Assumptions of ERP averaging/signal averaging

ERP is linear combination of signal plus noise

Signal is independent of noise

Signal is invariant across trials

Noise is random across trials

Categorical Targets

The target in an oddball task need not be the same physical stimulus. **It can be a member of some category**. In that case, P3 amplitude is related to the (subjective) probability of the relevant stimulus category, and not the probability of the individual stimulus

e.g., the number 2
even numbers
multiples of 2
members of the category: fruits, animals, green things, etc.
synonyms of “encourage”

ODDBALL TASK

Only 1 specific target letter

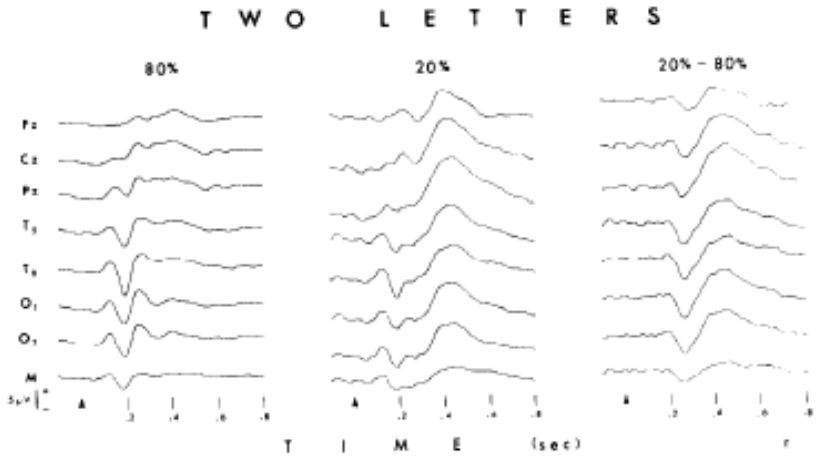


Fig. 1. Grand Mean ERPs obtained for 1-Target Oddball, at all recording sites, associated with the 80% standard stimulus (left column), the 20% target stimulus (middle column), and the difference waveforms obtained by subtracting the ERPs elicited by the non-target stimulus from the ERPs elicited by the target stimulus (right column). In this and subsequent figures, the arrow on the time scale indicates stimulus onset.

25 different target letters

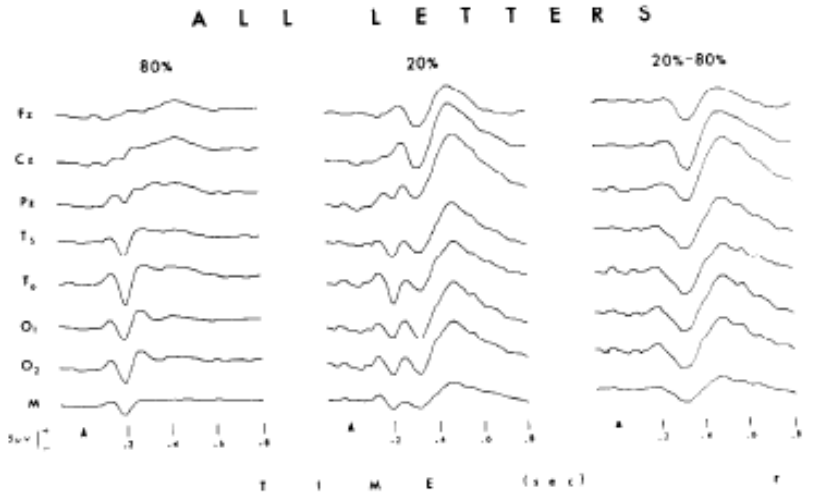


Fig. 2. Grand Mean ERPs obtained in 25-Target Oddball, at all recording sites, associated with the 80% standard stimulus (left column), the 20% target stimuli (middle column), and the difference waveforms obtained by subtracting the ERPs in the left column from the ERPs in the middle column (right column).

Note positive up

Ritter lab

Factors influencing P3 amplitude

- Subjective Probability

- Stimulus/event probability
  - global probability
  - sequential probability
  - temporal probability

- Motivational Significance (Stimulus Meaning, Salience)

- Task Relevance (attention)

Note: factors above are not necessarily independent of each other: subjective probability might be influenced by stimulus categorization, sequence, payoff matrix, interstimulus interval, among other factors

P3 and task relevance/attention

Effects of subjective probability and motivational significance are modulated by amount of attention paid to the stimulus.

Attention typically required to observe P3 to target events.

Stimuli that capture attention elicit large P3

Functional significance of P3b

- ***Context Updating (Donchin, Coles):*** reflects the updating of a mental model of the environment that is maintained in working memory by attentional systems; P3 elicited as soon as there is enough information to suggest a need to update working memory.

- ***Template Matching (Chao & Knight; Hillyard):*** match incoming stimulus to target representation in working memory

- ***Event categorization (Kok):*** engagement of event categorization network that is controlled by joint operation of *attention* and working memory. P3 amplitude reflects attentional capacity invested in **categorization** of a task relevant event

- ***Decision Monitoring (Verleger)*** has renounced his closure hypothesis and replaced it with the view that the P3 process bridges perceptual and response processing; specifically, P3 reflects monitoring that the first decision to classify some stimulus and act accordingly has led to appropriate processing steps.

Common across all views*: When a P3b is observed there has been conceptual encoding of stimulus into working memory.*

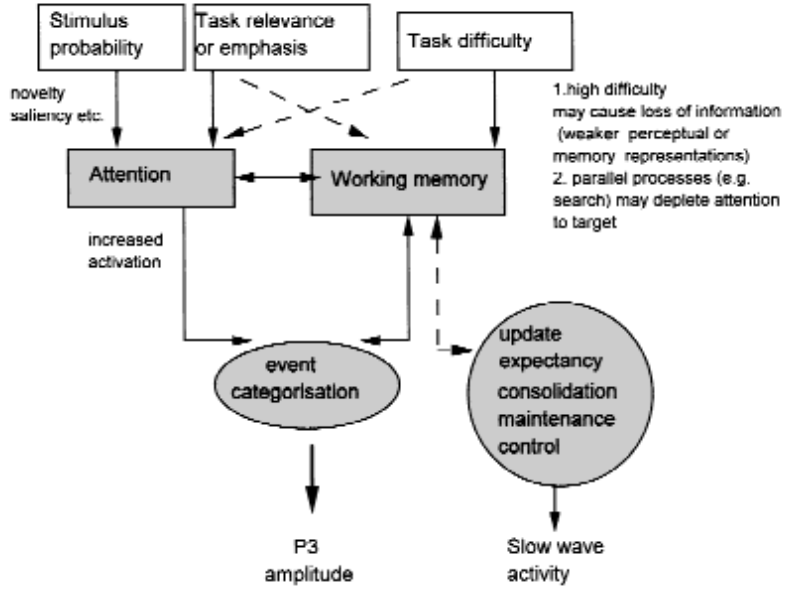


Figure 4. A simplified diagram describing the major determinants of P3 amplitude (white boxes), the underlying mechanisms (dark boxes), and their effects on the event categorization process. Event categorization is conceived of as a process that involves a comparison between the external stimulus and an internal representation, and that is elicited by target as well as nontarget (or even novel) stimuli. Low probability (or high saliency and novelty) of events and task relevance (left) are assumed to increase activation of neural assemblies associated with event categorization, thus leading to larger P3s. Conversely, task difficulty (right) is assumed to counteract this process, leading to smaller P3s. It is further assumed that slow wave activity is associated with a variety of working memory processes (e.g. encoding, update, search) that are under executive control and that run in parallel or precede event categorization. See text for further explication.

Kok

When a P3b is observed there has been conceptual encoding of stimulus into working memory.

Table 1. P300 amplitude and latency biological determinants.

FACTOR	AMPLITUDE	LATENCY	COMMENT
Natural			
Circadian	Indirect	Indirect	Circadian body changes affect P300 measures
Body Temperature	No	Yes	Increased temperature, decreased latency
Heart Rate	No	Yes	Faster heart rate, decreased latency
Food Intake	Yes	Some	Amplitude increases, latency shorter
Activity Time	Yes	Some	Food interacts with activity preference time
Ultradian	Some	Yes	90 min latency cycles
Seasonal	Yes	No	Seasons with light, increased amplitude
Menstrual	No	No	Neutral stimuli, no effects
Induced			
Exercise	Indirect	Direct	Affects overall arousal level
Tonic	Yes	Yes	Increases amplitude, decreases latency
Chronic	No	Yes	Decreased latency, variable results across studies
Fatigue	Yes	Yes	Decreased amplitude, increased latency
Drugs (Common)	Yes	Yes	Specific drug, arousal level, tonic/chronic use
Caffeine	Some	Yes	Amplitude increases if fatigued, latency decreases
Nicotine	Small	Yes	Weak amplitude effects, latency decreases
Alcohol			
Acute	Yes	Yes	Amplitude decreases, latency increases
Chronic	No	No	Social drinking: No permanent long-term effects
Alcoholism Risk	Yes	No	At-risk: smaller amplitudes with visual tasks
Constitutional			
Age	Yes	Yes	Modality, task, response parameters important
Children	Yes	Yes	Amplitude increases, latency decreases
Adults	Yes	Yes	Amplitude decreases, latency increases
Intelligence	Yes	Yes	Amplitude from complex tasks smaller for more intelligent, latency shorter for perceptual/speeded classification tasks for more intelligent
Handedness	Yes	Yes	Amplitude: left > right for frontal/central sites Latency: left < right for frontal/central sites
Gender	Small	Small	Amplitude: female > male, latency: female < male
Personality	Yes	No	Amplitude: introverts < extroverts
Genetic	Yes	Yes	Amplitude and latency genetically determined

Adapted from Polich, J., and Kok, A. (1995). Cognitive and biological determinants of P300: An integrative review. *Biological Psychology, 41*, 103-146.

Recent meal? Season? Exercise? Alcohol? At risk for alcholism?

According to Polich and colleagues:

Intrasubject test-retest reliability

P3 amplitude: .5-.8
P3 latency: .4-.7

Difficulty for cross session comparisons!

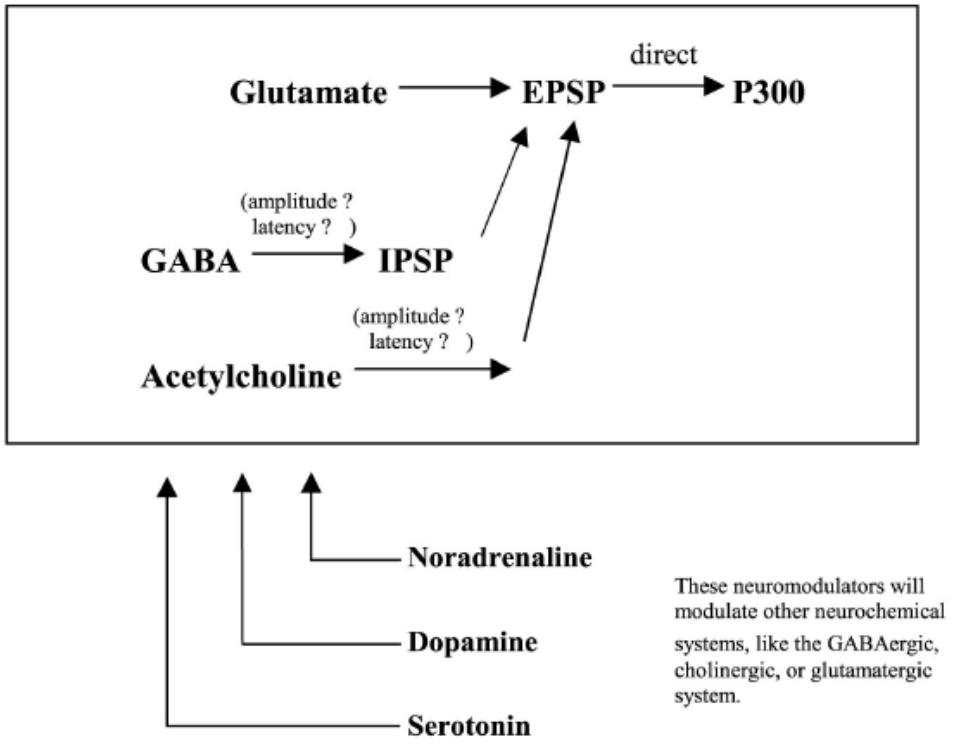
Lots of studies on pharmacological effects!

Table 1: The Effects of Pharmacological Manipulations on the P300 potential in humans.

Drug	Action	Modality	Effect on P300	Reference
Monoamines:				
MP	Increases CA activity	Visual	No effect on latency	Naylor et al. (1985)
Amph	Increases CA activity	Visual	No effect on latency	Halliday et al. (1987)
Cocaine	Increases CA activity	Auditory	Decreased amplitude No effect	Herning et al. (1985); Herning et al. (1987)
Yohimbine	Increases NE activity	Visual	Decreased latency	Halliday et al. (1994)
Clonidine	Decreases NE activity	Visual Auditory	Increased latency Decreased amplitude	Halliday et al. (1994) Duncan & Kaye (1987); Joseph & Sitaram (1989)
Antidepressants:				
Fluoxetine	Affects 5-HT	Auditory	Decreased amplitude	d'Ardhuy et al. (1999)
Tineptine	Affects 5-HT	Auditory	Decreased amplitude	
Clomipramine	Affects 5 HT, other monoamines, ACh systems	Auditory	Decreased amplitude, but showed no additional diminution after 8 days.	
Apomorphine	DA agonist	Auditory	No effect	Luthringer et al. (1999)
Methsergide	5-HT antagonist	Auditory	No effect	Meador et al. (1989)
Cholinergic:				
Scopolamine	ACh antagonist	Auditory Visual	Increased latency & Decreased amlitude Increased Amplitude	Meador et al. (1987; 1989) Callaway et al. (1985)
Benzodiazepine:				
Triazolam	BDZ hypnotic, GABA agonist	Auditory	Decreased amplitude	Hayakawa et al. (1999)

Abbreviations: MP, methylphenidate; Amph, amphetamine; DA, dopamine; NE, norepinephrine; 5-HT, serotonin; LC, CA, catecholamine; BDZ, benzodiazepine; GABA, gamma-amino butyric acid; ACh, acetylcholine.

Neurochemical substrates of P3 generation



Glutaminergic neurotransmission directly causes the EPSPs responsible for P3 activity. These EPSPs, and as a consequence the P3 are modulated directly and indirectly by acetylcholine and GABA. The, adrenergic system and with minor importance the dopaminergic and serotonergic systems have modulatory influence on indirect effects of ACH and GABA systems. Frodl-Bauch et al. 1999

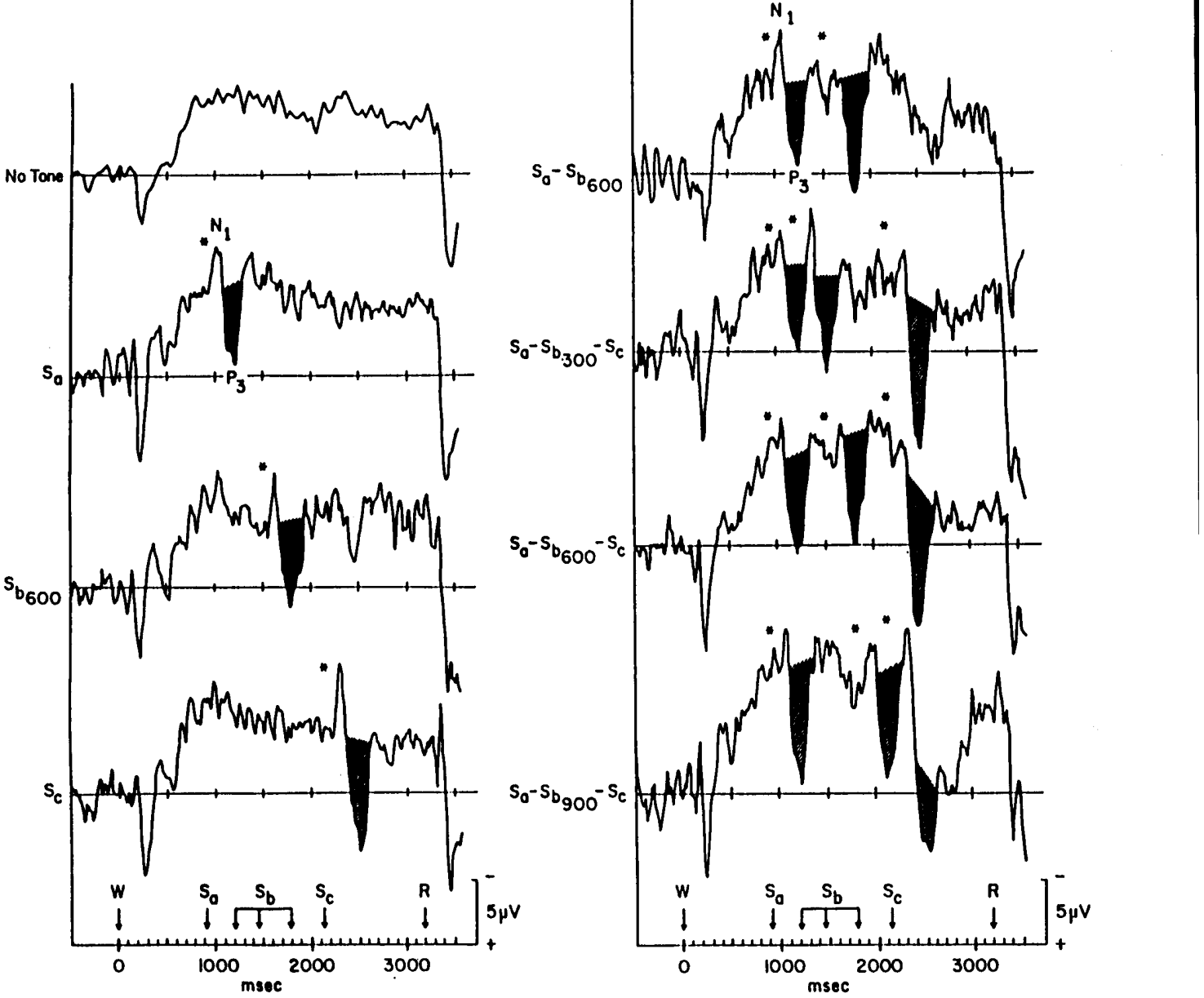


FIG. 29. Event-related potentials elicited by near-threshold tones presented on a random basis at specific times after warning flash (W). On each trial there could be either 0 (*top left tracing*), 1 (*second* through *fourth left tracings*), 2 (*top right tracings*), or 3 (*second* through *fourth right tracings*) tones presented at times indicated by •. Subjects reported the number of tones perceived after a subsequent response cue (R) appeared. *Arrows*, Sa, Sb, and Sc, time points at which tones might occur. The Sb stimulus could occur 300, 600, or 900 ms after the Sa stimulus. Grand-average vertex recordings from 5 subjects. [Adapted from Woods et al. (535).]

SIGNAL DETECTION

Attended, task relevant, target events elicit a P3 (P3b), what about task irrelevant, or infrequent or surprising or novel events?

Fractionating the P300

Squires, Squires & Hillyard (1975) – P3a (and P3b)

Courchesne et al. (1975) - novelty P3

Note positive up

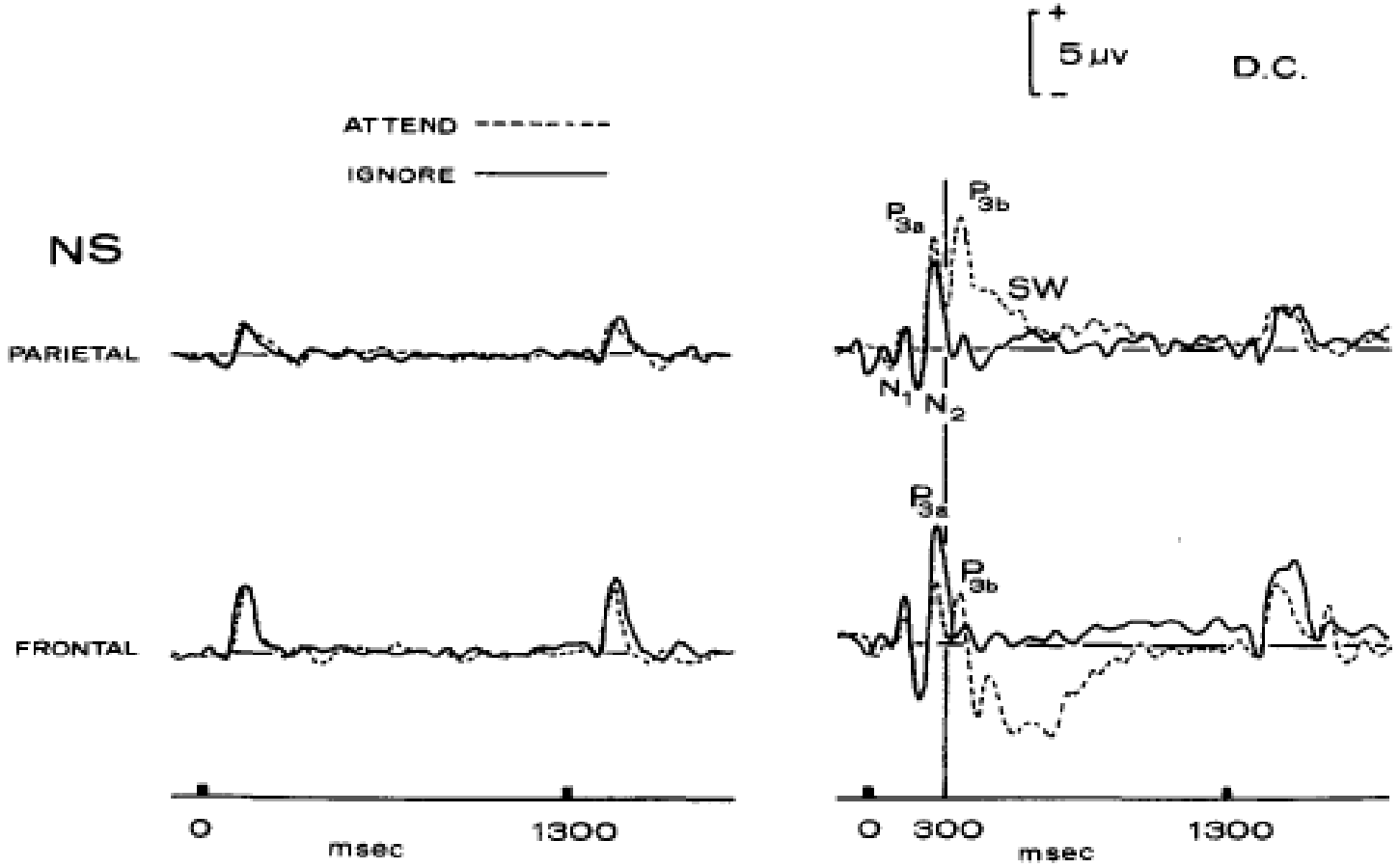


Fig. 6. D.C. recordings for subjects ES and NS at two electrode locations, parietal and frontal. The loud stimulus occurred frequently ($P = 0.9$) and the soft stimulus was rare ($P = 0.1$). On the left are responses to two consecutive loud stimuli (solid line for the ignore condition, dashed line for the attend condition). On the right are responses to the soft stimulus followed by a response to the loud.

ODDBALL PARADIGM: Loud Tone p=.9; Soft tone p=.1

Note positive up

Attention?
Probability?
Attn x probability?

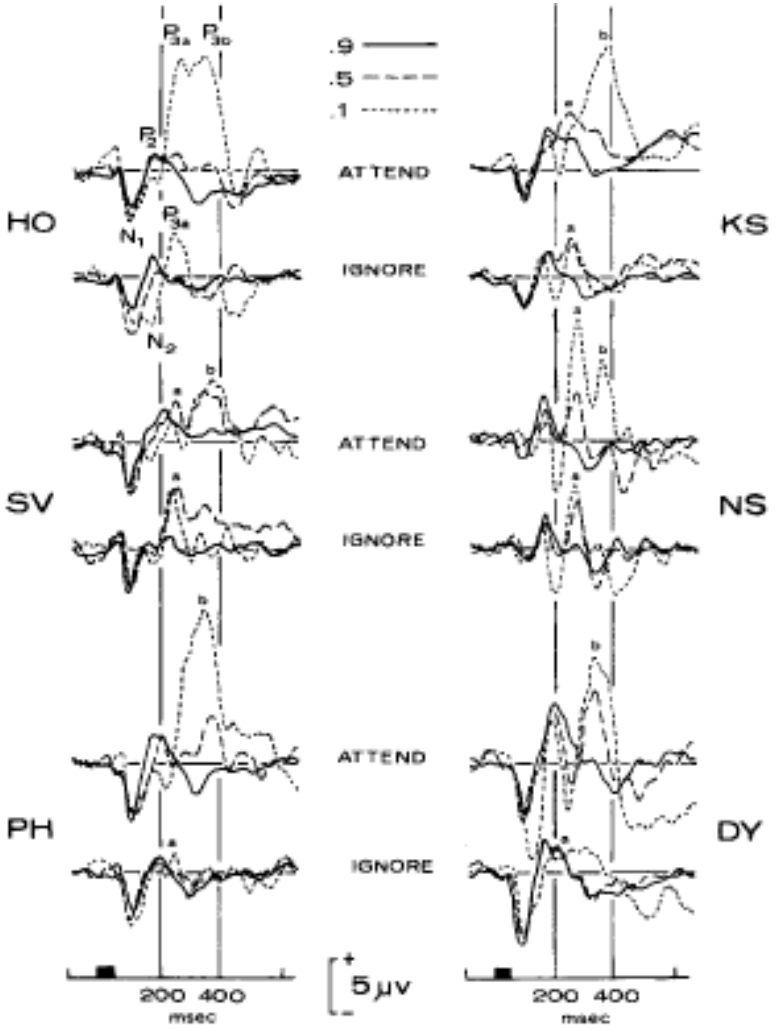


Fig. 2. The effect of stimulus probability on the vertex evoked responses in the ignore and an attend condition where that stimulus is counted, for six subjects. Responses associated with the three probabilities of each stimulus are superimposed. The components labeled by the abbreviations "a" and "b" are P_{3a} and P_{3b}, respectively. The vertical calibration is 5 μV for all subjects except NS, for whom it is 10 μV in all figures.

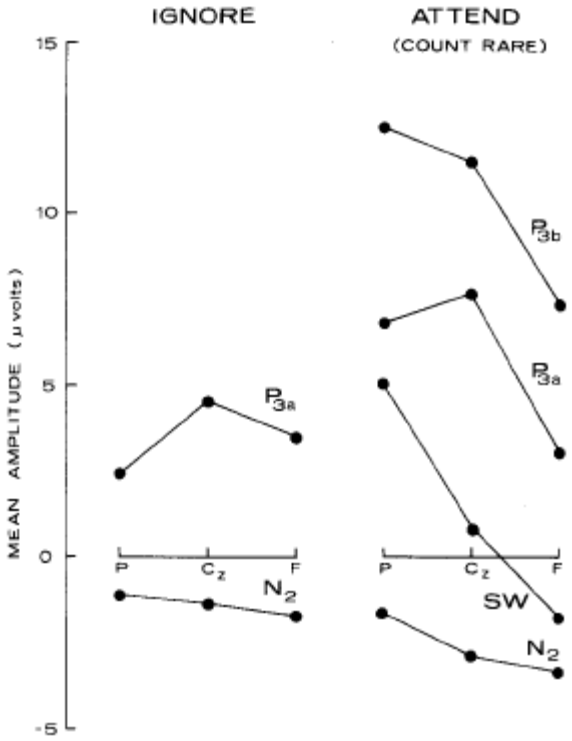
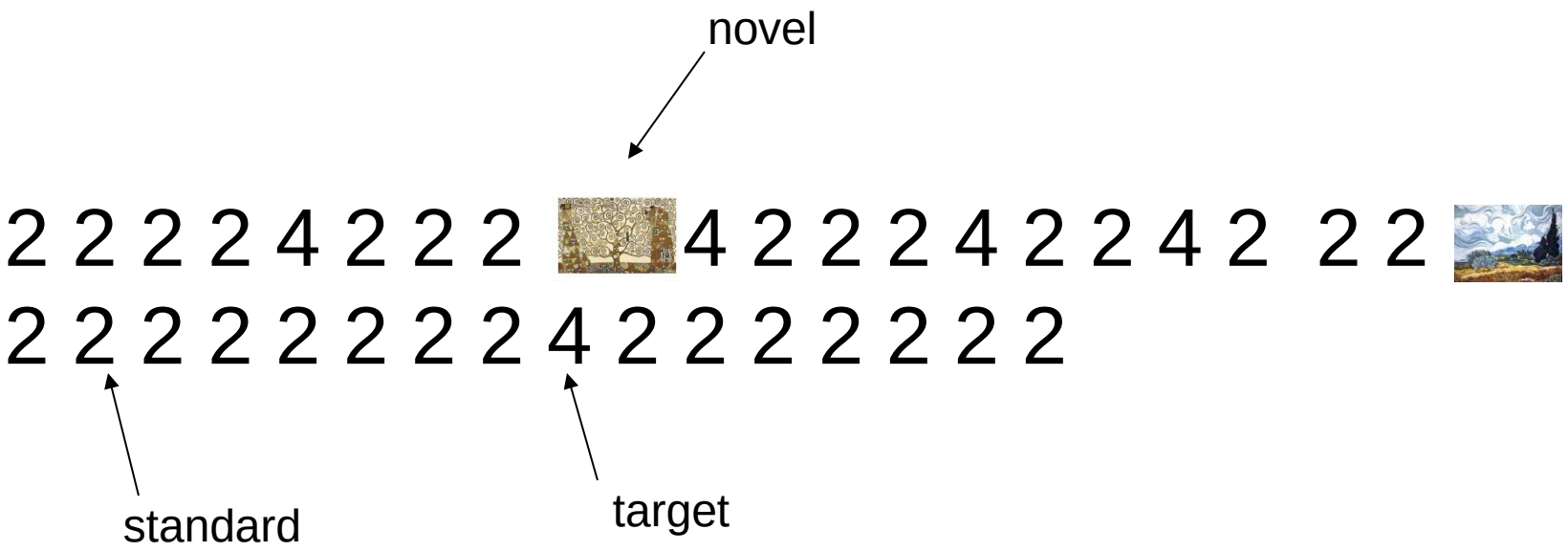


Fig. 5. The mean amplitudes of the late components evoked by infrequent stimuli ($P = 0.1$) at the three electrode locations, parietal (P), vertex (C_z), and frontal (F), averaged across subjects and across stimuli (loud and soft). "SW" stands for slow wave (see text for explanation).



Standard=80%, target=10%, novels=10%

Novels – colorful pictures shown only once each

Parietal P3 Frontal P3

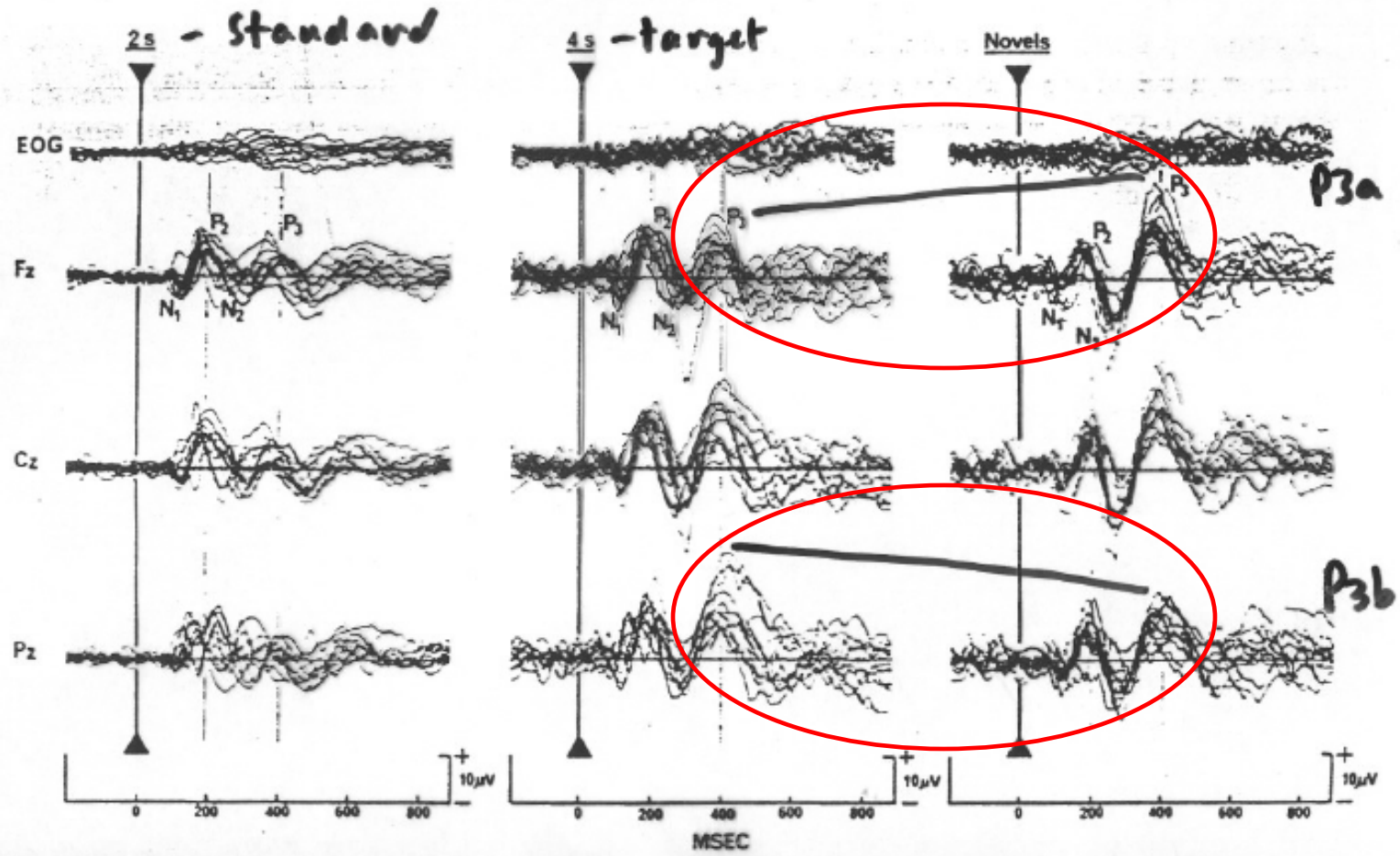
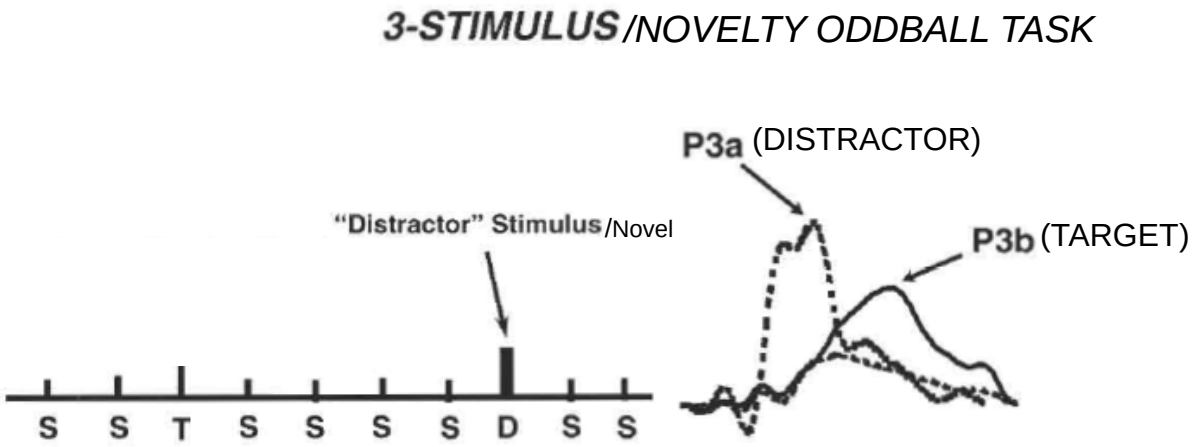


Fig. 2. Evoked responses to 2, *4*, and *novel* slides in the count-*4* condition. Each trace to the *4* and *novel* slides represents an average of 15 responses for one subject; those to the 2s are averages of 120 responses. 15 subjects. A.C. recordings.

Note positive up



From Polich

(S) **STANDARD**, HIGH PROBABILITY EVENT
(T) LOW PROBABILITY, **TARGET**, DEVIANT
(D or N) IMPROBABLE SERIES OF UNIQUE, UNEXPECTED, **DISTRACTOR** OR **NOVEL** EVENTS

P3a, novelty P3, frontal P3	**P3b, classical P3, target P3**
Occurs early 250-280 ms - 60-80 ms before P3b	Occurs ~300+, variable latency - after P3a
Fronto-central or flat distribution	Centro-parietal distribution
Habituates with repetition	Does not habituate with repetition
Deviant, oddball non-target event, even without attention	Task relevant, target events, w/ attention, or capturing of attention
3-stimulus (novelty oddball) task, (standard, improbable target, & improbable or novel deviant)	Oddball task, binary decision, signal detection, attention tasks, visual search task, memory search tasks
Associated with novelty or orienting	Associated w/ expectancy, context updating, event categorization, decision making
Involuntary shifts of attention to changes in environment	Voluntary shifts of attention to changes in environment; involuntary if noxious
Lateral prefrontal cortex, hippocampus	Temporo-parietal junction

VISUAL

Note positive up

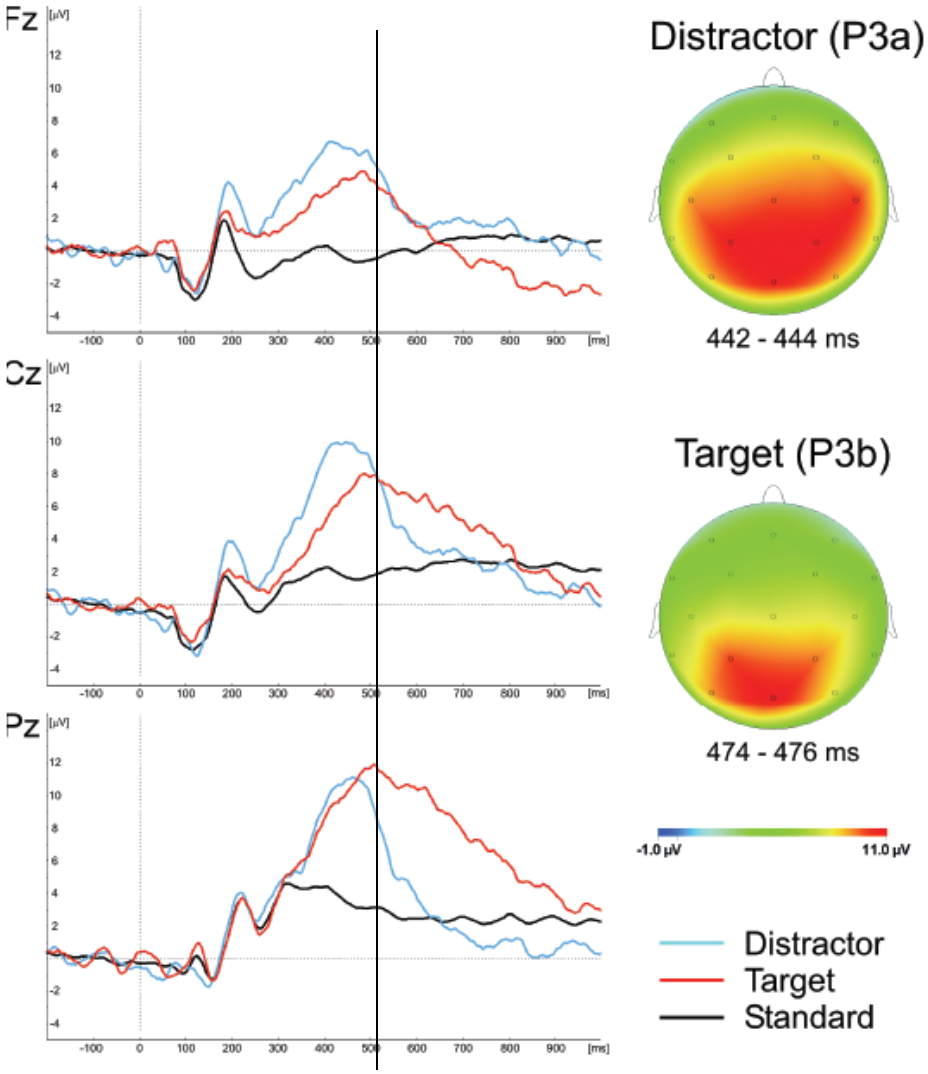
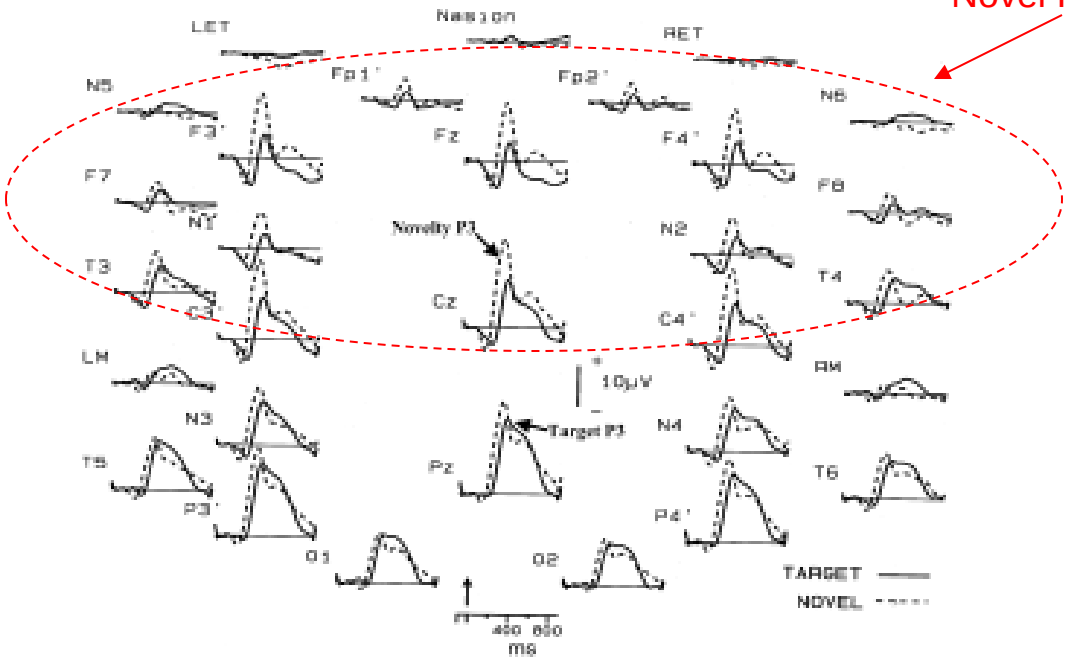


Fig. 2. *Left* panel, Grand average event-related potentials from three midline electrodes (Fz, Cz, Pz) of the distractor, target, and standard stimuli of a visual three-stimulus oddball paradigm. *Right* panel, Scalp potential maps at 442–444 and 474–476 ms after stimulus onset (corresponding to the respective peak latencies) for distractor and target stimuli. Small circles indicate electrode positions on the scalp. Note the earlier peak of the P3a and its more frontal topography. From Bledowski, Prvulovic, Goebel, and others (2004) with kind permission of Elsevier.

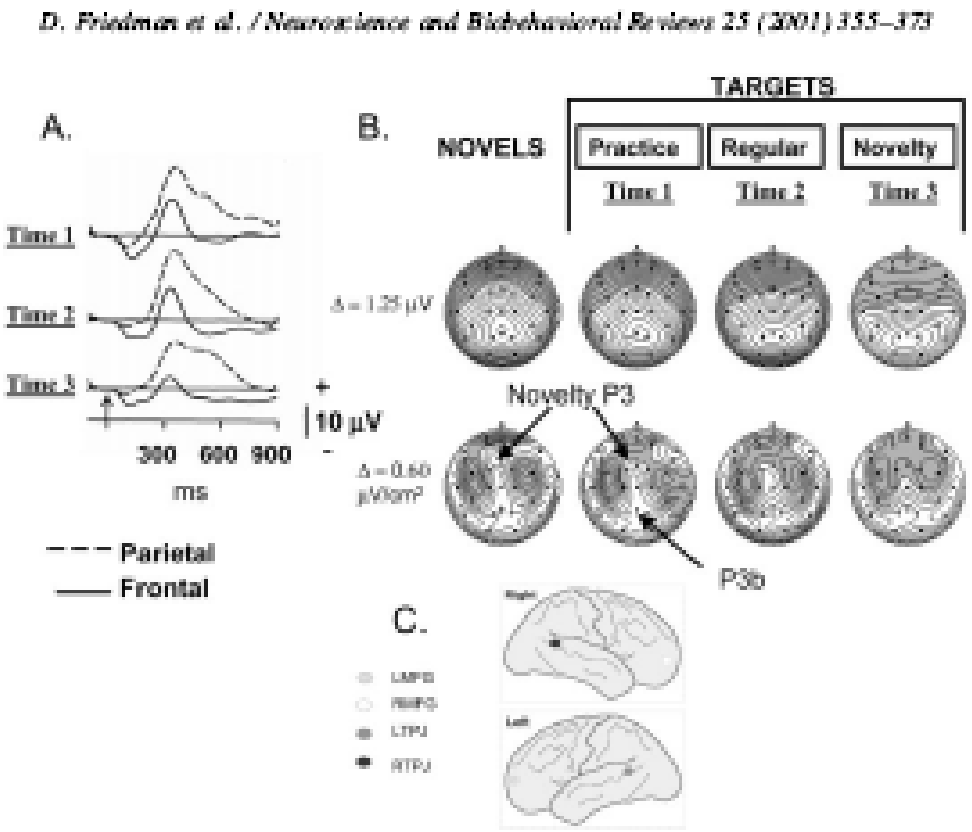
Friedman & Fabiani: 3 stimulus novelty (auditory) oddball task

Novel P3 larger especially frontally



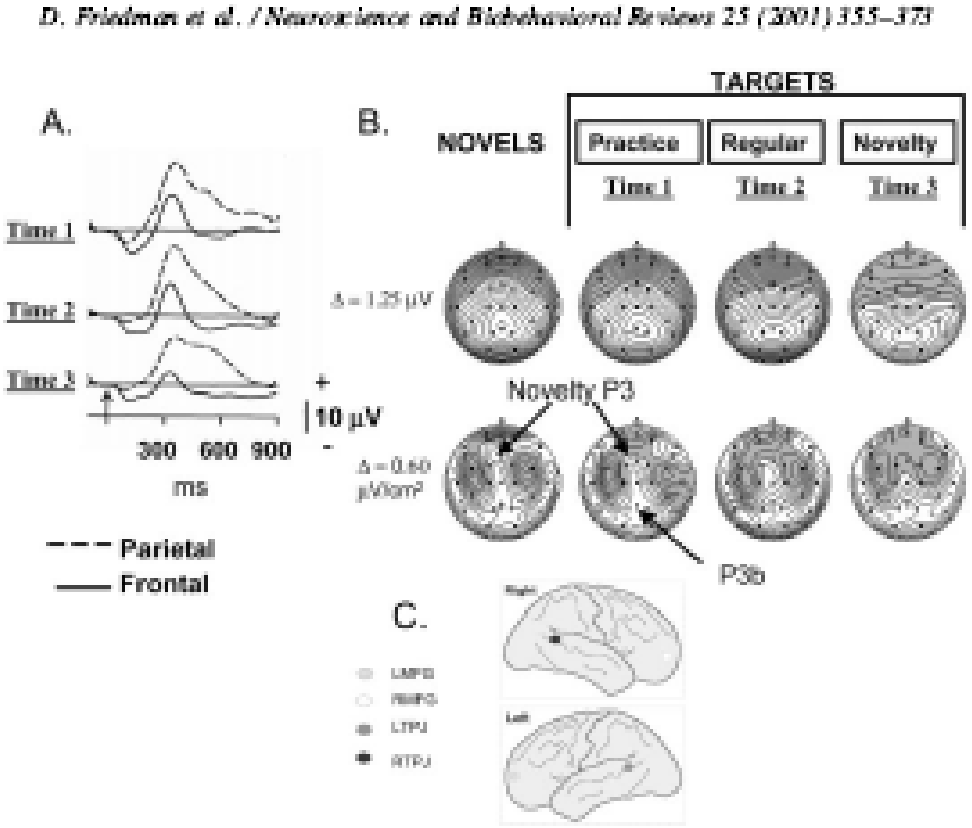
Note positive up

Target and Novelty P3 across time



Note positive up

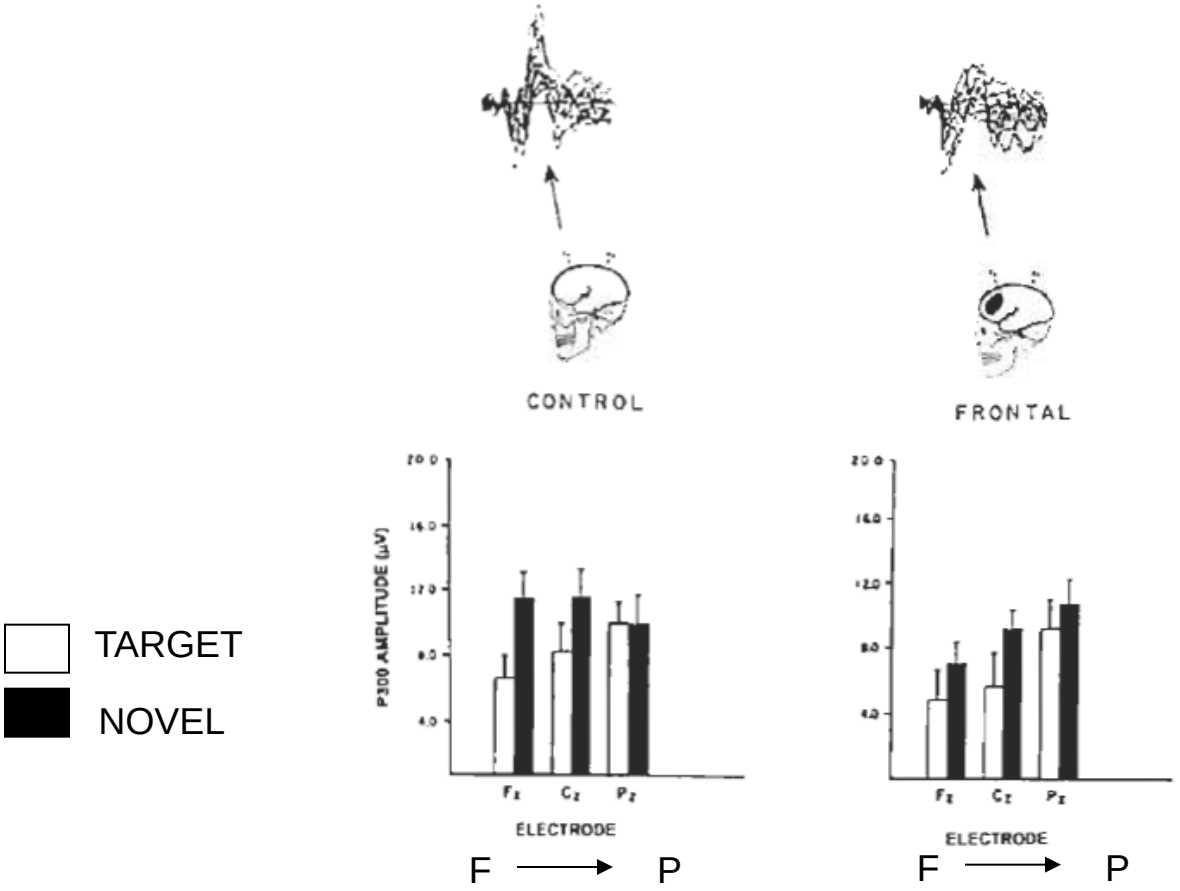
Target and Novelty P3 across time



A. Frontal P3 decreases with time; Parietal P3 unchanged with time
B. Over time, frontal component of target P3 disappears

P3a & P3b not only have different scalp distributions but differ functionally: vary in response to habituation, familiarity, attention

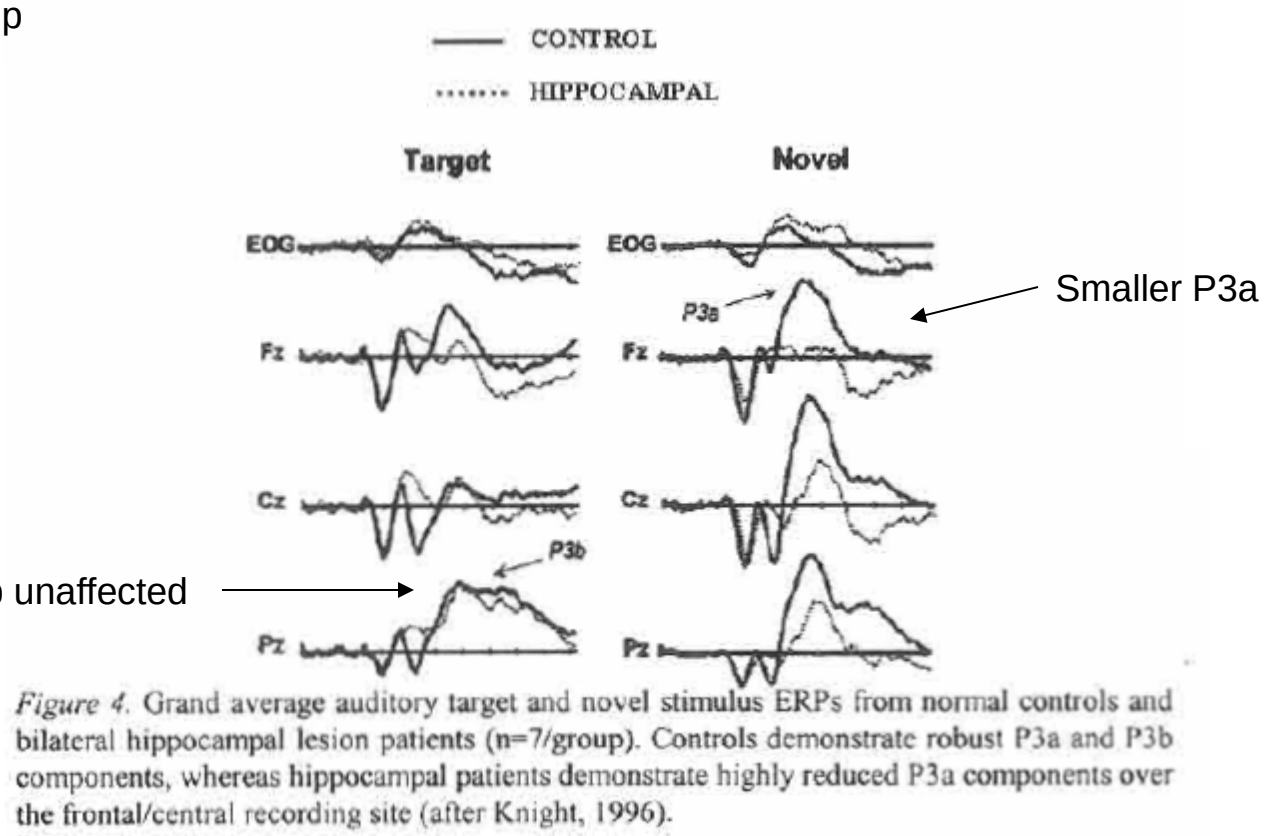
FRONTAL LESIONS



Frontal lesions reduce P3a but not P3b

HIPPOCAMPAL LESIONS

Note positive up

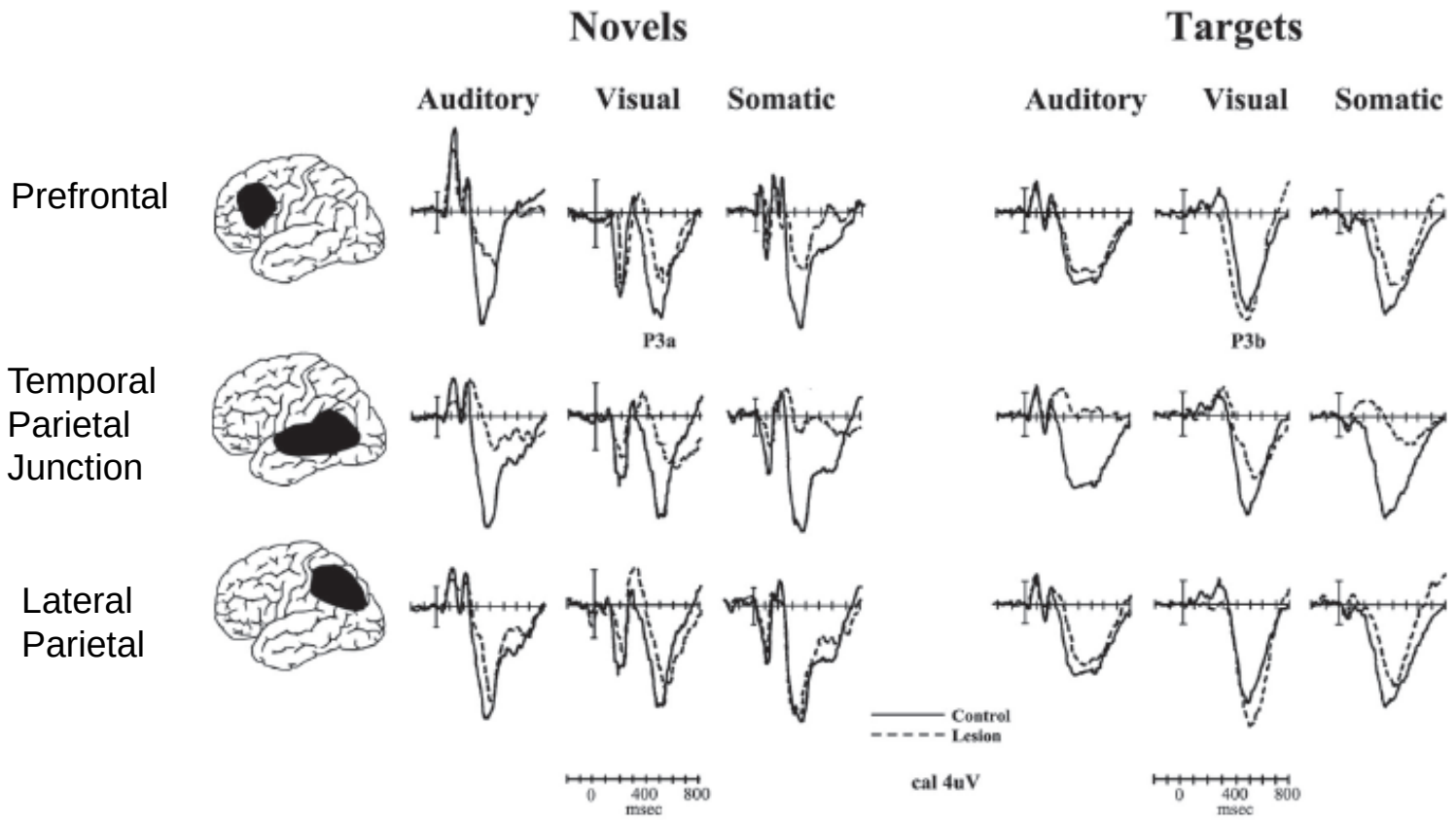


Smaller P3a

P3b unaffected

Figure 4. Grand average auditory target and novel stimulus ERPs from normal controls and bilateral hippocampal lesion patients (n=7/group). Controls demonstrate robust P3a and P3b components, whereas hippocampal patients demonstrate highly reduced P3a components over the frontal/central recording site (after Knight, 1996).

Knight hypothesis: P3a generation requires frontal lobe attention mechanism and hippocampal processes driven by novelty information processing


Novels
Targets
Auditory
Visual
Somatic
Auditory
Visual
Somatic
Prefrontal
Temporal Parietal Junction
Lateral Parietal
P3a
P3b
Control
Lesion
0
400
800
msec
cal 4uV
0
400
800
msec

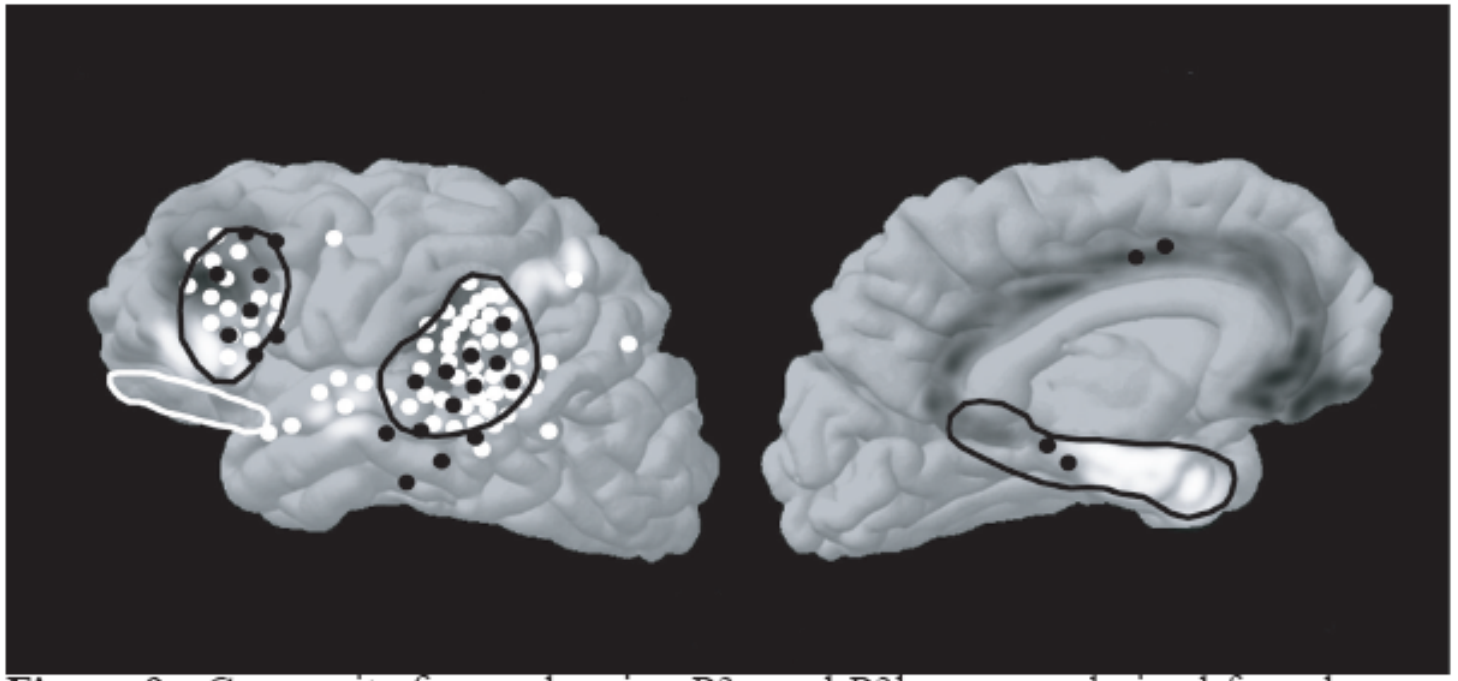


Figure 9. Composite figure showing P3a and P3b sources derived from human lesion studies, intracranial recordings, and fMRI studies. See figures 2, 3, and 8 for details.

Outline – lesion, shading – intracranial recordings, dots – fMRI; white-P3b, black-P3a

P3 composed of two functionally distinct potentials (P3a, P3b). Multiple cortical (and some subcortical generators) give rise to each.

Possible P3 generators – converging evidence

Intracranial recordings

(1) steep gradients and polarity inversions in medial temporal lobe structures (hippocampus, amygdala)
(2) Many cortical areas, especially
  (a) temporal parietal junction (TPJ) including supramarginal gyrus and caudal parts of superior temporal gyrus and adjacent areas
  (b) lateral prefrontal gyrus

Lesion data

(1) Hippocampal damage does NOT affect P3b, does reduce P3a
(2) TPJ damage reduces P3b and P3a
(3) Prefrontal damage reduces P3a

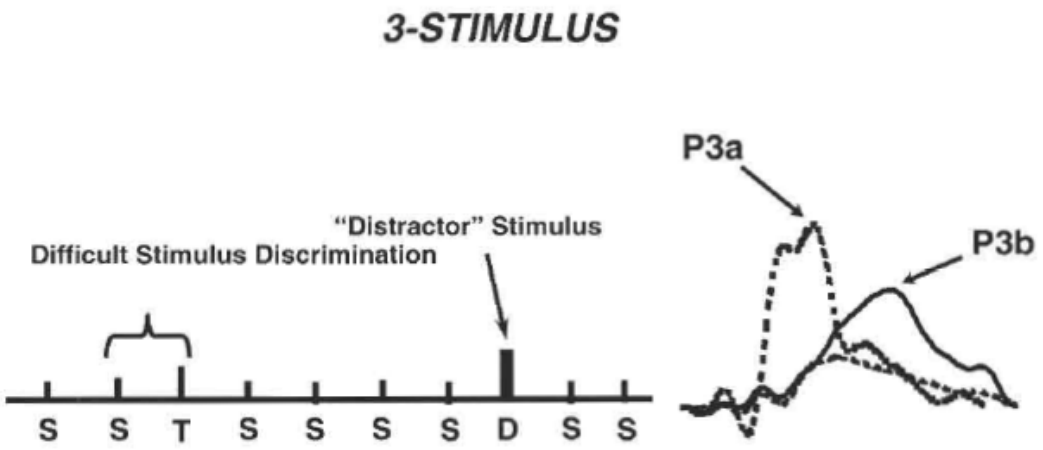
Functional Imaging

(1) Prefrontal cortex
(2) TPJ region
(3) Thalamus

**probability sensitivity seen in supramarginal gyus, right medial frontal gyrus, thalamus, insula

Is novelty necessary or sufficient to elicit P3a/frontal P3?

Note positive up



HYPOTHESIS: ***If standard-target discrimination is difficult then a distractor elicits P3a , even if it is not novel!***

Note positive up

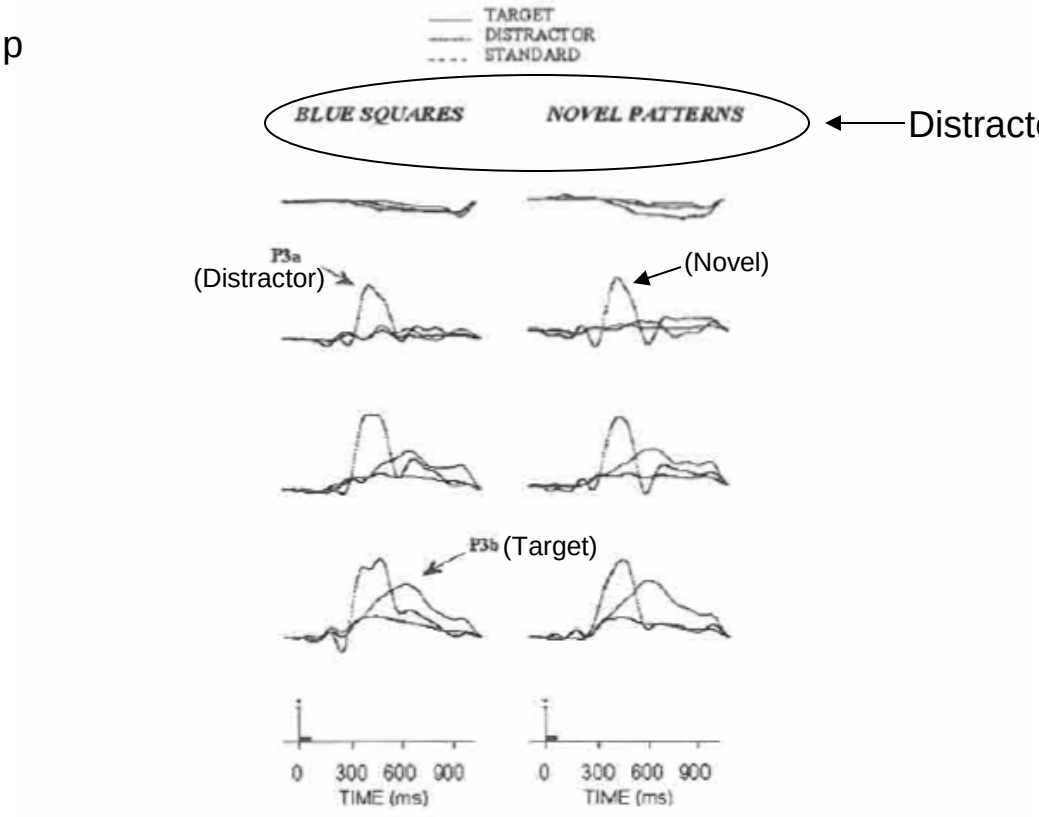
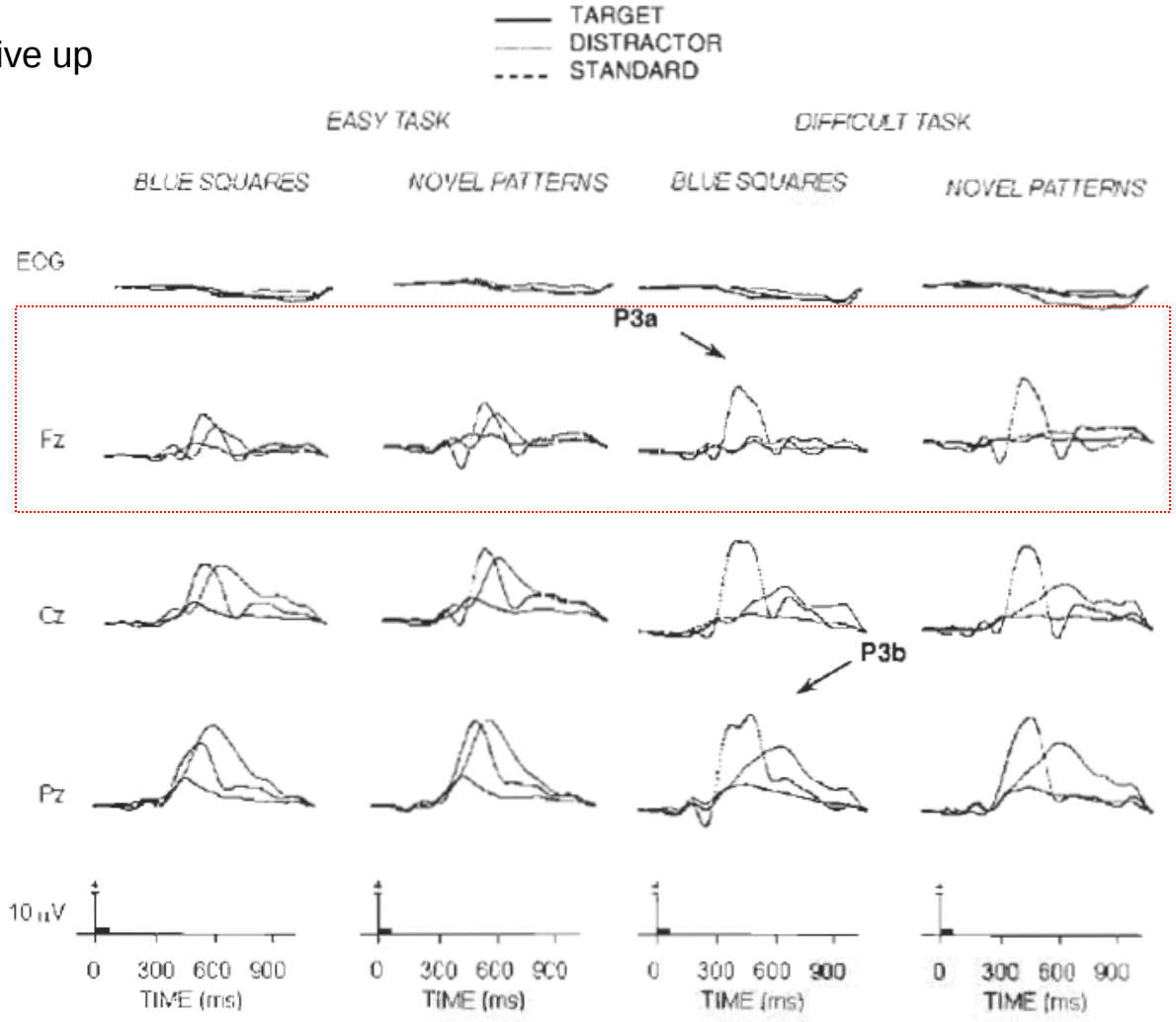


Figure 2. Grand average ERPs (n=12) from different three-stimulus oddball stimulus conditions. Subjects to respond to a target stimulus 5.5 cm diameter target circle and do not respond to a standard stimulus 5.0 cm diameter circle or to the distractor stimuli. The distractor stimuli were 23.0 cm wide squares that were all blue and always the same or different color novel patterns, with the two distractor stimulus types presented in separate conditions. (*Polich*)

Standard-Target Discrimination: 5.5 cm target vs 5.0 cm standard

Note positive up



(Polich)

P3a subcomponent is produced when the attentional focus required for the primary (standard-target) discrimination task is interrupted by an infrequent nontarget stimulus event: the distractor does NOT have to be novel. It is, however, important that the standard-target discrimination be difficult (Polich).

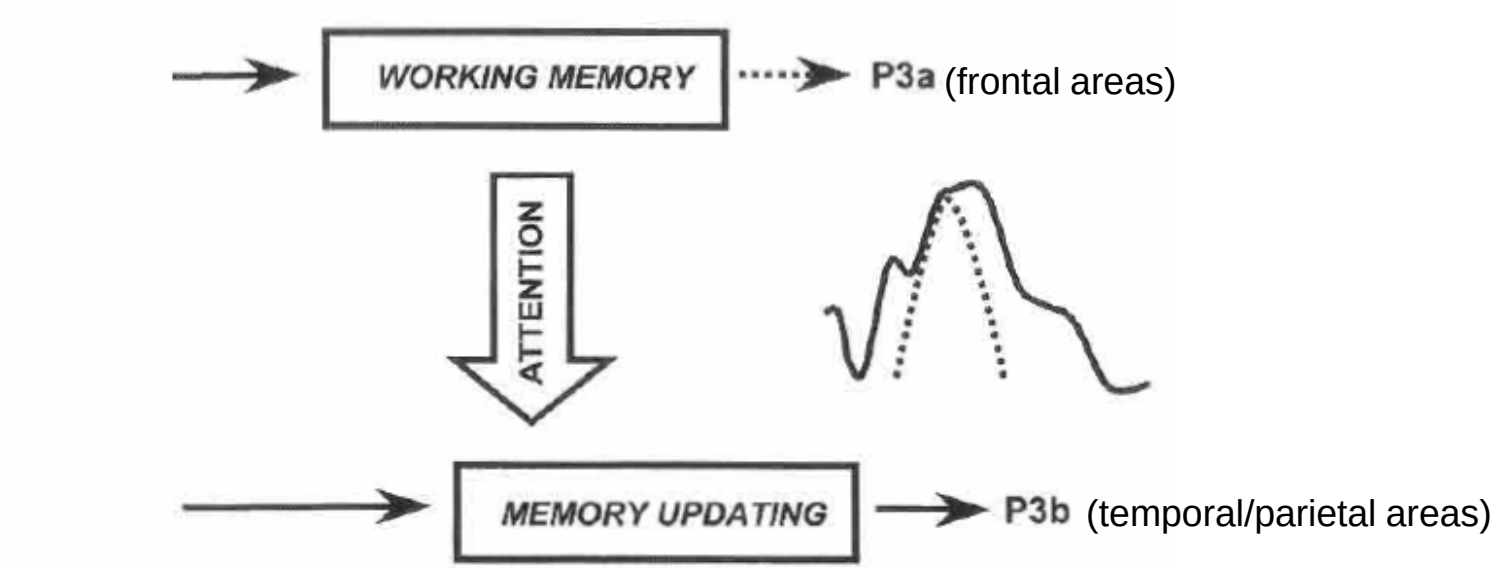


Figure 5. Schematic model of cognitive P300 activity. Sensory input is processed in parallel streams, with frontal lobe activation from attention-driven working memory changes producing P3a and temporal/parietal lobe activation from memory updating operations producing P3b. See text for explanation.

P3a and P3b arise from interaction between frontal attentional control over contents of WM and subsequent LT storage operations. (Polich).

Note positive up

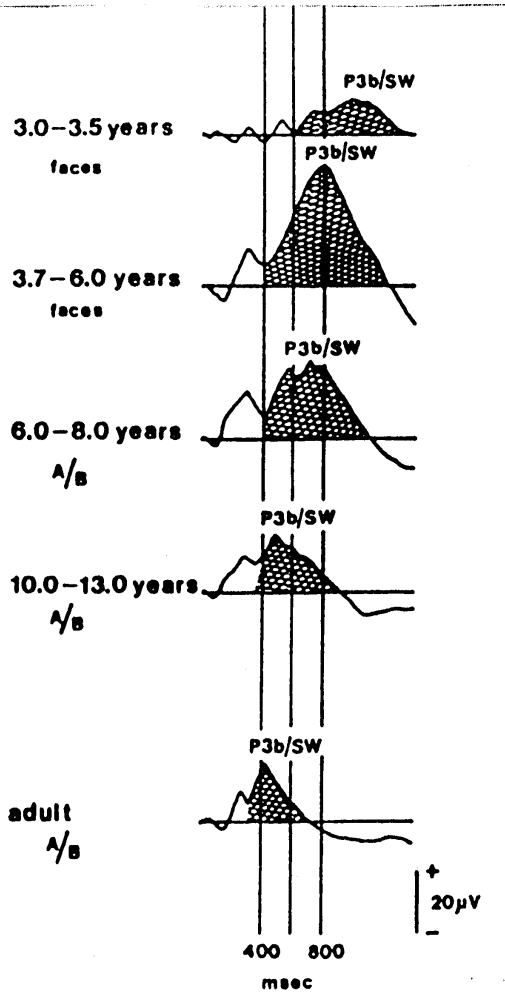
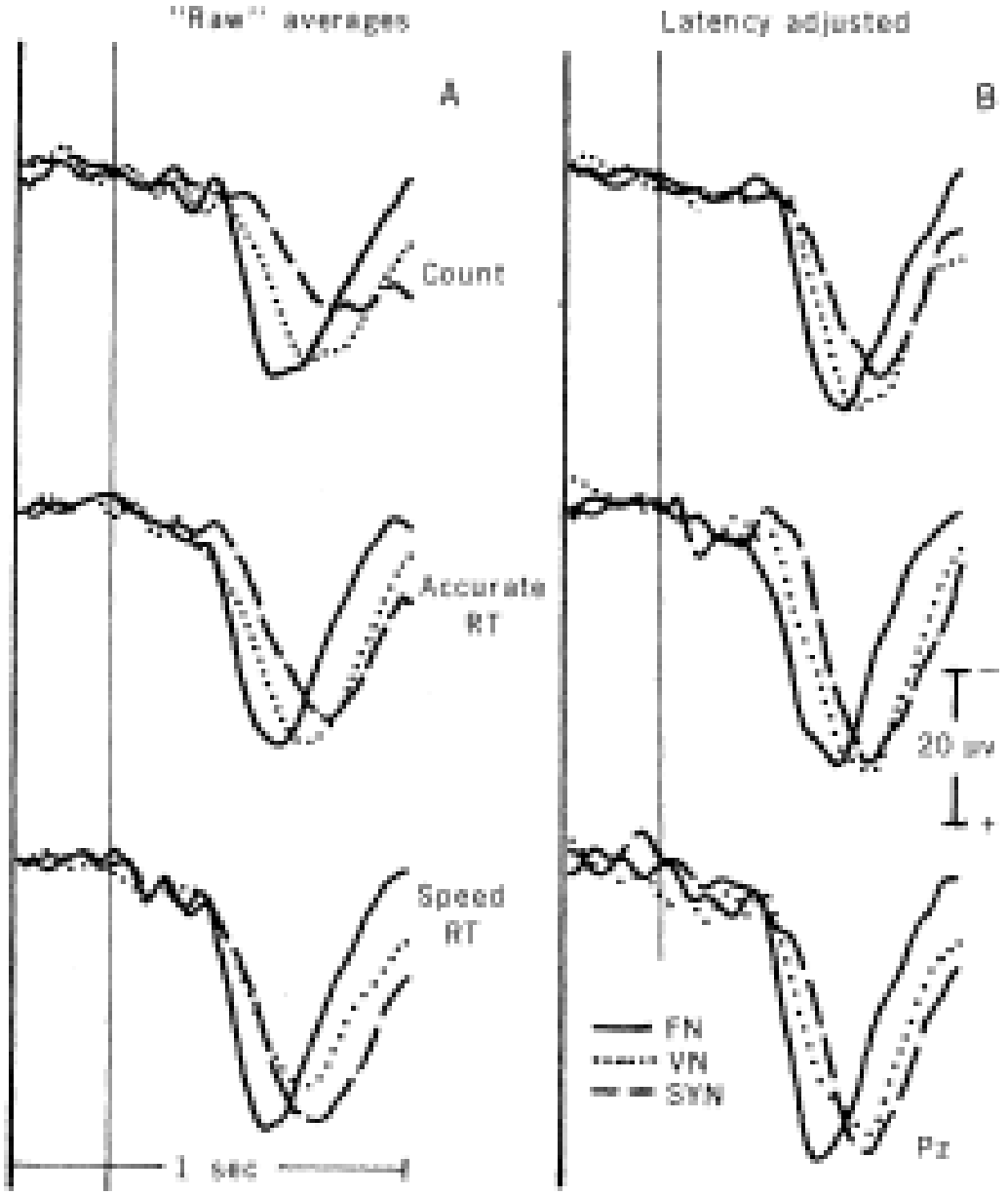


FIGURE 9-9. Normal development of P3b (P3b/SW complex) from early childhood to adulthood. P3b (P3b/SW complex) evoked by target stimuli ("target present" events) in subjects of different ages. These stimuli occurred infrequently in sequences of nontarget stimuli. P3b (P3b/SW complex) is shaded. Waveforms for 3- to 3.5-year-olds and 3.7- to 6.0-year-olds are from Courchesne, Ganz, and Norcia (1986) in which the target stimuli were human faces. Waveforms for 6- to 8-year-olds, 10- to 13-year-olds, and 24- to 36-year-olds are from Courchesne (1978) in which the target stimulus was the letter A and the nontarget stimulus was the letter B. Adapted from Courchesne, Ganz, and Norcia (1986).

P3 latency as an index of stimulus evaluation (categorization) of time

Stimulus evaluation time + Response preparation, selection, execution = RT



Kutas, McCarthy, Donchin

P3b latency seems to variy with ease of stimulus categorization

What is P3-RT relation?

X-errors

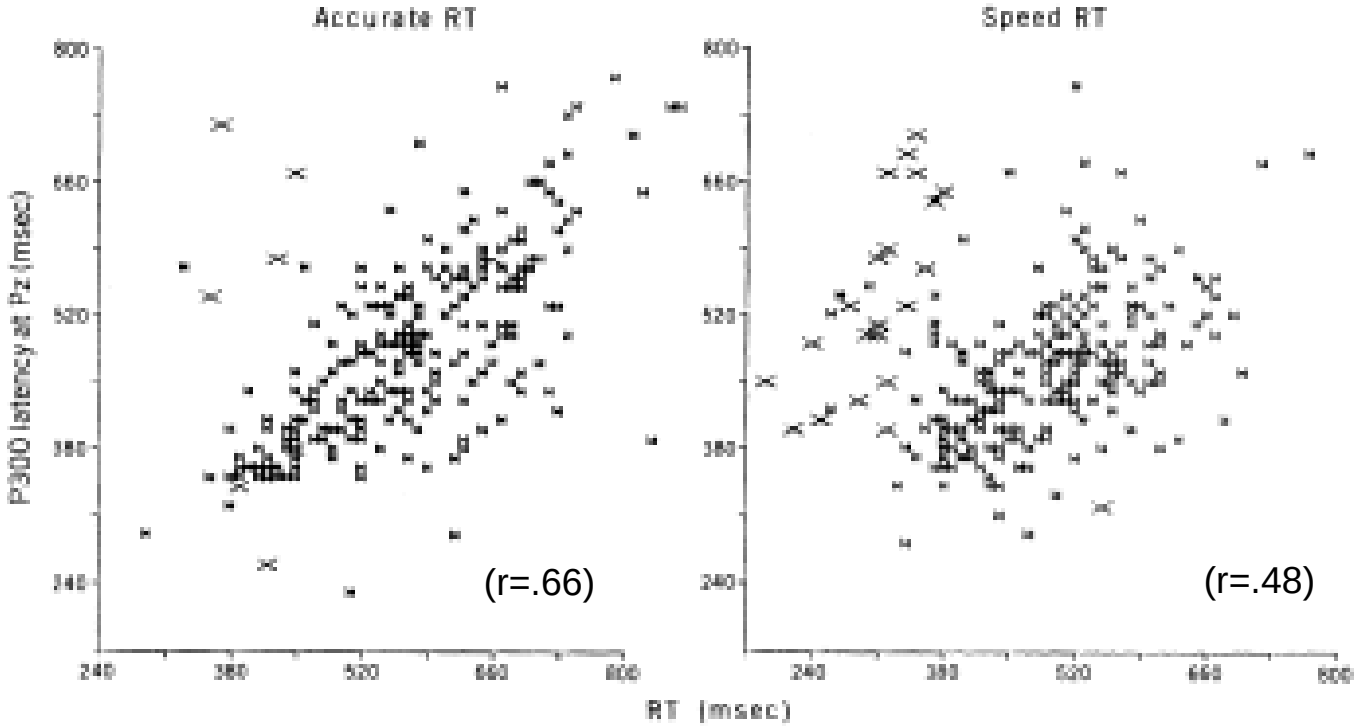


Fig. 2. Single-trial P300 latency plotted against reaction time, on the same trials, for the accurate and speed RT conditions. The *X*'s mark trials on which errors were committed. The observed error rate was 3 percent for the accurate RT condition and 9 percent for the speed RT condition. As a binary choice was required, it is reasonable to assume that the observed error rate is approximately half the actual rate. The linear regressions describing these data were $y = 0.57x + 156$ with $r = .66$ ($F = 185.65$, d.f. = 240) for the accurate RT condition and $y = 0.38x + 276$ with $r = .48$ ($F = 69.86$, d.f. = 239) for the speed RT condition.

(Kutas, McCarthy & Donchin)

Test P3 latency = stimulus evaluation time hypothesis

Additive Factors Approach
Need 2 variables whose effects on RT are additive (under assumption that if variables effect independent serial stage, then reaction times should be additive, otherwise interactive)
- factor 1: stimulus discriminability
- factor 2: stimulus-response compatibility

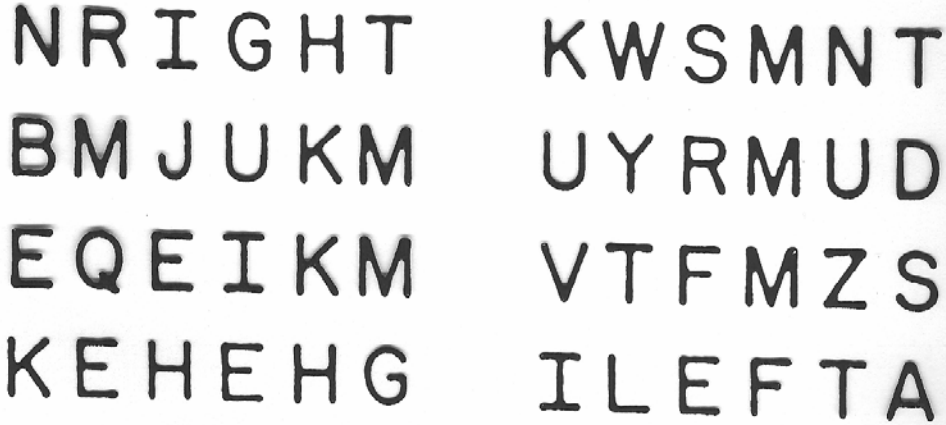
Prediction:

RT = stimulus discrimination time + response selection time
P3 latency = stimulus evaluation time only

NO NOISE

(a) (b)

NOISE



(c) (d)

Reaction Times

	compatible	incompatible	
No noise	624	716	(92)
Noise	891	981	(90)
	(167)	(165)	

Effect of noise?
Effect of S-R compatibility?
Additive or interactive?

Reaction Times

	compatible	incompatible	
No noise	624	716	(92)
Noise	891	981	(90)
	(167)	(165)	

Noise adds about 165 ms, regardless of compatibility
Incompatibility adds about 90 ms, regardless of noise.

Additivity taken to reflect noise and incompatibility affect different processing stages!

P3b peak latency

	compatible	incompatible	
No noise	589	617	(28)
Noise	792	796	(9)
	(203)	(179)	

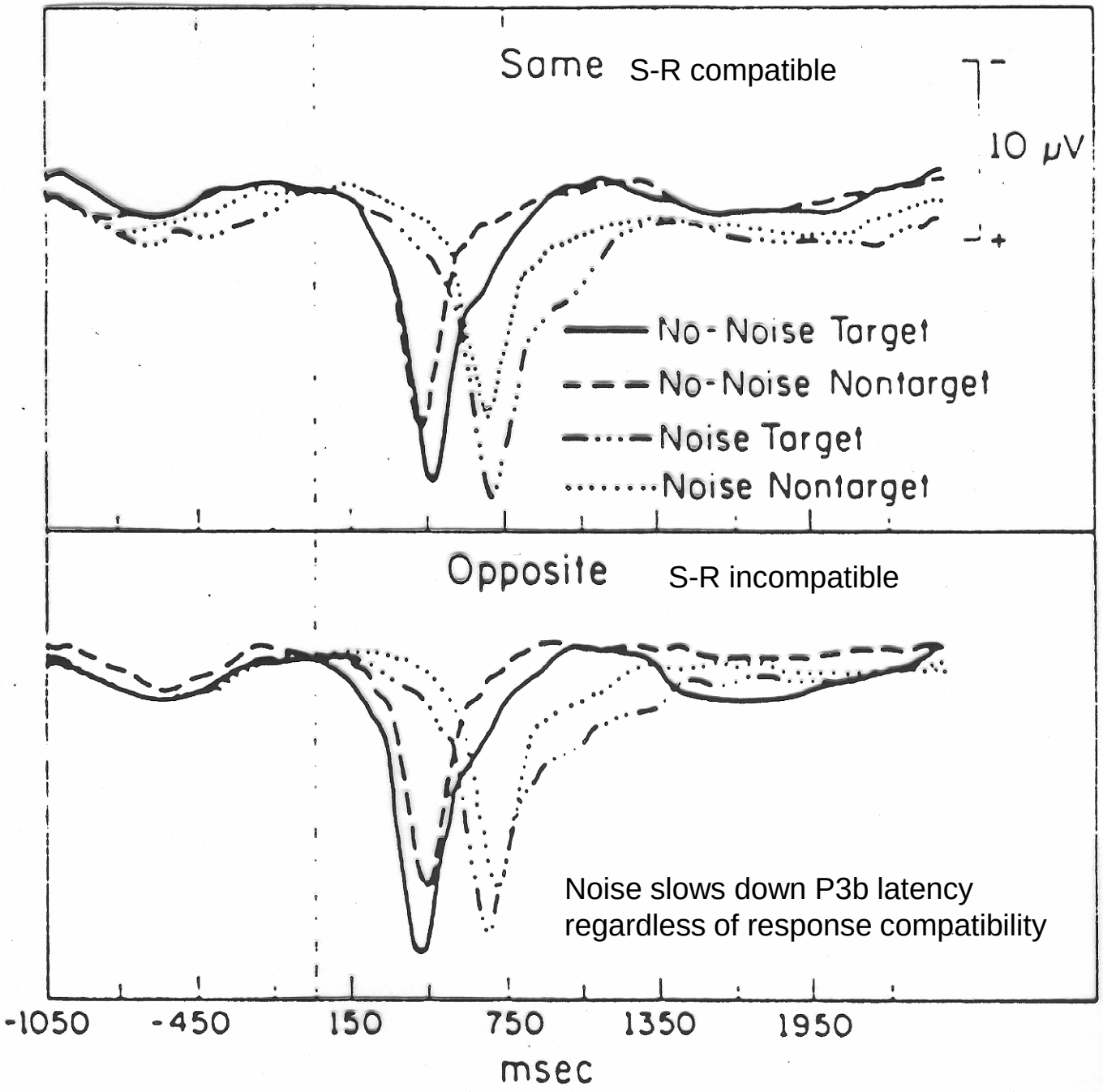
N.S.

Effect of noise?
Effect of S-R compatibility? N.S.
Additive or interactive?

P3b peak latency

	compatible	incompatible	
No noise	589	617	(28)
Noise	792	796	(9)
	(203)	(179)	

Note that P3b peak latency occurs pre-RT. Noise adds about 190 ms on average, regardless of stimulus-response compatibility.
Incompatibility has no reliable effect.


Same
S-R compatible
10 μV
No-Noise Target
No-Noise Nontarget
Noise Target
Noise Nontarget
Opposite
S-R incompatible
Noise slows down P3b latency
regardless of response compatibility
-1050
-450
150
750
1350
1950
msec

A A L E F T

A A A A A A

A A A A A A

A A A A A A

(A-A)

B B D C A A

D R I G H T

B A B D A A

C D C C B A

(A-D)

B D G E F F

A C E F A B

L E F T G A

B C E E D A

(A-G)

K W S M N T

U Y R M U D

V T F M Z S

I L E F T A

(A-Z)

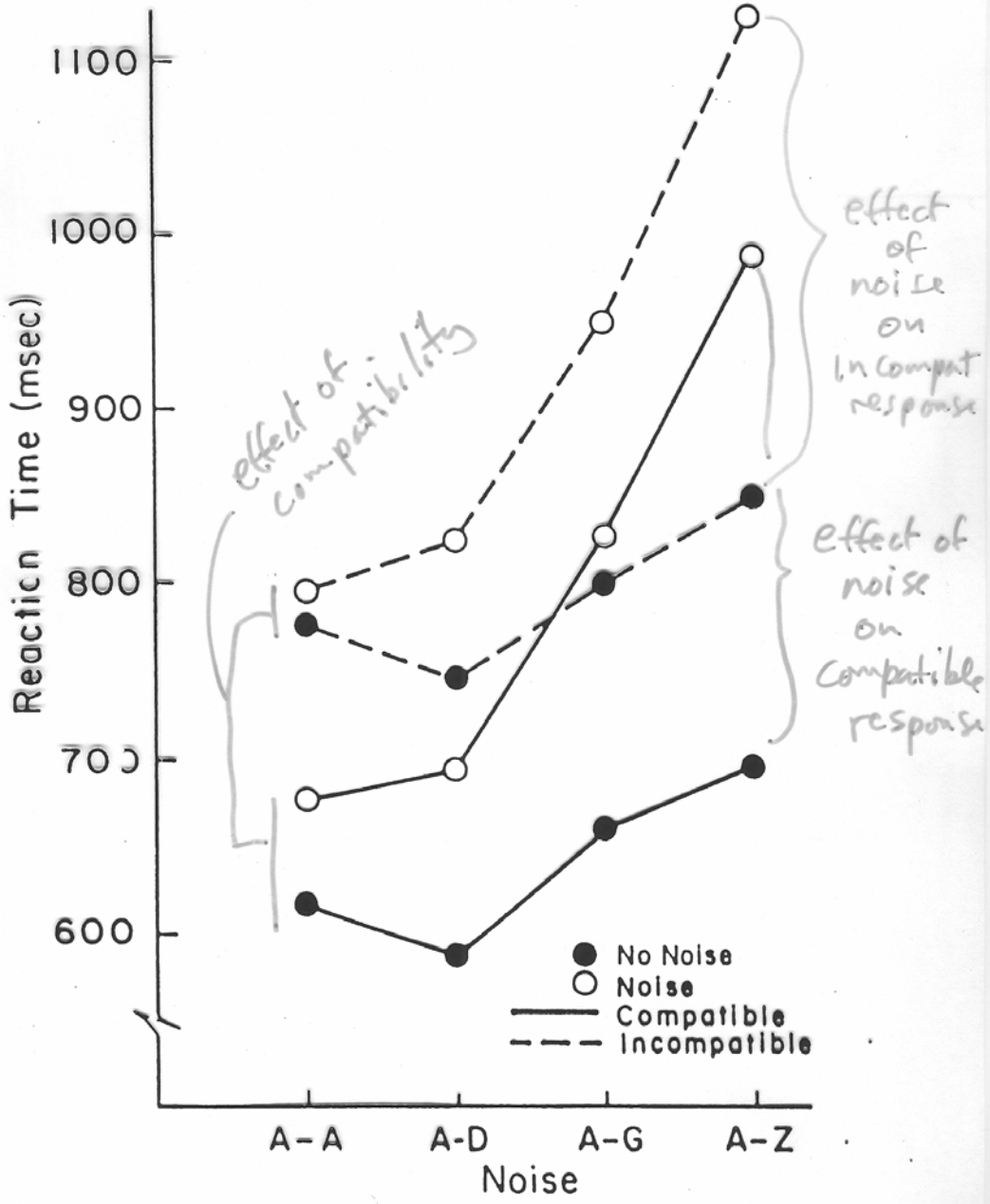
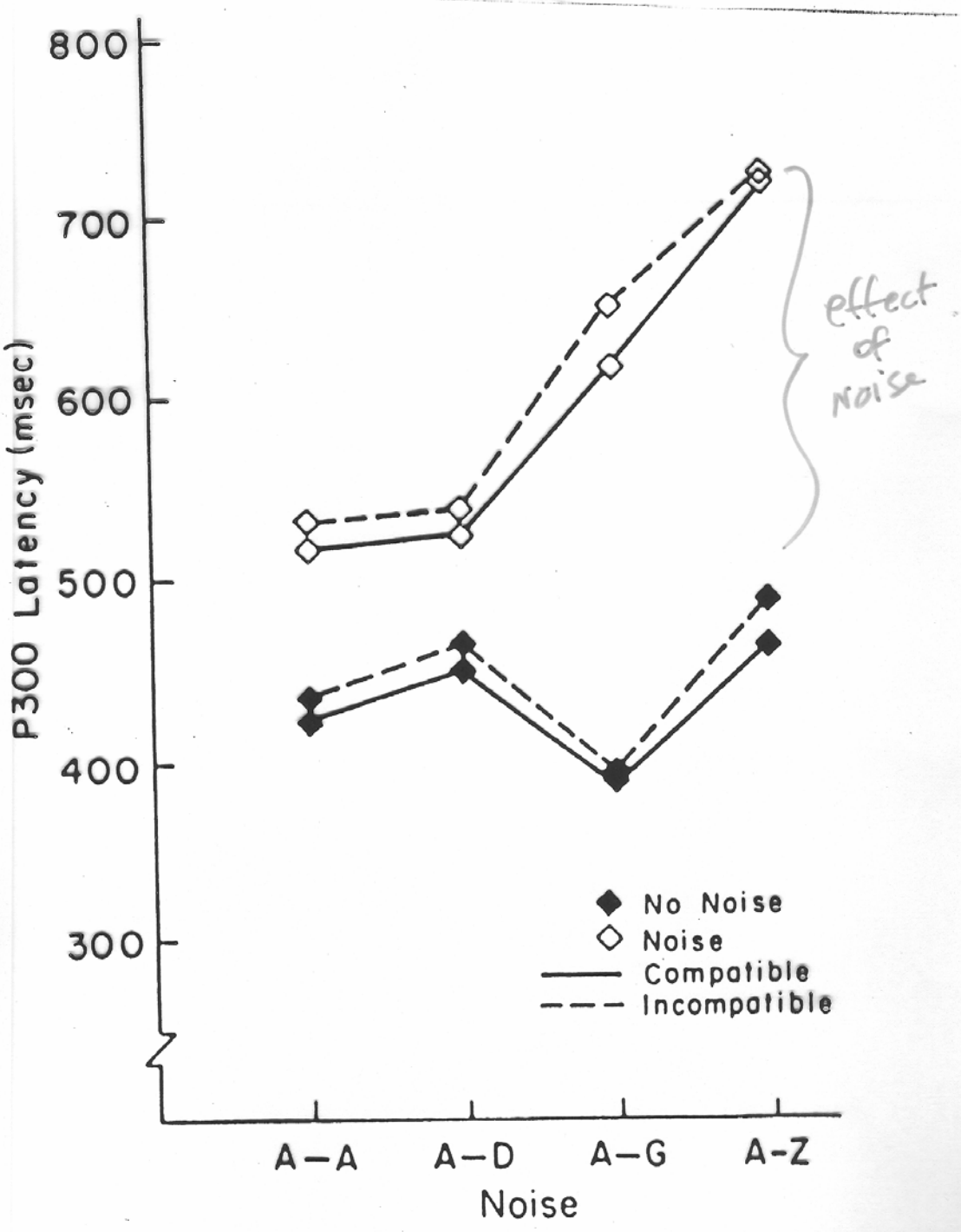


Figure 8. RT (in ms) results from Experiment 2.


800
700
600
500
400
300
P300 Latency (msec)
effect of noise
No Noise
Noise
Compatible
Incompatible
A–A
A–D
A–G
A–Z
Noise

P3b latency and stimulus evaluation time

Varies with difficulty of categorization task

Is correlated with but dissociable from reaction times

Is more sensitive to perceptual-conceptual (stimulus related/evaluation) processes than response-related processes, i.e., ***P3b latency is not (well-)correlated with variance in RT due to response-related processes***

P3b provides metric for decomposition of stages of information processing that complements RT

Decomposing the P3b

There have been suggestions that even the P3b is not a unitary process e.g., Falkenstein distinguishes P390 and P540

P390: central, modality dependent, stimulus-related
P540: modality independent, response-related

Note positive up

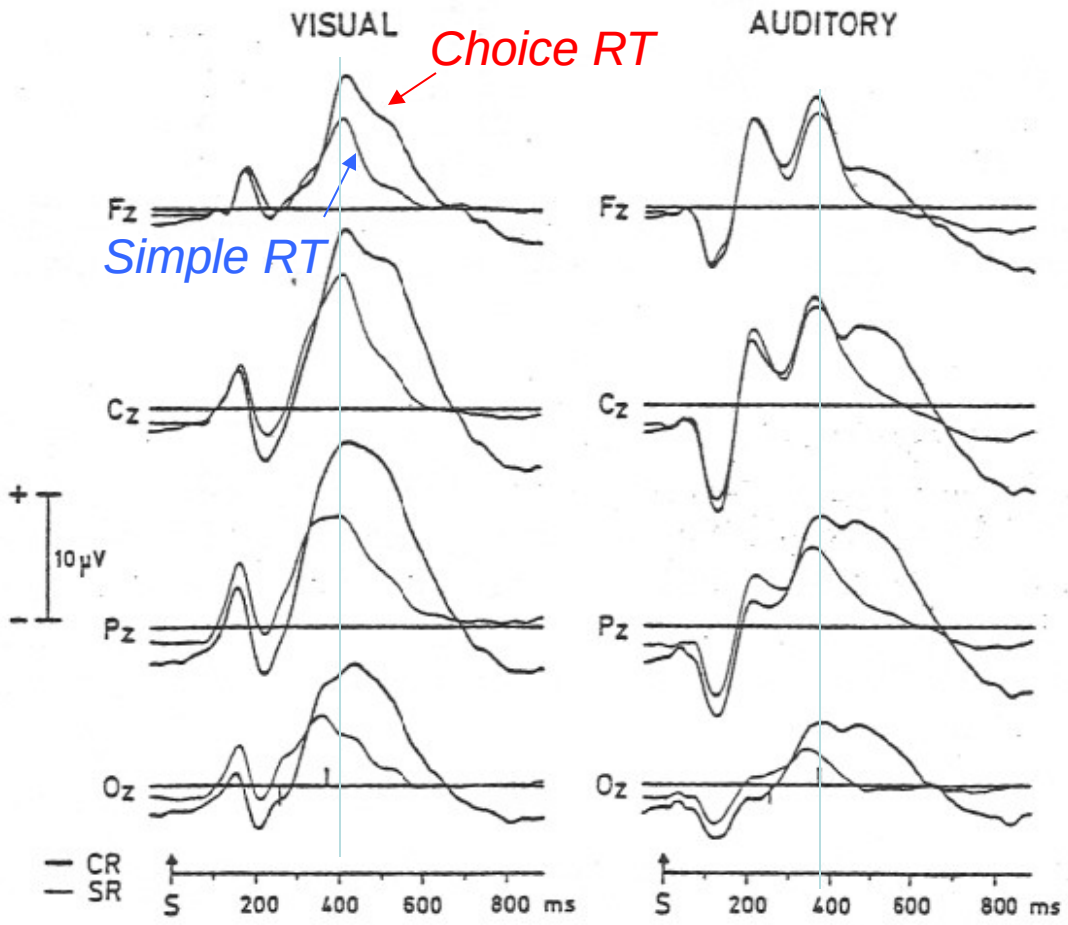


Fig. 1. Grand means of the ERPs after visual (left panel) and auditory stimuli (right panel): heavy lines, 2-way choice reaction (CR) task; thin lines, simple reaction (SR) task. The associated reaction times are given as vertical heavy (CR) and thin (SR) bars in Oz. (S = stimulus onset.)

Note positive up

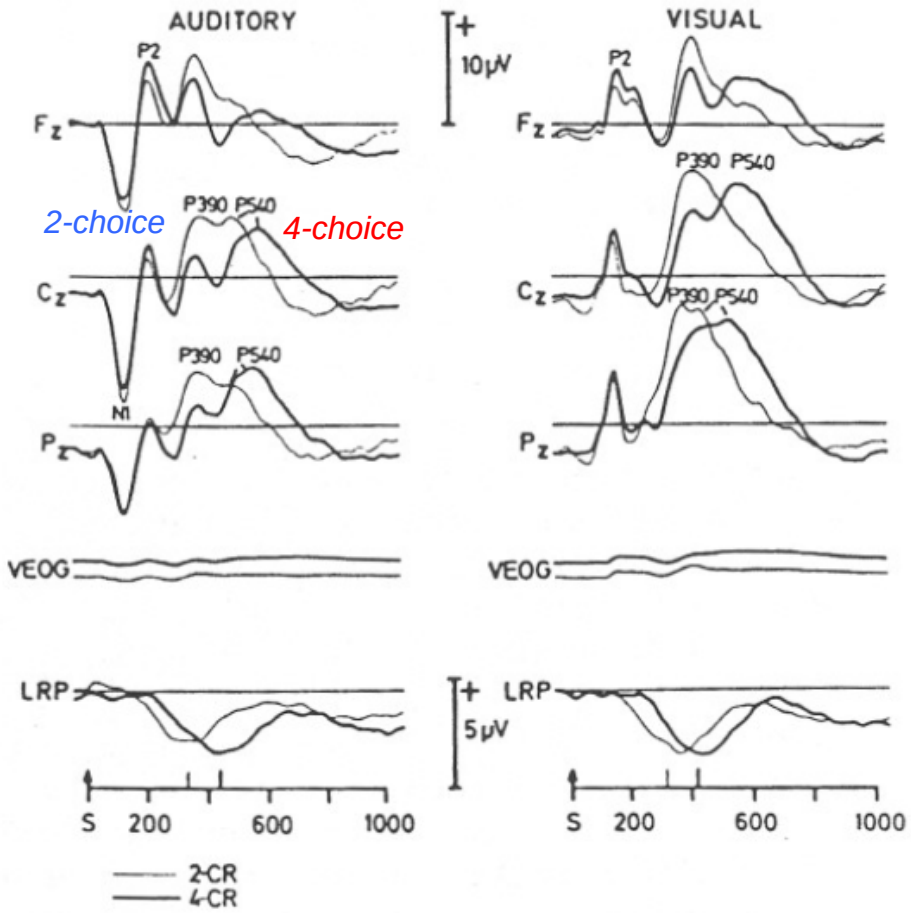


Fig. 3. Grand means across 11 subjects of the ERPs of the *choice* reaction tasks after auditory (left panel) and visual stimuli (right panel). Thin lines: 2-CR (2-choice task), heavy lines: 4-CR (4-choice task). Two separate positive peaks are visible, which are most separated on 4-CR reactions to auditory stimuli. The lowest traces show the lateralized readiness potential. The associated choice reaction times are given as vertical thin (2-CR) and heavy bars (4-CR) on the abscissa. For further details refer to legend of Fig. 2.

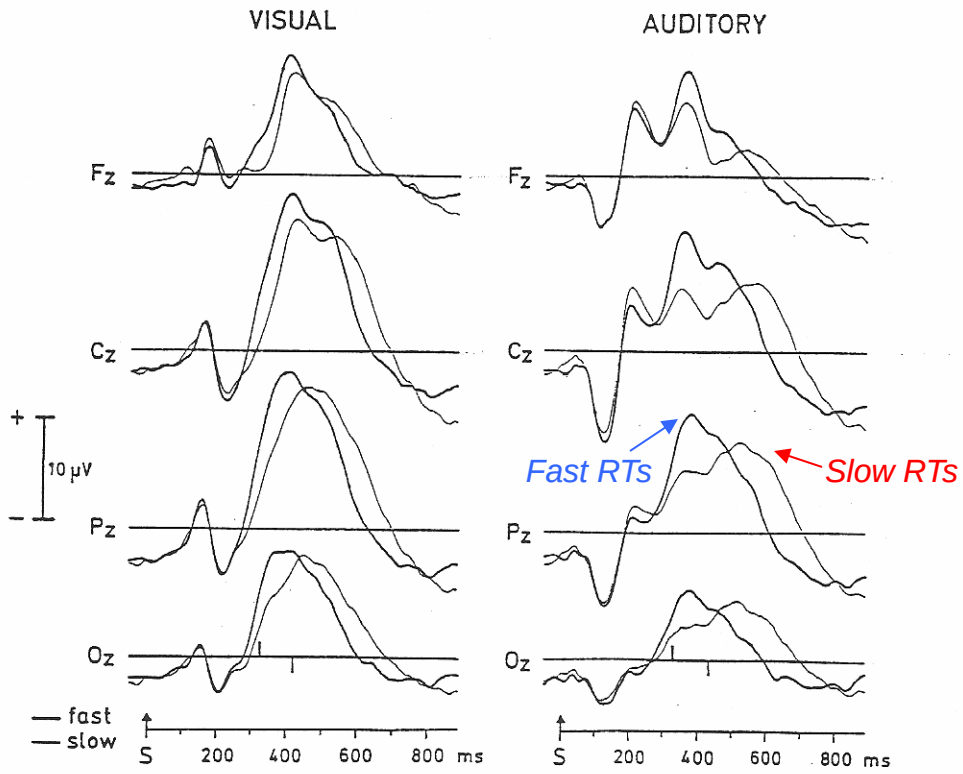


Fig. 2. Grand means of the ERPs of the choice reaction tasks after visual (left panel) and auditory stimuli (right panel): heavy lines, fast choice reactions (RT below median); thin lines, slow choice reactions (RT above median). The associated reaction times are given as vertical heavy (fast) and thin bars (slow) in Oz.