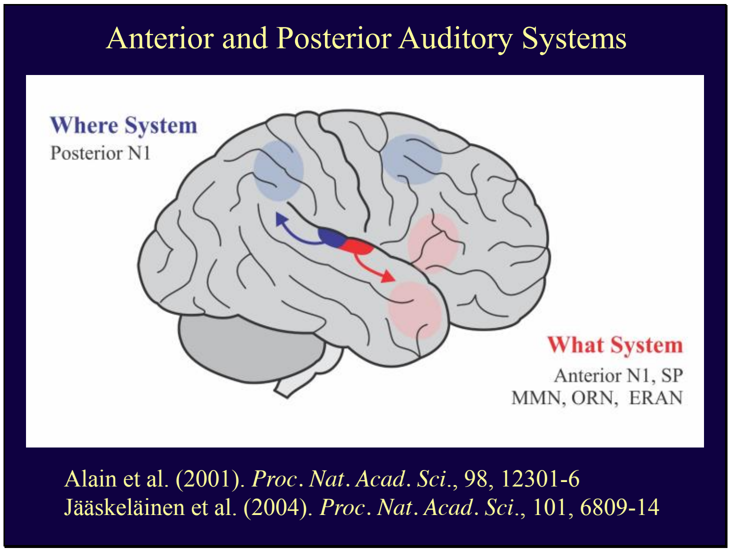
What is the meaning of it all? This is what you come to wonder when you get older. The following three slides will tell you what I understand about the workings of the auditory regions of the temporal lobe. This is a very simplified view of what happens in the cortex when input comes from the thalamus or from another region of cortex. Thalamic input typical causes an initial positive wave at the surface as the deeper regions of the cortex are activated. This is followed by ascending activation of the dendrites which results in a surface negative wave. Cortico-cortical connections give surface negative waves.

Slide 29



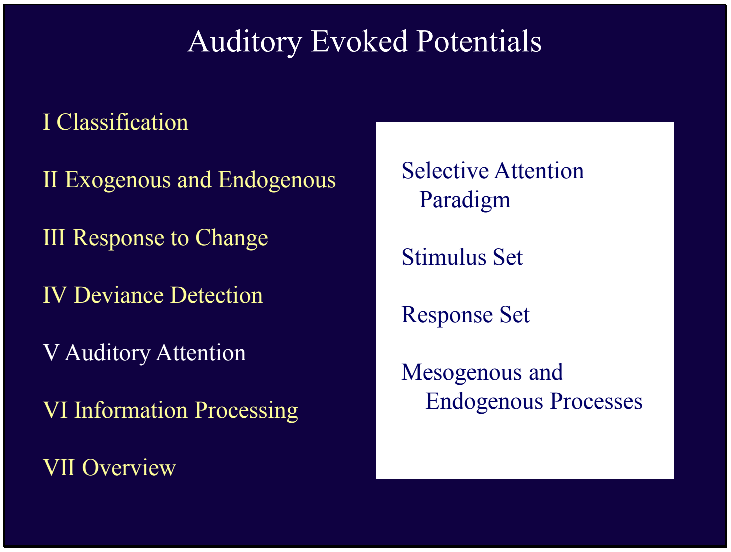
This is the superior surface of the left temporal lobe. The auditory cortex, located on Heschl's gyri is surrounded by closely connected belt and parabelt regions. I suggest that the activation of these areas proceeds from the primary regions to the belt and then to the parabelt. In the parabelt regions some of the fields will be oriented laterally rather than vertically. Thus we record from the vertex an N1b wave and from the temporal scalp a later N1c wave. The areas of the cortex are likely highly specialized so that particular regions in the belt or parabelt may process particular auditory features.

Slide 30



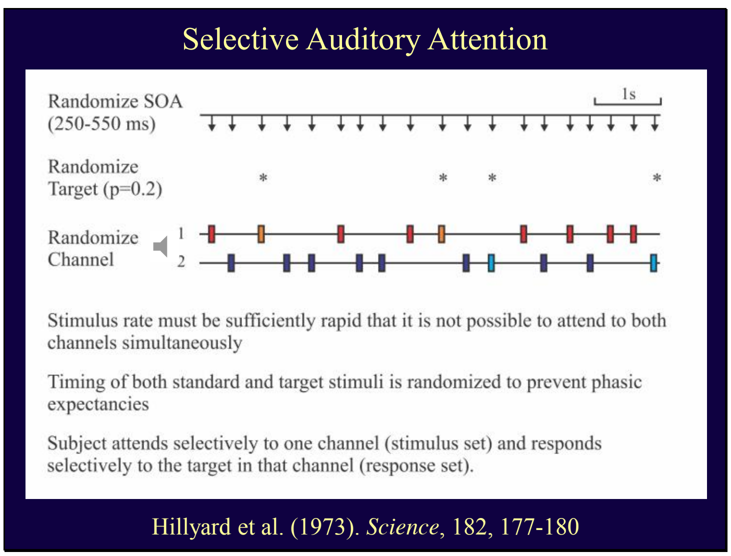
There is also a division between the posterior and anterior systems. The posterior system is concerned with detecting a sound and diverting attention to it. It reacts early and rapidly to tell us that a sound has occurred and where it is coming from. It mediates an early N1 wave. The anterior system is concerned with analyzing the nature of the sound. It reacts more slowly and tells us what the sound might be. It mediates multiple different negative waves – the anterior N1, the sustained potential. the MMN. the ORN. and the event-related anterior negativity (associated with musical processing).

Slide 31



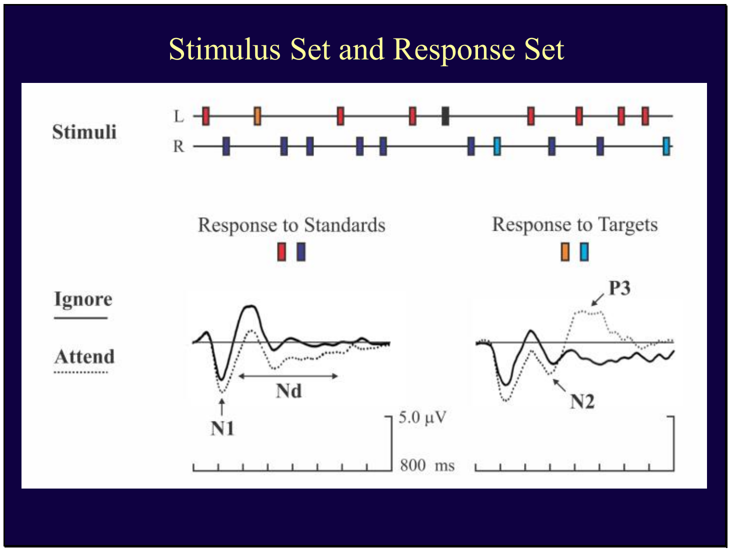
Now we understand how the auditory cortex functions, how does auditory attention work? We shall consider the process of selective attention and try to see these in the light of mesogenous and endogenous.

Slide 32



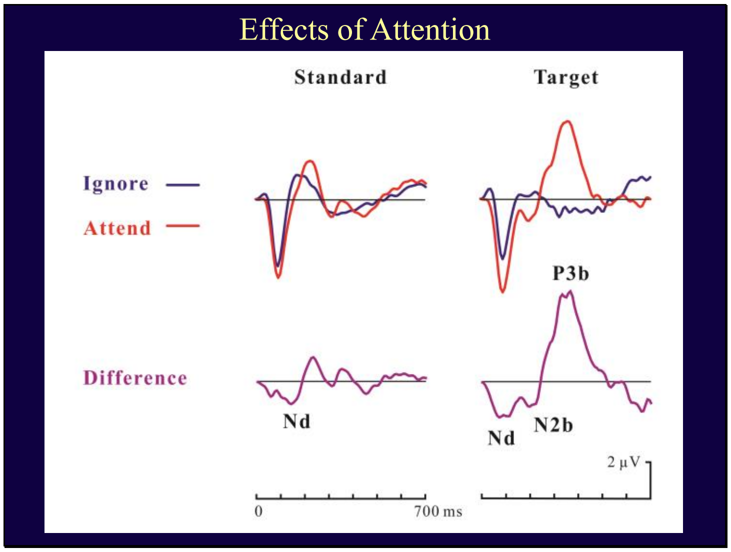
This slide illustrates the basic paradigm to study auditory attention. Stimulus rate … The timing … Subject … The sounds in this auditory example are presented in two different frequency channels. It is like a cocktail party for droids. The paradigm more typically presents the two channels in separate regions of space, but that is difficult in a lecture where the audience has no earphones. Selective attention is also difficult to tune. Therefore the example presents a train of low frequency sounds at the beginning so that you can settle your attention on the low frequencies.

Slide 33



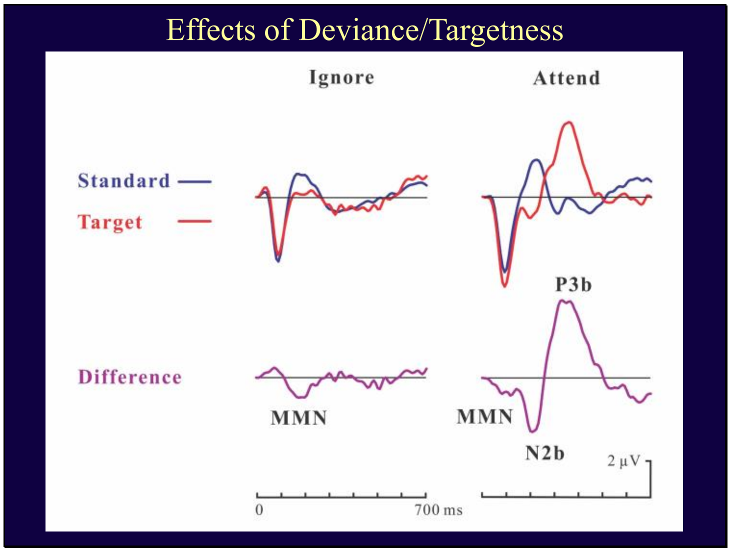
The basic findings are that the stimuli in the attended auditory channel evoke an enhanced N1 and a more prolonged negative wave that has been called the processing negativity or the Nd – the negative difference wave because it is measured in the attend-ignore difference waveform. The response to the targets elicits an additional N2 and P3 complex.

Slide 34



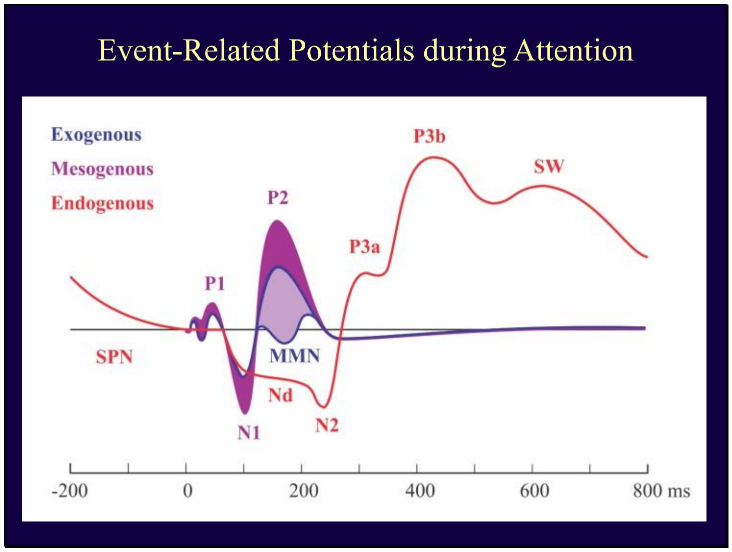
This shows the attend-ignore difference waves. For the standard an Nd wave by itself. For the target this leads into the N2-P3 complex as the target is successfully discriminated from the standard.

Slide 35



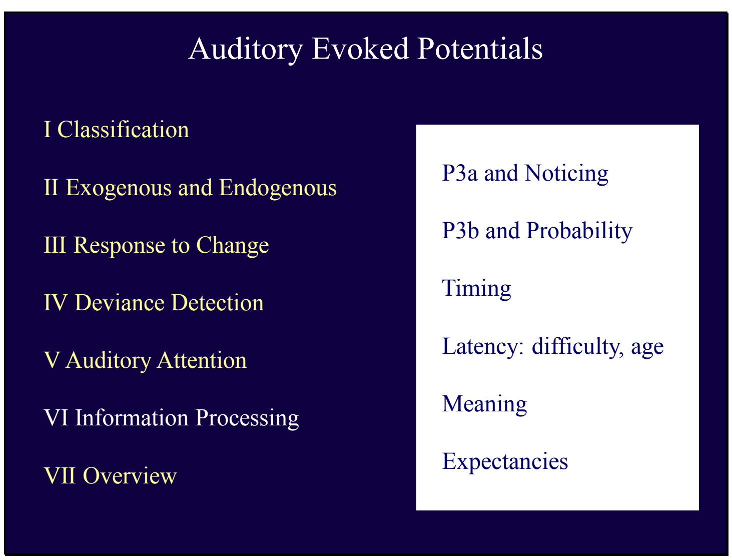
This shows the same waveforms but superimposed to compare target and standard. The difference waveform when the stimuli are ignored shows a MMN. For the attended stimuli the MMN leads to the N2-P3 complex.

Slide 36



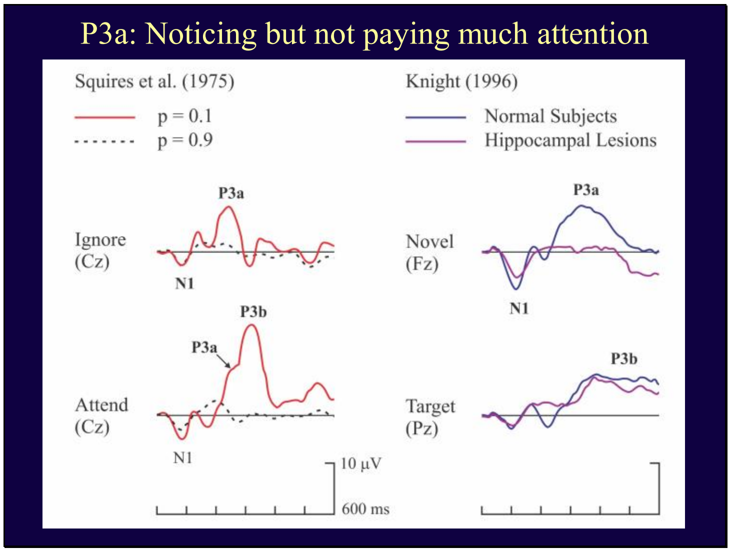
So we can return to the ancient Hillyard-Picton classification. There are a set of exogenous waves that are evoked by the stimuli – the N1, P2 and MMN. The N1 and P2 are affected by attention – we have therefore considered them mesogeonous. The Helsinki theory of the MMN is that it is not affected by attention. Since there is clear evidence that the MMN is sometimes susceptible to attention, I have made it mildly mesogenous. Superimposed on these waves are the endogenous components that reflect expectancies – the stimulus preceding negativity, processing – the Nd, detection – the N2, and the various responses to detection – P3a for noticing, P3b for updating working memory and Slow Waves for updating longer memories.

Slide 37



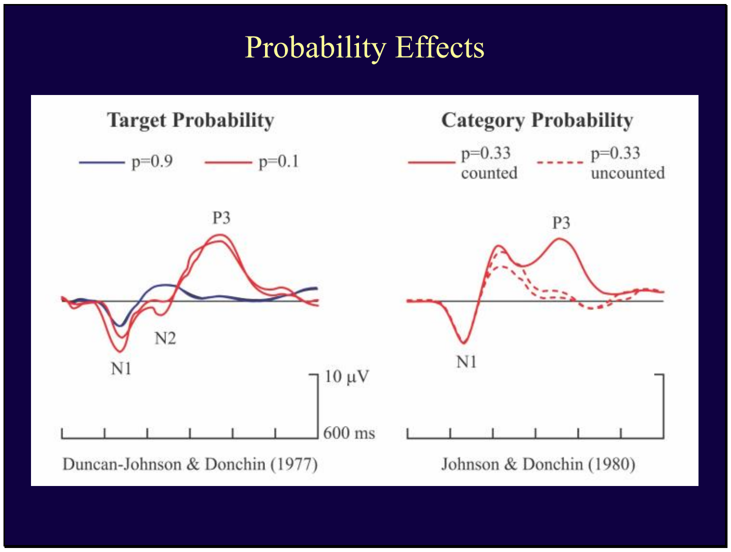
We have considered how the brain attends to auditory stimuli in order to obtain information. In our final set of slides we shall look at how this information is processed. Information is typically measured in terms of the inverse of the probability and so we shall be concerned with the EPs to the attended improbable target.

Slide 38



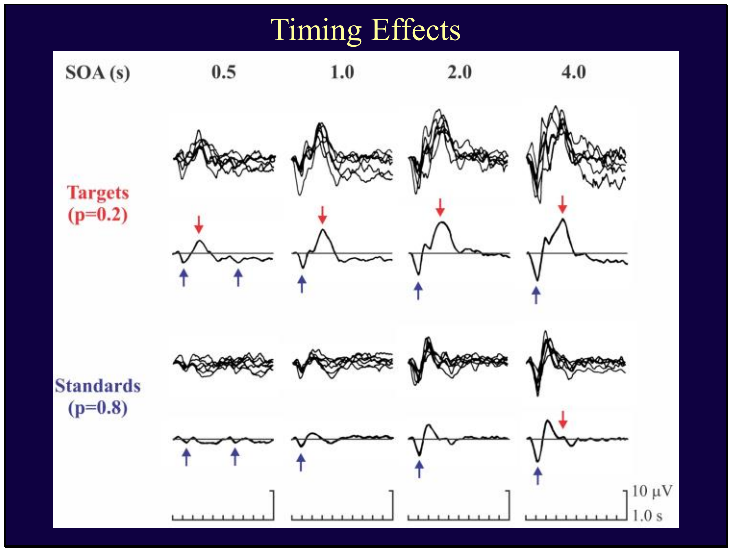
The first set of waves evoked by an informative stimulus is the N2-P3a complex. This is evoked by the improbable stimulus even when it is unattended. It appears to indicate that the stimulus has been noticed but deemed unworthy of further processing. It can be large when the stimulus is quite novel – then it is called the novelty P3. When the stimulus is task-relevant the P3a is followed by a P3b wave. These waveforms come from a Squires, Squires and Hillyard paper. The P3a seems to be generated in or dependent upon activity in the hippocampus. Bob Knight showed that patients with hippocampal lesions showed no P3a to novel stimuli but were still able to generate a P3b when detecting a target.

Slide 39



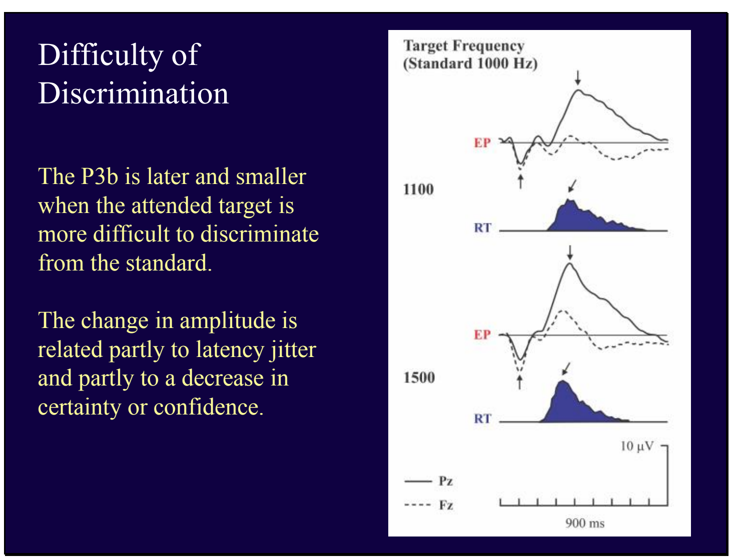
The P3 wave depends on the probability of the target. Even if the task is changed to detect the more probable stimulus it is the improbable one that elicits the P3. The probability depends on how the subject categorizes the stimuli. When there are three equiprobable stimuli but only one is to be counted, the P3 follows the counted stimulus. The others are categorized together as not to be counted.

Slide 40



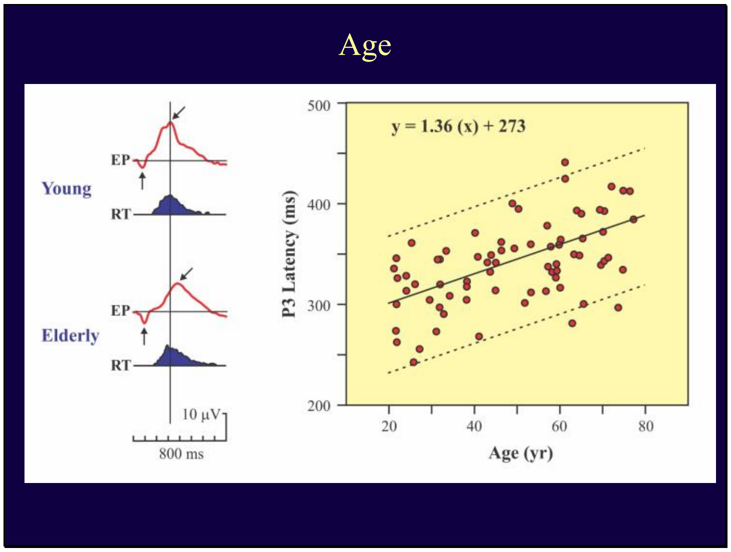
The P3 wave varies with the timing of the stimulus. If the target occurs with the same stimulus probability of 0.2 but with a longer SOA, the average interval between targets will be longer - every 20 seconds when the SOA is 4 seconds as compared to every 2.5 seconds when the stimuli come every half second. Recent findings by Gonsalvez and Polich (2002) have shown that the P3 wave on any given trial depends on the interval from the previous target.

Slide 41



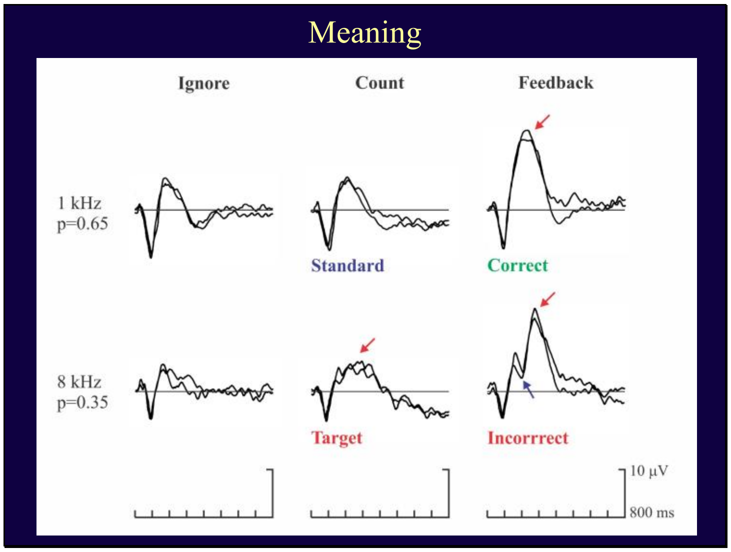
The P3b is later … The latency of the P3 depends on the time taken to discriminate between the target and the standard.

Slide 42



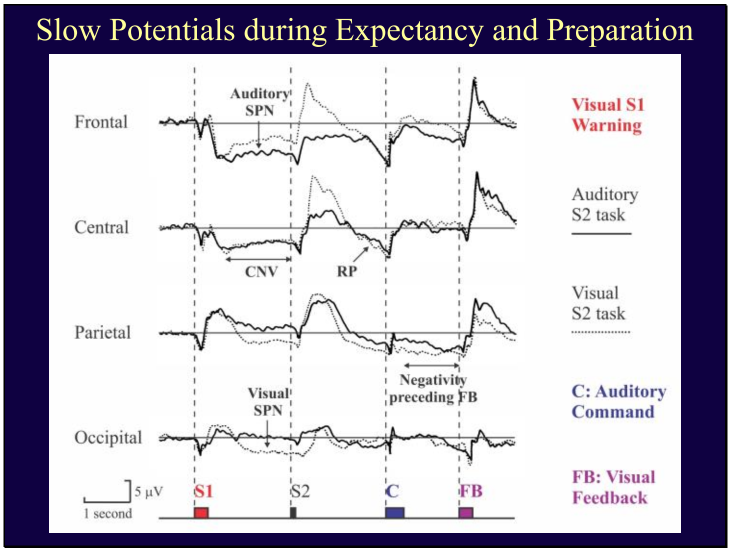
The term P300 comes from the normal latency of the P3 in an easy discrimination at the age of 20. The latency of the P3 wave increases with increasing age. Every birthday you can celebrate a 1.4 ms slowing in your P3. Interestingly this slowing can occur without concomitant slowing in motor speed.

Slide 43



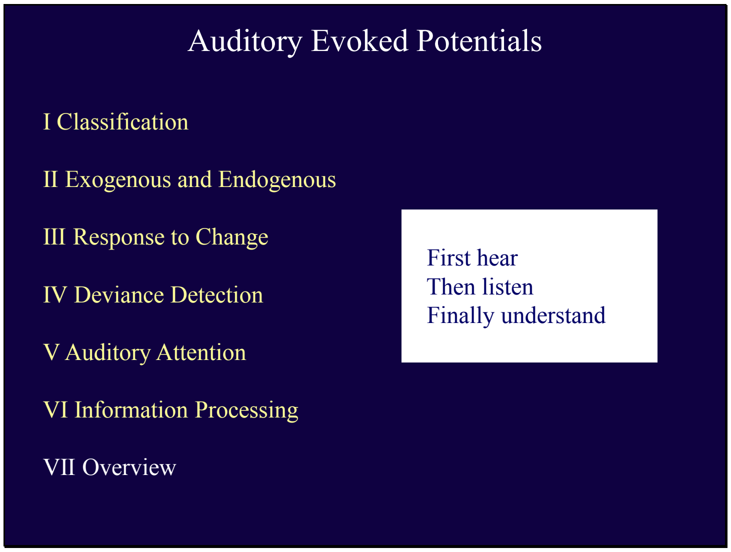
A final comment about the P3 is that its amplitude varies with how much the information means. In this experiment the same stimuli could be ignored, counted or used as feedback in a perceptual task. The P3 is much larger when the stimulus means more. Information that warrants a change in behavior also elicits a large N2 wave. A similar wave occurs in a go-nogo task when a subject inadvertently goes in response to the nogo stimulus.

Slide 44



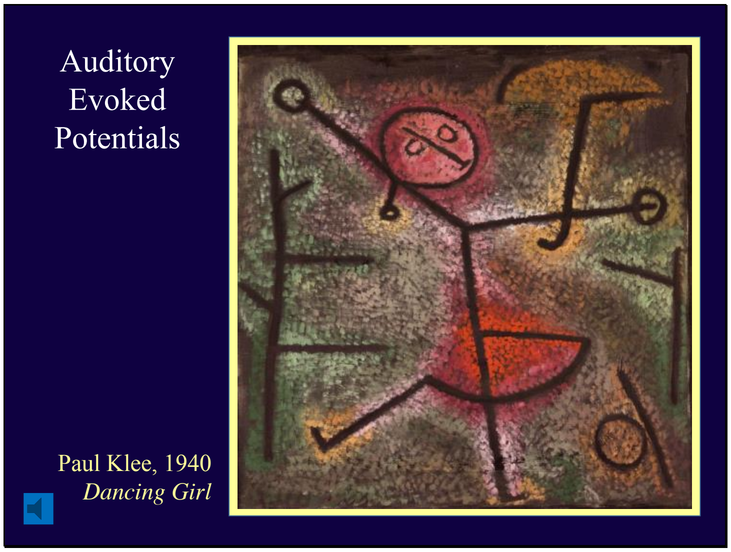
A final data slide shows an array of endogenous stimuli as the subject attends to a warning stimulus, gets ready to perform a sensory task, makes the decision, prepares to respond, responds and then awaits feedback. The sensory preceding negativity is frontal for the auditory task and posterior for the visual task. A contingent negative variation links the warning to the task stimulus. A Bereitschaftspotential or readiness potential precedes the motor response. The negativity preceding feedback is parietal in its distribution. Large positive waves follow the discriminated stimulus and the feedback. Thus can we follow the workings of the human brain.

Slide 45



We have considered the different components of the auditory EPs, concentrating on the distinction between exogenous, mesogenous and endogenous components. The N1-P2 is a response to simple change such as the onset or offset of a sound. The MMN relates to a change in stimulus from those that have been occurring before. Attention brings a host of endogenous components: stimulus preceding negativity, Nd, N2, P3. The largest of these is the P3 wave which is related to the processing of information into meaning.
The overview is hear, listen, understand – exogenous, mesogenous, endogenous.

Slide 46



One of Paul Klee's last paintings. If we listen properly to the music that we hear, we understand that we should dance