ATTENTION

The mind is ***capacity-limited*** and as a result continuously assigning priority to some sensory information over others, and this ***selection*** process makes a profound difference for conscious experience and behavior.

Attended stimuli more likely to control behavior

- discriminated more quickly, accurately
- better-remembered
- assoc w/ more reports of awareness

ATTENTION

Attention is not a process under the control of ***a*** brain area or even ***a*** brain system. There is a *whole host of attentional mechanisms* capable of selecting relevant information at multiple stages of processing. Attention more generally is a set of processes that control the flow of information through the nervous system – a set of processes that operate by modulating activity of other systems (perceptual, memory, response)

ERP data have been particularly useful in providing timing information that is critical for understanding the dynamic operation of different attentional processes.

ERP (sometimes in combination with other neuroimaging techniques) have shed light on mechanisms underlying

- visuospatial attention,
- visual search,
- automatic capture of attention
- voluntary control of attention

ATTENTION PARADIGMS

Filtering paradigm

Spatial cueing paradigms

Visual search paradigm

Dual task paradigm

VISUAL ATTENTION-RELATED COMPONENTS

P1, N1, N2pc, SN, EDAN, LDAP, ADAN

N2pc – N2posterior contralateral
SN – selection negativity
EDAN – early directing attention negativity
LDAP – late directing attention positivity
ADAN – anterior directing attention negativity

Attention influences almost all ERP components/effects

Why use ERPs, in particular, to study attention?

1. Can be recorded in the absence of any overt response, and thus used to ***examine even unattended stimuli*** (even actively ignored stimuli)
2. High temporal resolution allows determination of when and how attention begins to affect processing, and to track timecourse of various attentional processes

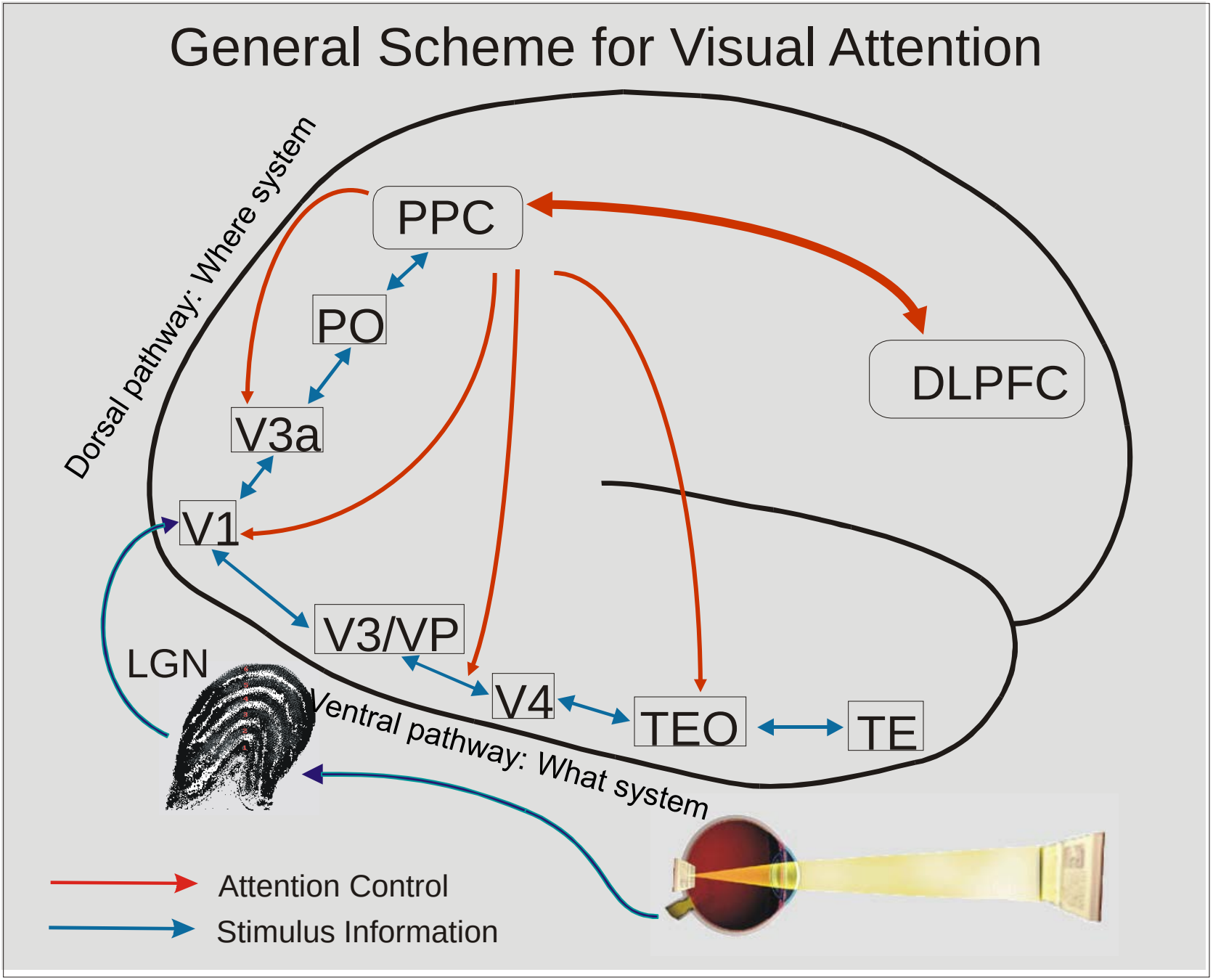
Visual-Spatial Attention

May be directed voluntarily to a specific region of the visual field or captured automatically by a salient event

Improves the perception of stimuli at attended locations (i.e. within the “spotlight” of attention)

So when and where in the visual pathways are the attended inputs enhanced by spatial attention?

General Scheme for Visual Attention



Single unit and neuroimaging data show attention related modulations in many visual areas in the ventral and dorsal visual streams including V1, V2, V3, V4,MT, IT .

In other words many areas are modulated by attention at some point, but when, how, and with what mechanism(s)?

Selective attention refers to the fact that at any given point in time, some sensory stimuli seem to be processed differentially relative to others as reflected in e.g., faster and more accurate responses. Thus, there is either enhanced processing of “attended” stimuli or suppressed processing of “unattended” stimuli, or both.

Selectrive attentionn is processes by which brain selects some sources of inputs for enhanced processing

Factors to control for in ERP studies of selective attention

1. **Avoid physical stimulus differences**: Stimuli in attended and unattended conditions should be, at least on average, the same.

2. **Avoid arousal – attention confound**. Use task conditions under which responses to attended and unattended stimuli are as similar as possible. Often means that responses to both are recorded concurrently, and attended and unattended stimuli are presented randomly.

3. **Avoid anticipation**: Random rather than predictable presentation of attended and unattended stimuli.

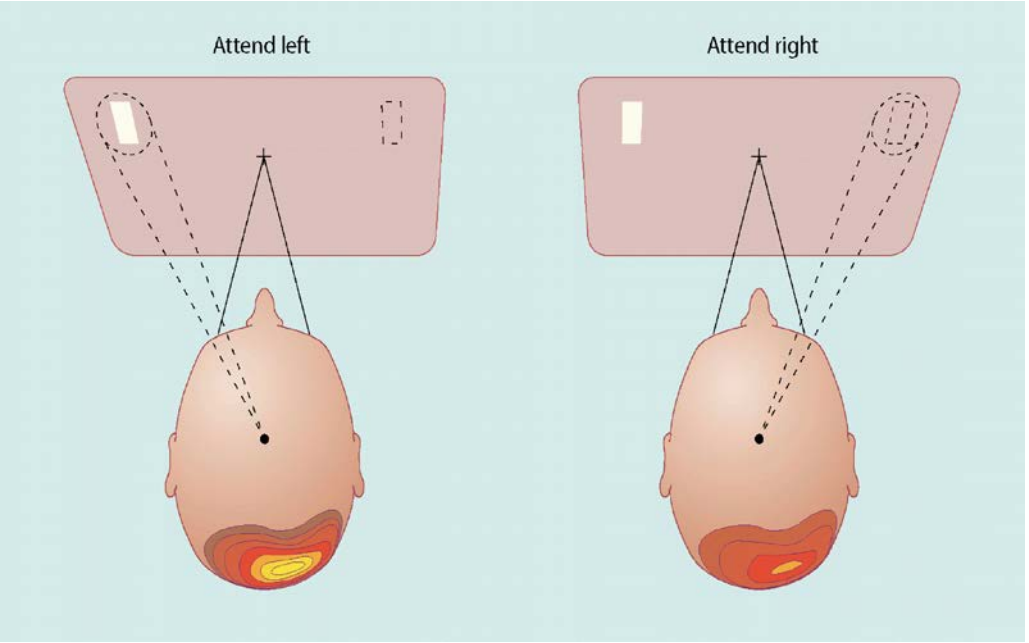
4. **Increase need for selectivity**. Stimuli need to be presented fast enough that the task will be difficult so that participants will be unable to shift their attention from trial to trial and/or divide their attention across the to-be-attended and to-be-unattended stimuli

Filtering Paradigm

ATTEND LEFT ATTEND RIGHT

Standard, Non-target, Frequent (80%)

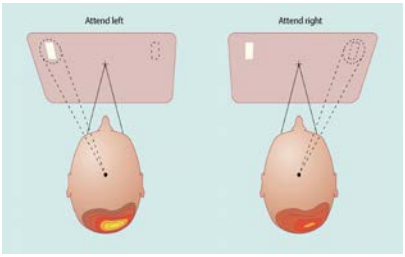
Target, Infrequent (20%), longer or shorter duration or height, etc., requires response



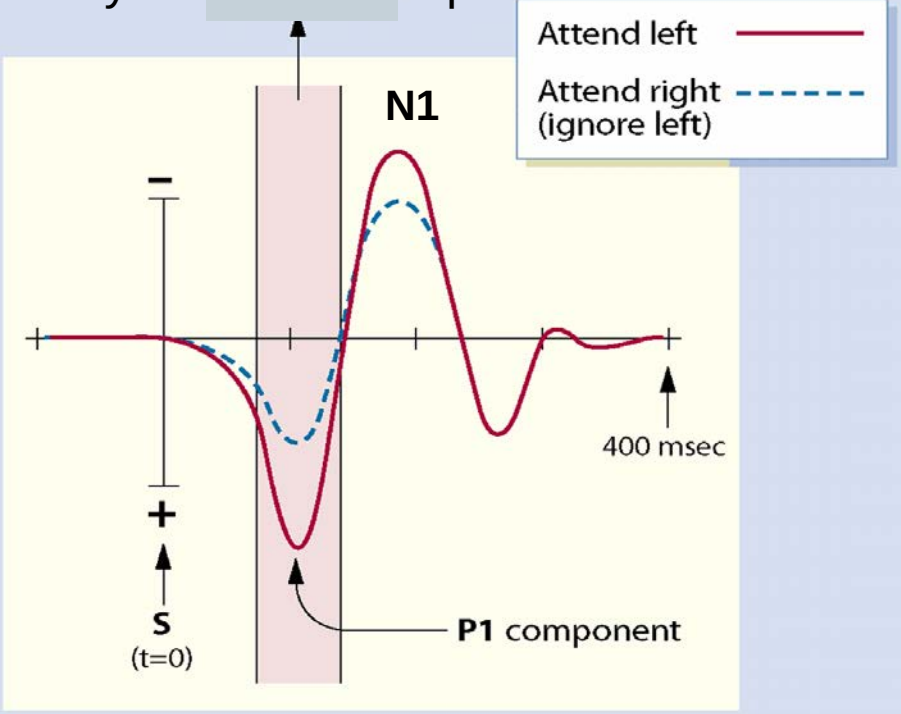
Fixate center. Move attention not eyes!

Compare the ERPs to same physical stimulus (target or standard) when it is and is not attended.

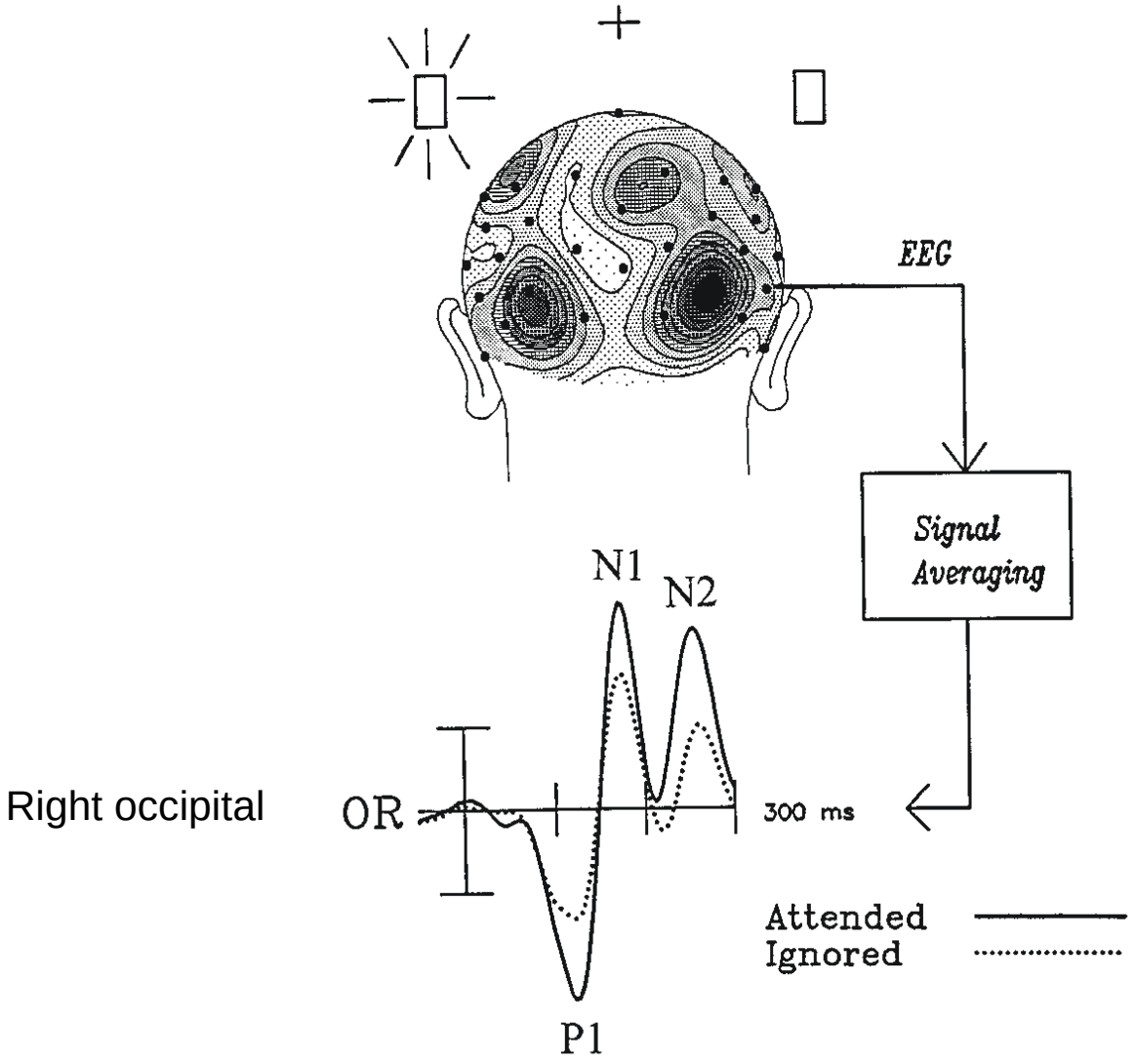
FILTERING PARADIGM



Sensory visual evoked potentials



Spatial Attention Modulates Early Sensory EP Components



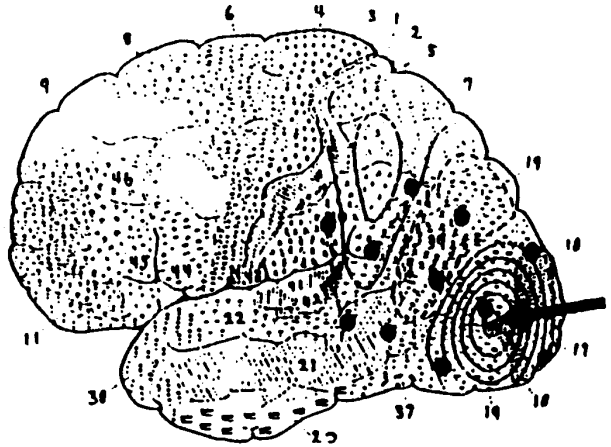
Mangun, Hillyard & Luck Attention & Performance 1990

Upper Right Stimuli

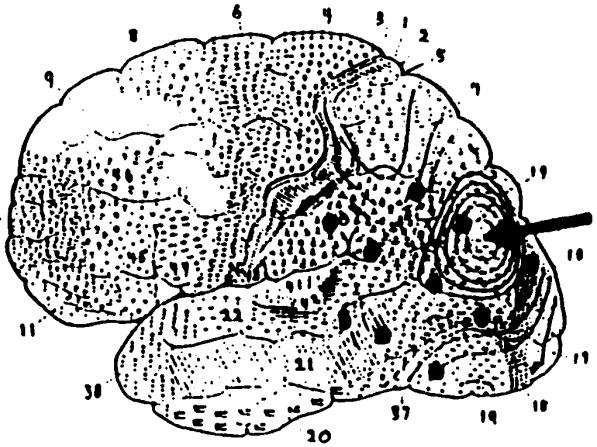
Scalp Current Density

Aka CSD – current source de
-- 2nd spatial derivative
-- current flow

P110



N180



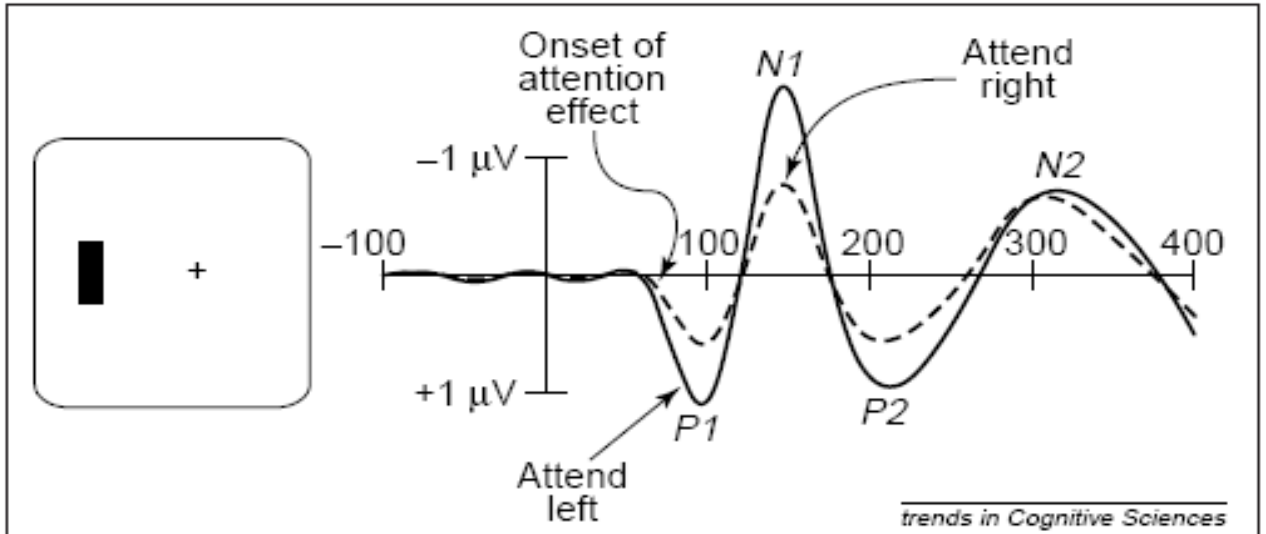


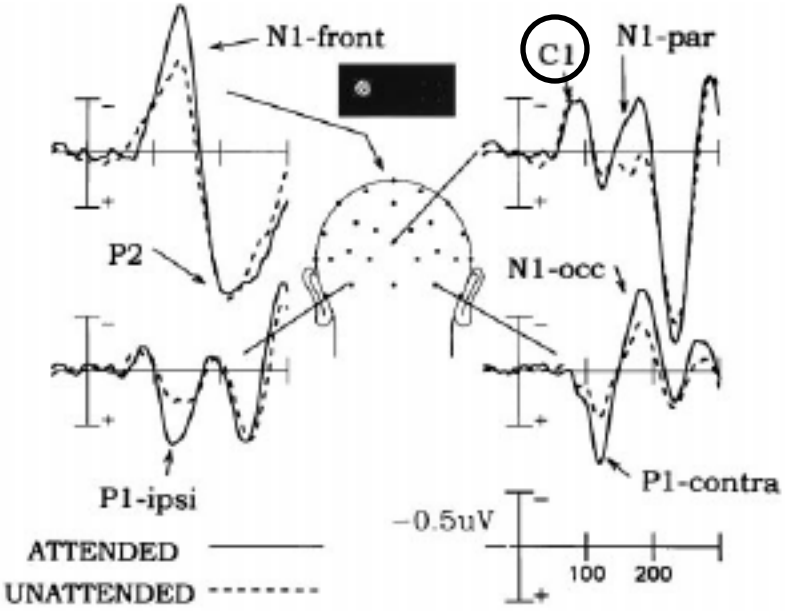
Fig. 1. Paradigm for using ERPs to study attention. Stimulus display (left) and idealized results (right). Subjects fixate a central cross and attend either to the left or right visual field. Stimuli are then presented to the left and right visual fields in a rapid sequence. In this example, the ERP elicited by a left visual field stimulus contains larger P1 and N1 components when the stimulus is attended ('Attend left') than when it is ignored ('Attend right').

Visuospatial selective attention: stimuli in attended location show
- enhanced P1 (80-130 ms) over posterior scalp
- enhanced N1 (150-200 ms) over posterior scalp

Modulations in amplitude of exogenous EP components with little or no change in component latency or scalp distribution: implies <u>sensory gain mechanism</u> – voluntary focussing of attention involves gain control within early visual pathways – increase size of small sensory signal relative to brain's internal noise.

frontal

occipital



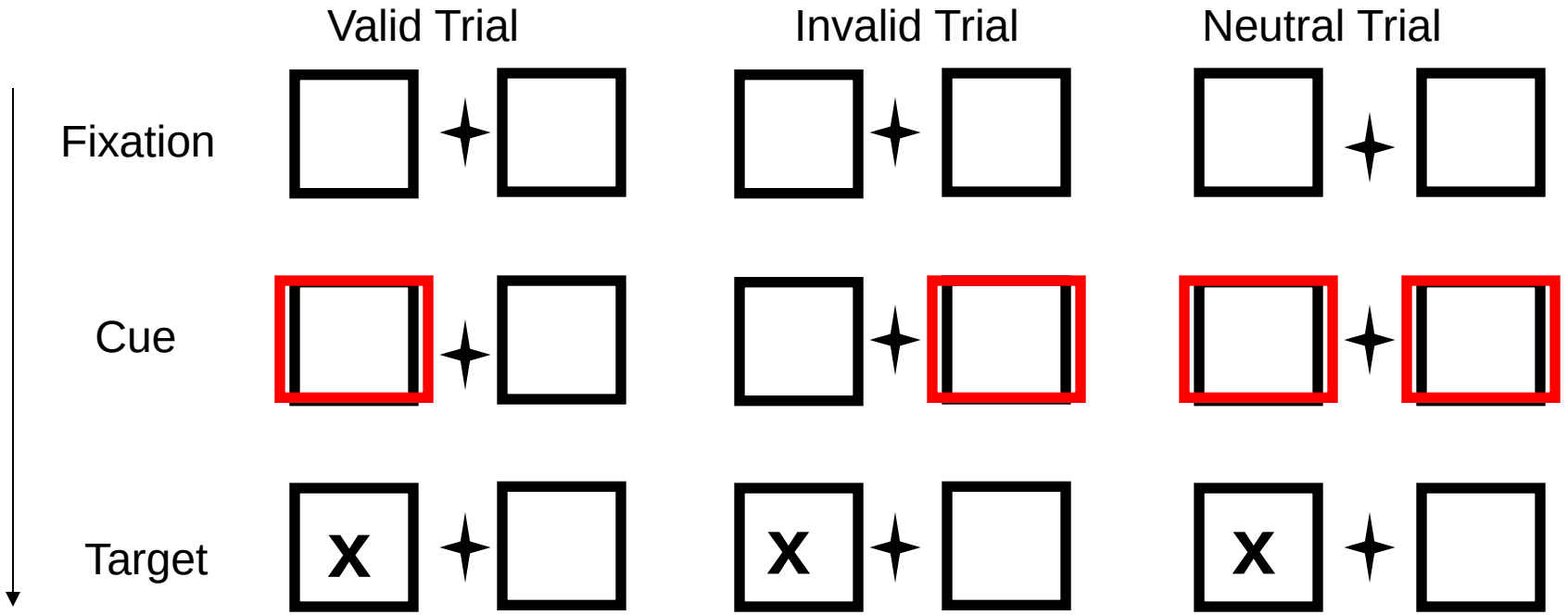
parietal

FIG. 1. Grand average visual ERPs over 17 subjects recorded from four scalp sites in response to small circular checkerboard stimuli in a spatial attention task. Stimuli were flashed in a rapid, randomized sequence to the left and right visual fields while subjects attended to one visual field at a time. ERPs shown are in response to left field flashes, with waveforms superimposed for attend-left (solid lines) and attend-right (dotted lines) conditions. Note that attending to the stimulus location produces an increased amplitude of the P1 components (80–130 ms) over the contra- and ipsilateral occipital scalp, as well as of multiple N1 components (120–200 ms) over frontal (front), parietal (par), and occipital (occ) scalp areas. In contrast, the earlier C1 component (50–90 ms), which was localized to primary visual cortex, did not change as a function of attention. Abscissa, time base in milliseconds. Reproduced with permission from Clark and Hillyard (32) (Copyright 1996, by MIT Press).

There are multiple N1 components/subcomponents sensitive to attention: e.g., frontal N1, parietal N1, occipital N1 – not all functionally or anatomically identical.

VISUOSPATIAL CUEING PARADIGM

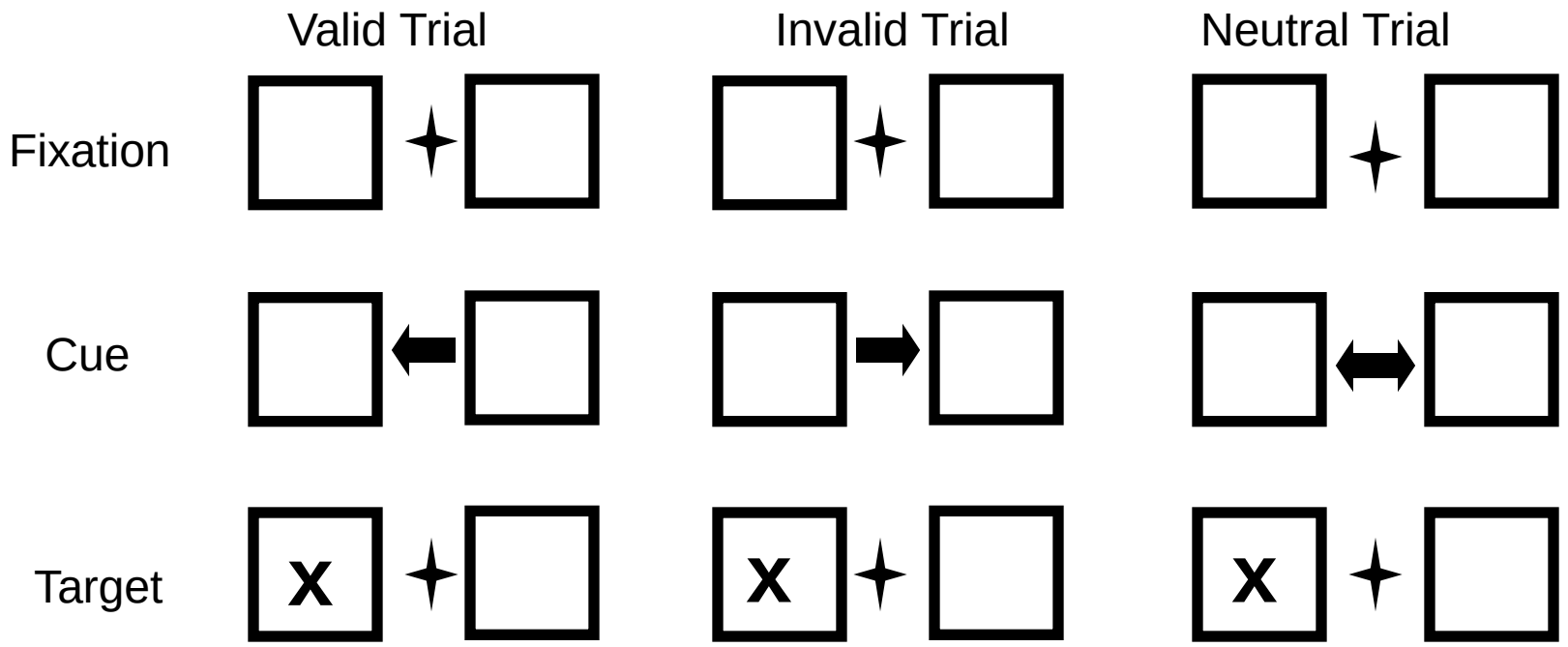
PERIPHERAL CUE



Critial factors: peripheral or symbolic cue
cue to target interval

VISUOSPATIAL CUEING PARADIGM

CENTRAL CUE



Critial factors: peripheral or symbolic cue
cue to target interval

occipital

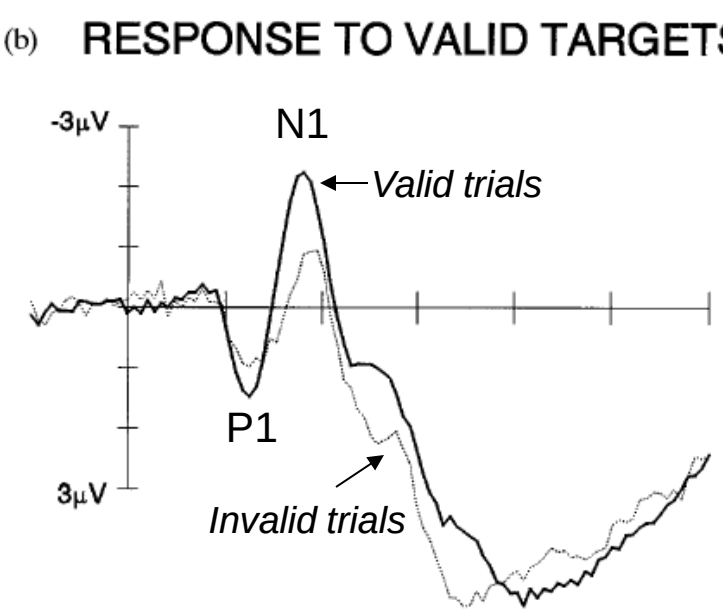
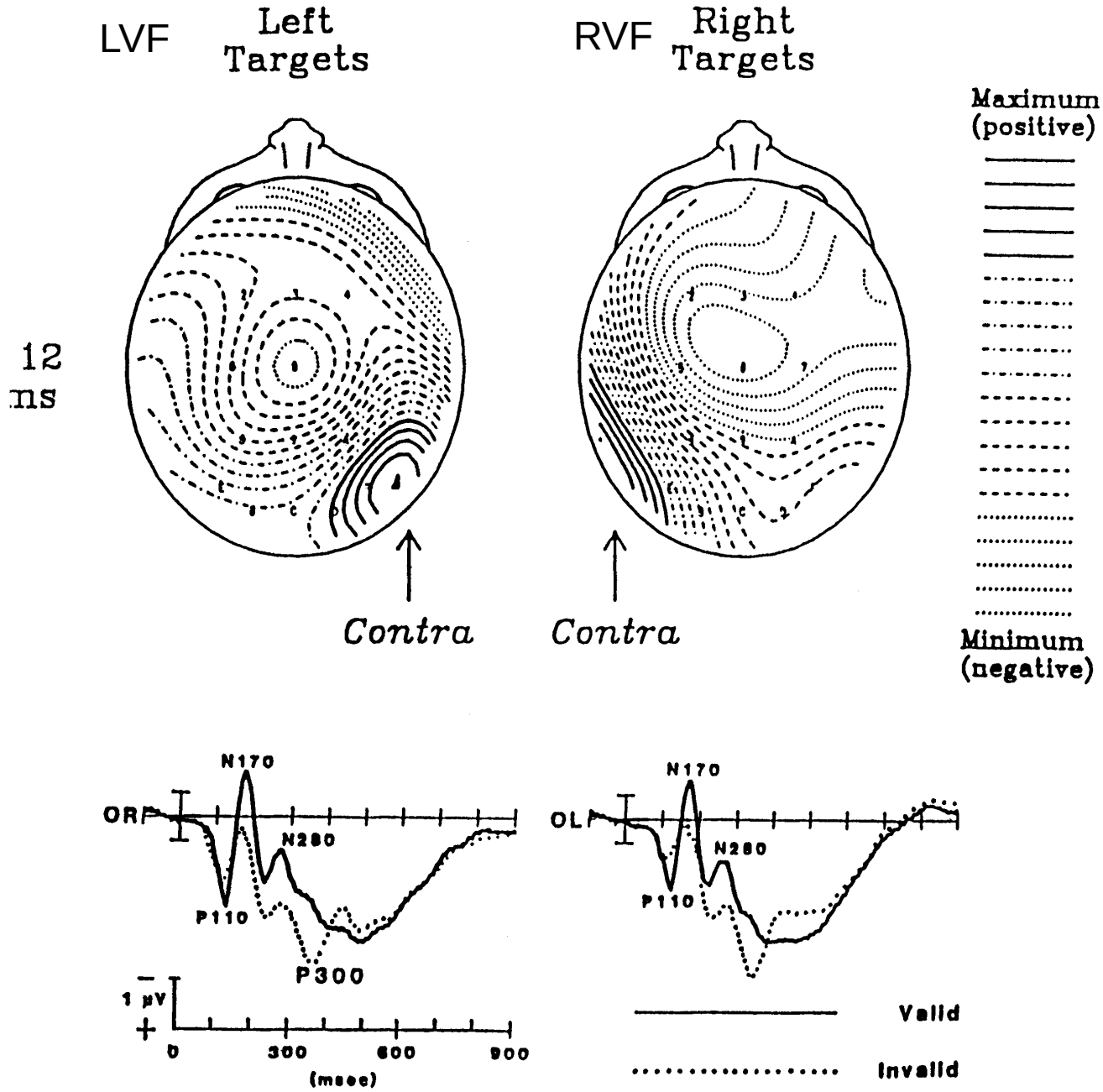


FIG. 3. Grand-averaged ERPs elicited at occipital electrodes ipsilateral to the location of the target stimulus in a trial-by-trial cueing experiment by valid trials (solid lines) and invalid trials (dotted lines). (a) ERPs elicited in a condition where responses were required in valid and in invalid trials. (b) ERPs elicited in a condition where responses were required in valid trials only.


SCALP TOPOGRAPHY OF P1 VALIDITY EFFECT
LVF
Left Targets
RVF
Right Targets
Maximum (positive)
12 ns
Contra
Contra
Minimum (negative)
N170
ORP
N280
P110
P300
1 μV
0
300
600
900
(msec)
N170
OLP
N280
P110
Valid
Invalid

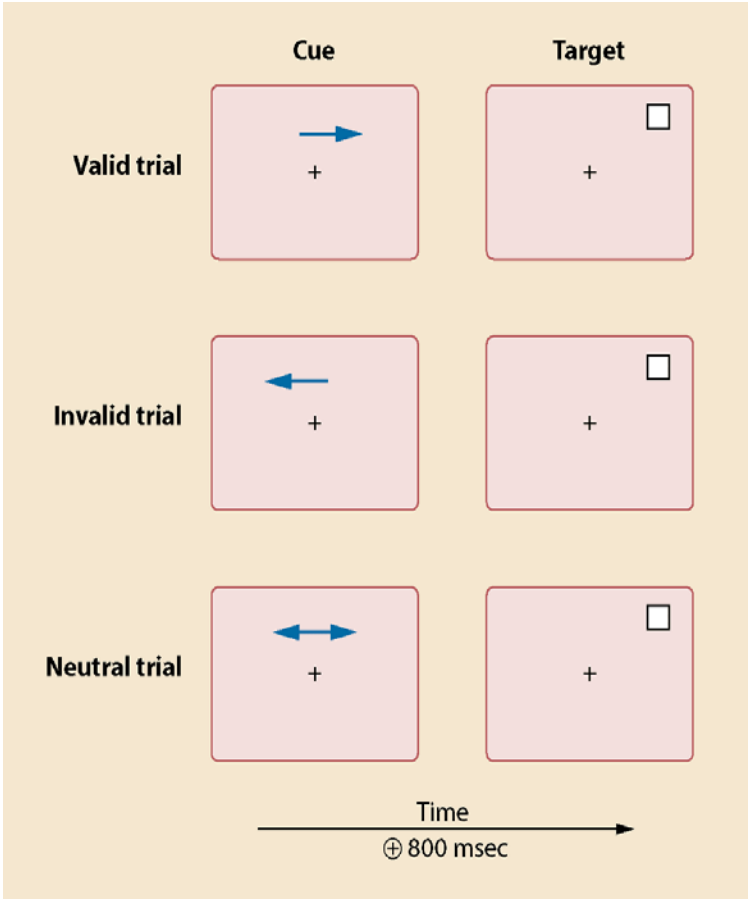
Visual Spatial Attention

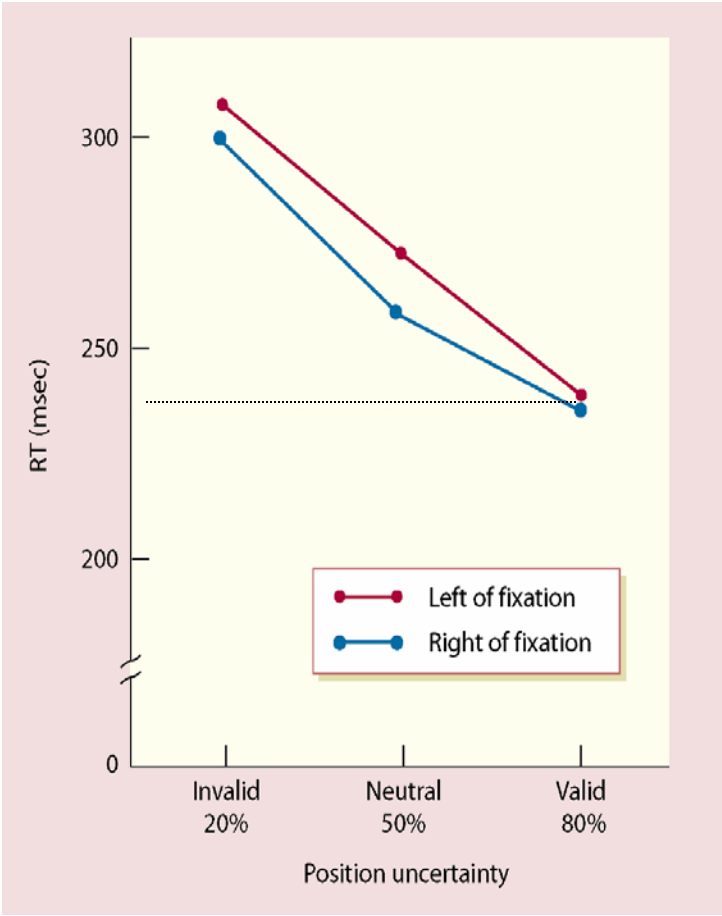
Filtering Tasks, Cuing Tasks, Visual Search Tasks

P1 and N1 amplitude enhancement seems to be a general characteristic of the spatial focusing of attention across many tasks. Attended stimuli elicit larger P1-N1 components than at unattended locations whether the stimuli are presented continuously in randomized sequences (filtering task) or cued on each trial as to the most probable location of the subsequent target stimulus (cueing task).

In ***trial-by-trial cueing tasks***, *enhanced P1-N1 amplitudes to target stimuli at valid (precued) locations have been associated with speeded reaction times and improved detectability of target signals, which lends support to the hypothesis that these ERP amplitude modulations reflect sensory information that is used for perceptual judgments.*

Similar P1-N1 modulations have been found in ***visual search tasks,*** *e.g.,* in which participants have to deploy focal attention to identify the shape of a target defined by its color in an array.





Note: fastest RTs are 200 ms+
i.e., beyond P1, N1 modulations

Conclusions

1. Spatial attention modulates amplitude of early P1 (80-120 msec) and N1 (140-200 msec) components in visual cortex.

2. Spatial attention acts like a ***sensory gain control mechanism***: relative amplification of attended-location inputs and suppression of unattended-location inputs at an early stage of processing; this reflects quantitative rather than qualitative effect ….

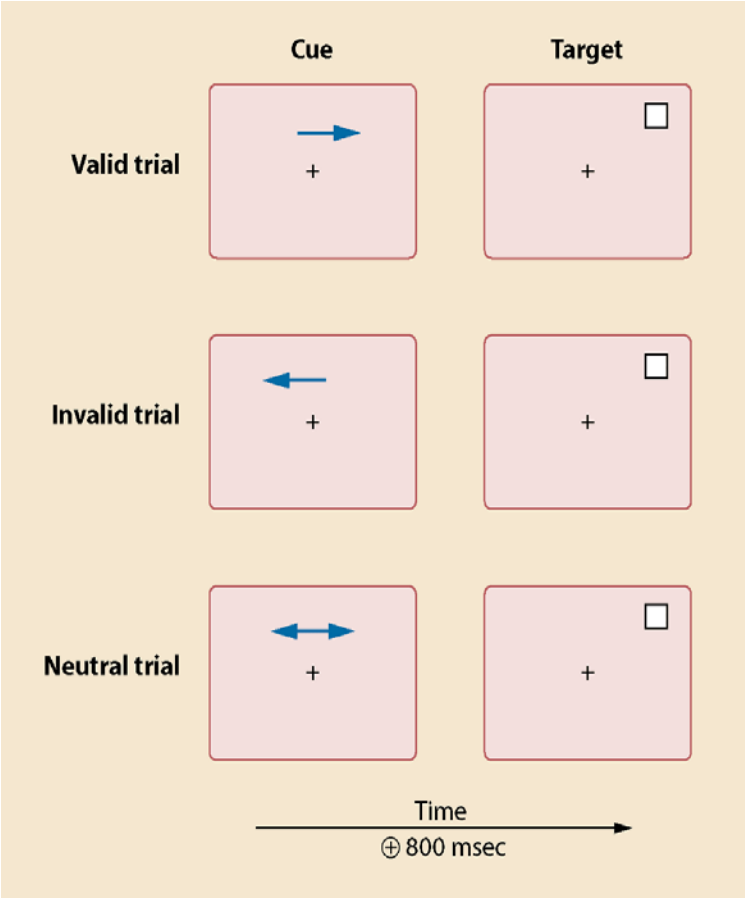
   …and it's early!.

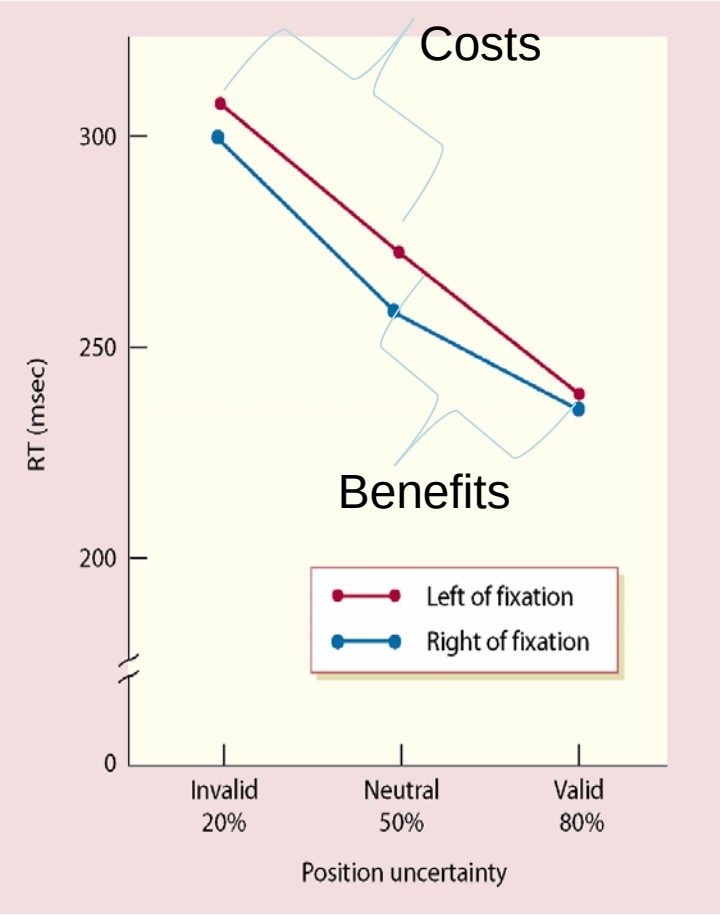
Early studies of attention using ERPs were used to assess two main theories about how attention influences processing.

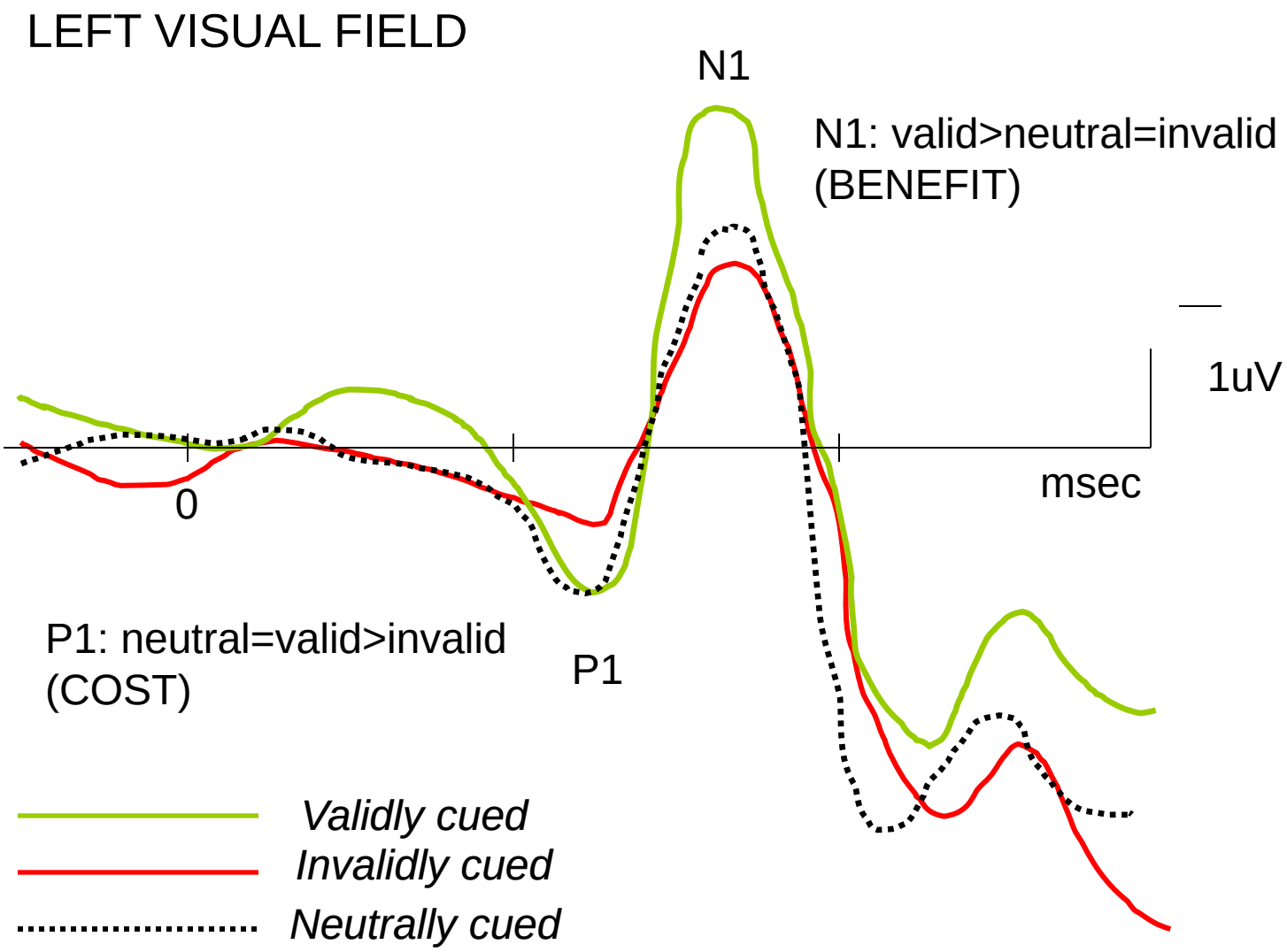
Early selection models: attention acts to filter out unattended information during perceptual processing. Some sensory information is not fully processed – selection of information takes place in a "stimulus set" such that the locus of selection is early in the information processing stream.

Late selection models: all perceptual information is fully analyzed. Attention then acts on the "response set" changing the response criterion associated with attended vs unattended stimuli such that the locus of selection is relatively late. Limit is in memory, decision or response not sensory processing system.

Behavior reflects combined influence of early and late stages!


Cue
Target
Valid trial
Invalid trial
Neutral trial
Time
⊕ 800 msec


Costs
Benefits
RT (msec)
300
250
200
0
Left of fixation
Right of fixation
Invalid
20%
Neutral
50%
Valid
80%
Position uncertainty


LEFT VISUAL FIELD
N1
N1: valid>neutral=invalid
(BENEFIT)
1uV
0
msec
P1: neutral=valid>invalid
(COST)
P1
Validly cued
Invalidly cued
Neutrally cued

Benefits of valid cue, of correctly allocating attn

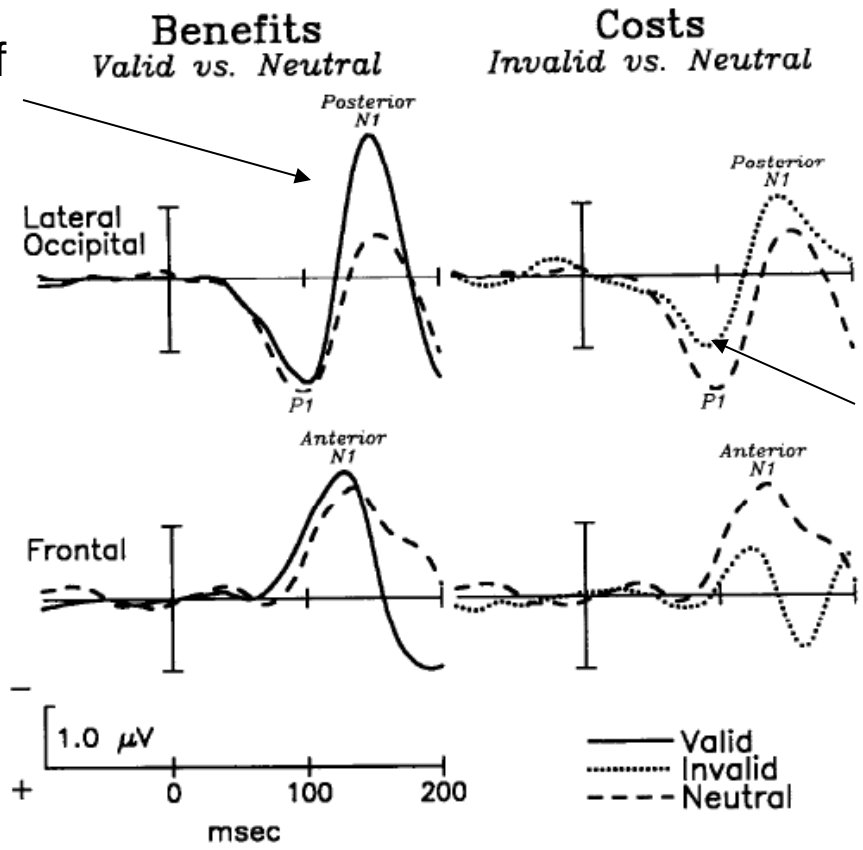


Figure 6. Lateral occipital and frontal waveforms from Figure 5, presented on expanded scales to make the early attention effects clearer. The left traces compare valid and neutral trials to show the benefits of attention, whereas the right traces compare invalid in neutral trials to show the costs of attention.

costs of invalid cue, e.g., need to switch misdirected attn

Luck et al. 1994

P1 and N1 are both affected by spatial attention and occur close in time but reflect different aspects of spatial attention. Best seen in cuing paradigms (attention directed to specific locations by explicit verbal instructions or symbolic cues).

N1 component

- larger for valid than invalid, ***but only when discrimination of stimulus features is required (not with simple detection).***

→ enhanced at attended location relative to neutral, but not suppressed relative to neutral at ignored location – ***benefits of attention***

Valid> Invalid = Neutral

- Benefit of attention correctly pre-allocated to a location
- related to discrimination
- inferior occipital temporal cortex of ventral stream, ~150 ms

P1 component

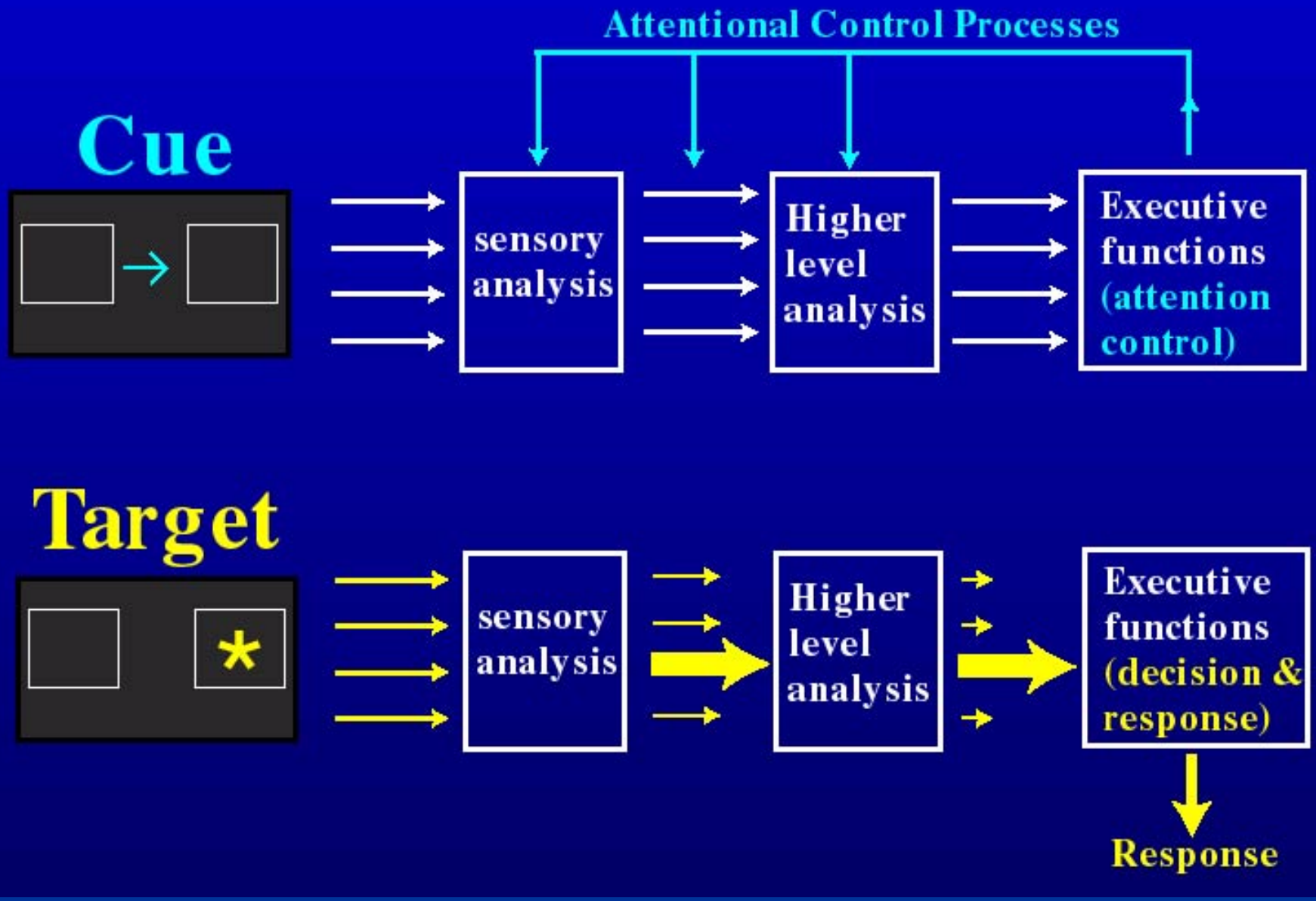
- larger for valid than invalid, whether or not discrimination required

→ suppressed at ignored location relative to neutral, but not enhanced relative to neutral at attended location – ***cost of attention***

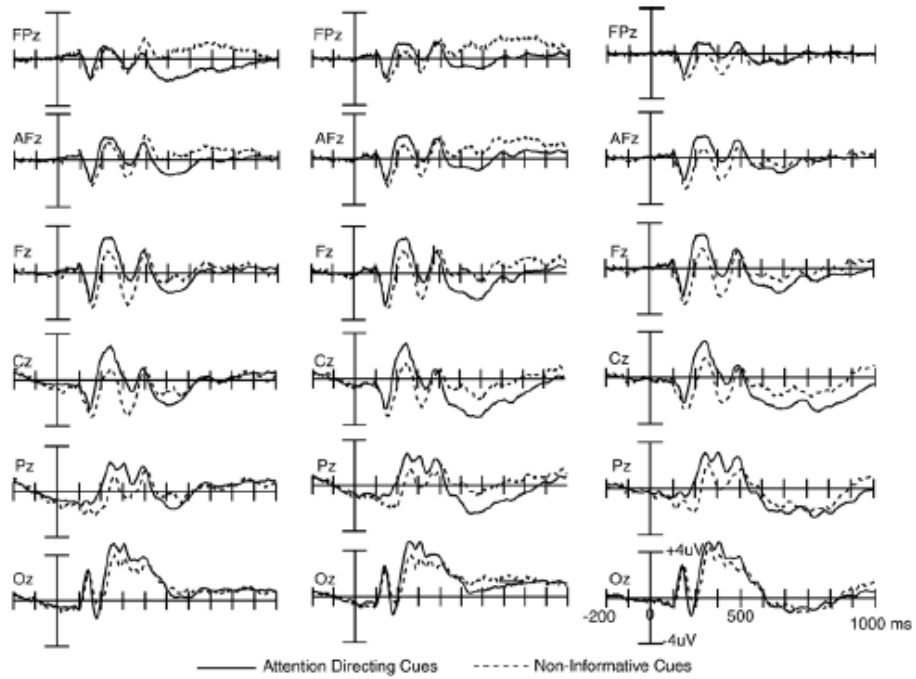
Valid = Neutral > Invalid

- Need to shift attention when it has been misdirected
- early sensory gain control, suppress noise at ignored location

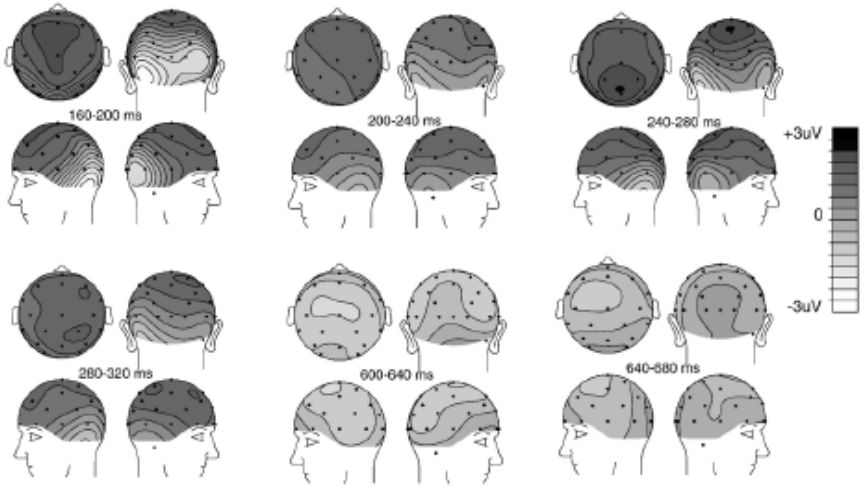
Cueing Paradigm: Cue-Target Interval


Attentional Control Processes
Cue
sensory analysis
Higher level analysis
Executive functions (attention control)
Target
*
sensory analysis
Higher level analysis
Executive functions (decision & response)
Response

CUE-TARGET INTERVAL IN SPATIAL CUEING TASK (INFORMATIVE VS NONINFORMATIVE CUE)



a) Short Cue-Stimulus Interval b) Intermediate Cue-Stimulus Interval c) Long Cue-Stimulus Interval



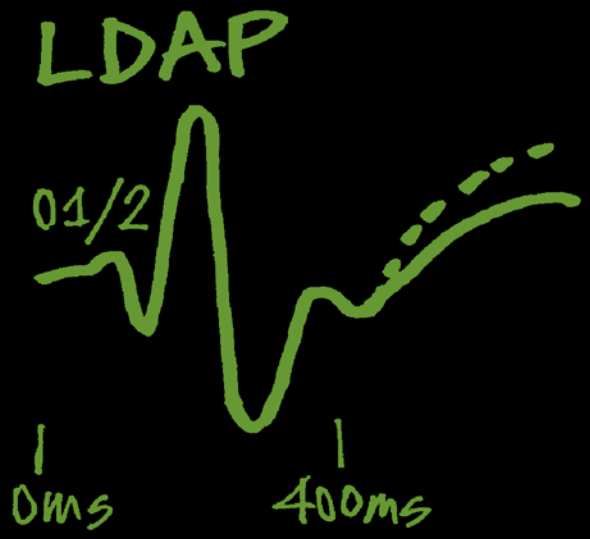
d) Scalp Topographies Based on the Long Cue-stimulus Interval in 40 ms Bins

Broadly distributed positivity
~140 ms to informative cue

ERP deflections

Anterior Directing Attention Negativity

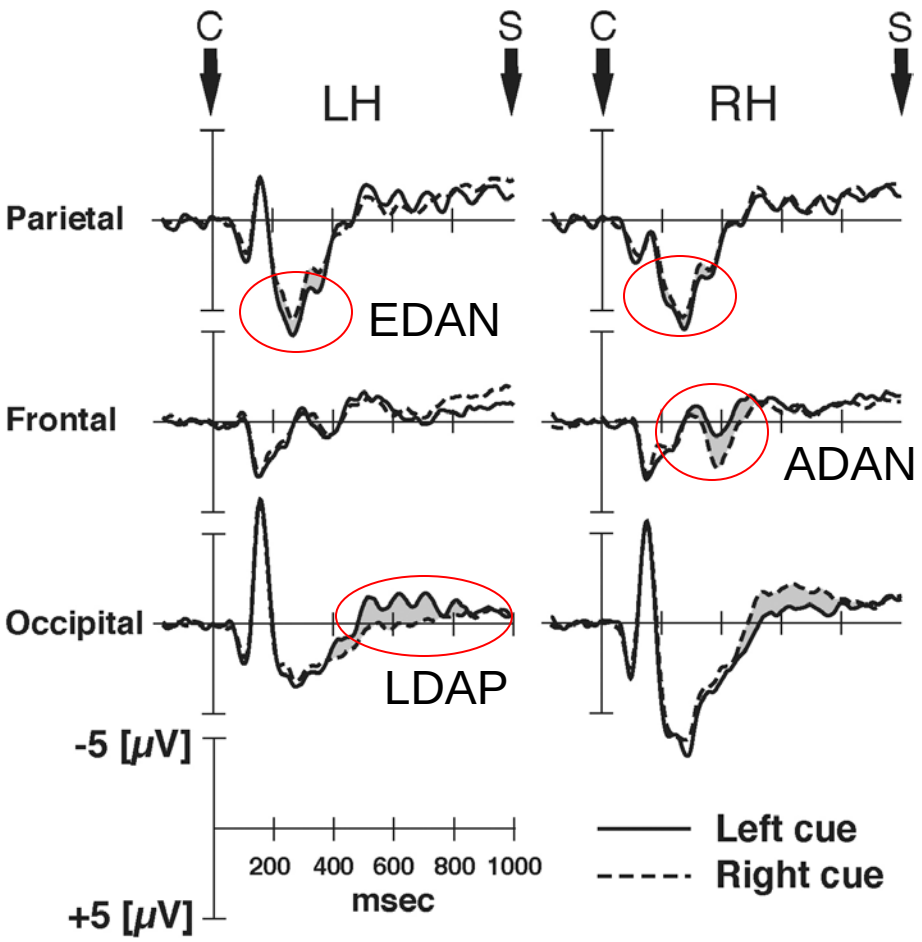
- In studies where attention is cued to either left or right, the ADAN is largest over contralateral frontal sites. In the somatosensory modality, the ADAN follows where your hand is. If your hands are crossed, the ADAN appears on ipsilateral sites. It seems to operate on somatotopically defined cordinates. A version of ADAN was called EDAN by Harter et al. (1989), supposedly the correlate of the decoding of the attentional cue ("early" directing...)
- The ADAN is bigger in response to stimuli in the lower visual field

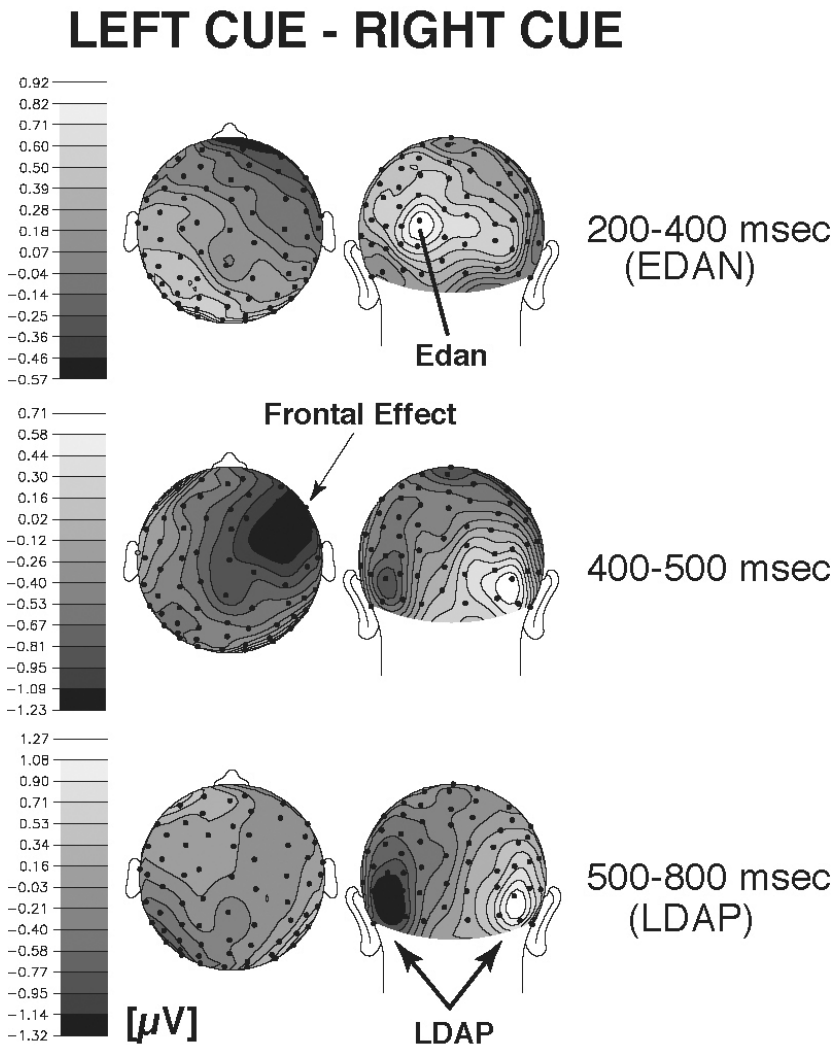


Late Directing Attention Positivity

- In contrast to the ADAN, the posterior LDAP component reflects feature encoding based on **external** representation of space. It does not depend on where your hand is, and some think that it reflects preparatory activation of sensory-specific visual areas. LDAP is bigger for upper-field stimuli
- **Comment:** Some researchers wonder how robust these effects are. If you are interested to learn more detail about this issue, Eimer et al. (2004) is a good start

ATTENTIONAL CONTROL MECHANISMS DURING CUE-TARGET INTERVAL?





Multiple ERP effects to Cues in Spatial Cueing Task

EDAN – early directing attention

posterior parietal negativity, 200-400 ms after cue
control process that acts on sensory areas to modulate excitability of neurons in attended regions of space (Harter)

- appreciation of the meaning of the symbolic cue and resulting redirecting of attention, originating from parietal areas.

LDAP – late directing attention positivity

occipital positivity, 500-700 ms after cue
scalp distribution similar to P1
excitability modulation (Harter); biasing of neural activity in visual regions that may be responsible for subsequent selective processing of stimuli in attended locations (i.e., priming of visual processing regions in response to instructive cues. biasing of activity in visual sensory areas, driven by a supra-modal attention directing process.

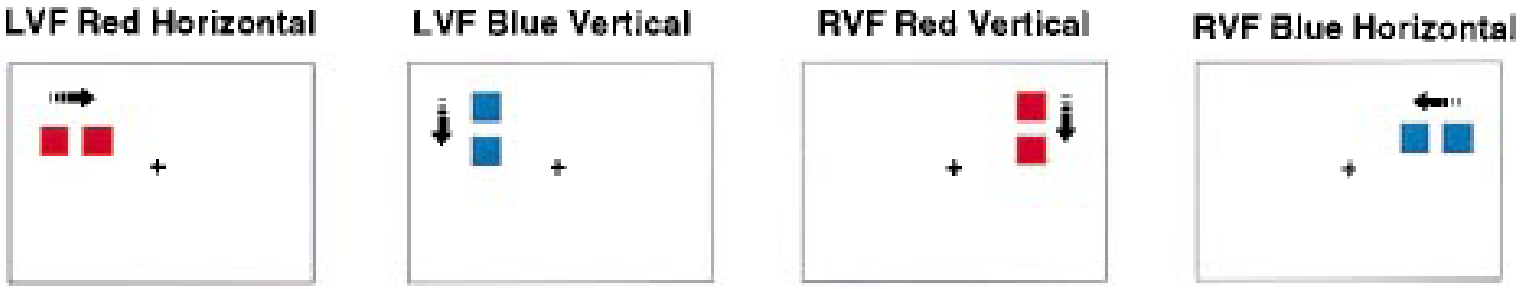
ADAN – **anterior directing attention negativity**

frontal effect between EDAN and LDAP

Is space/location special?

What about selection based on other visual features?

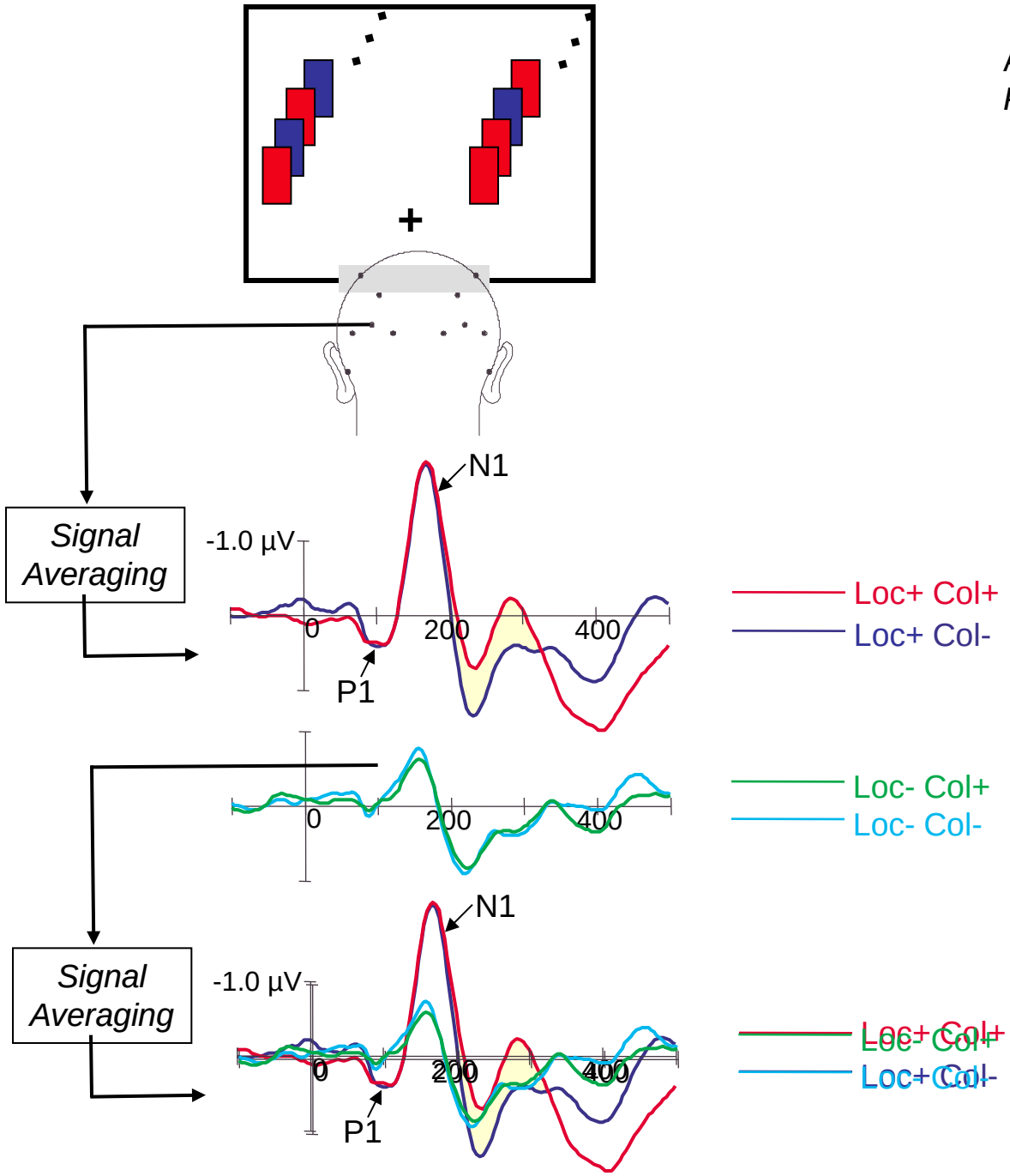
How completely is information at unattended locations suppressed by spatial attention? For example, is processing of stimulus features such as color suppressed at unattended locations?



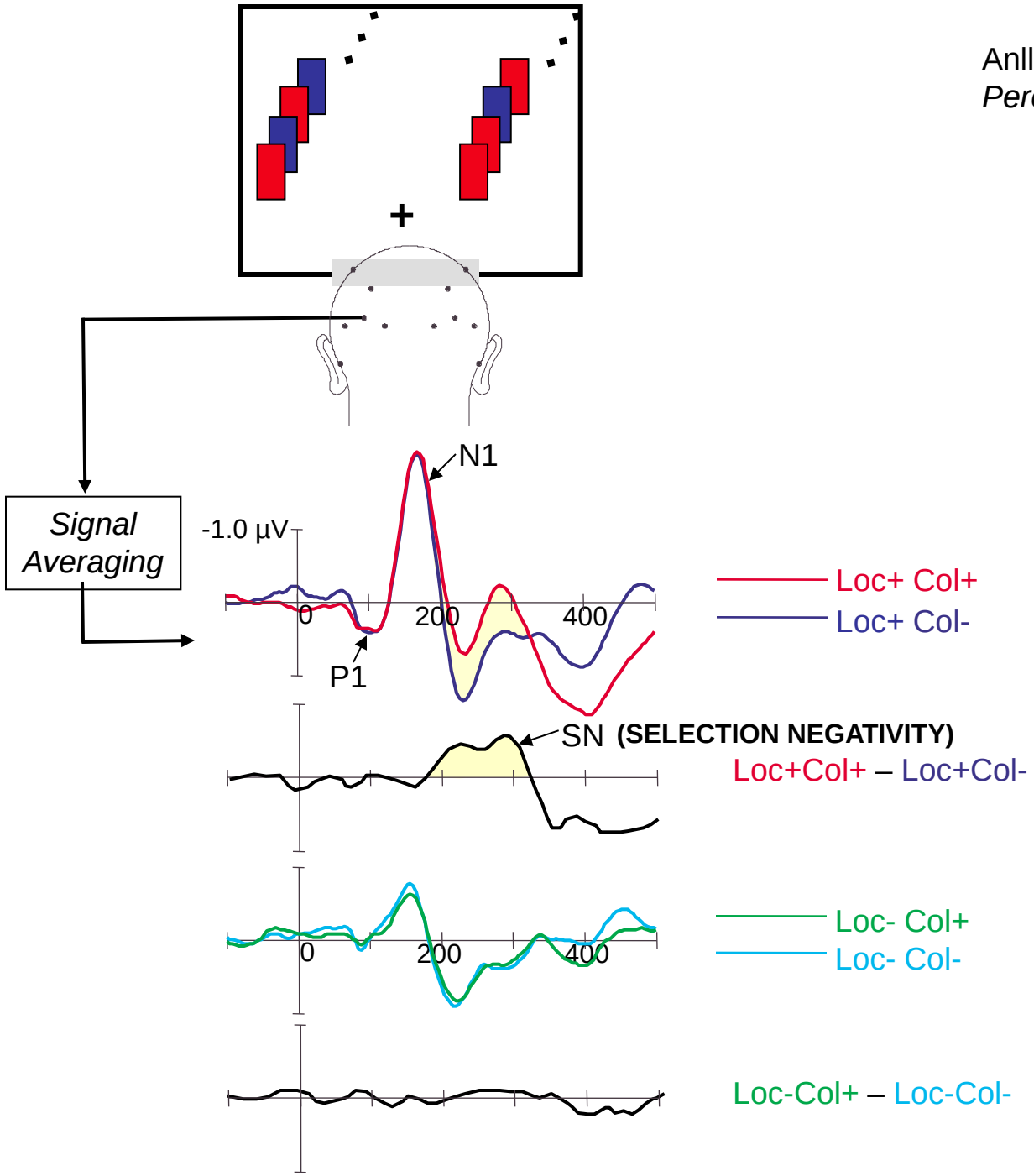
Location: right or left visual field
Color: red or blue
Movement Direction: vertical or horizontal
Target: slow versus fast apparent movement
Task: respond to slow moving target in attended location and color

Anllo-Vento & Hillyard

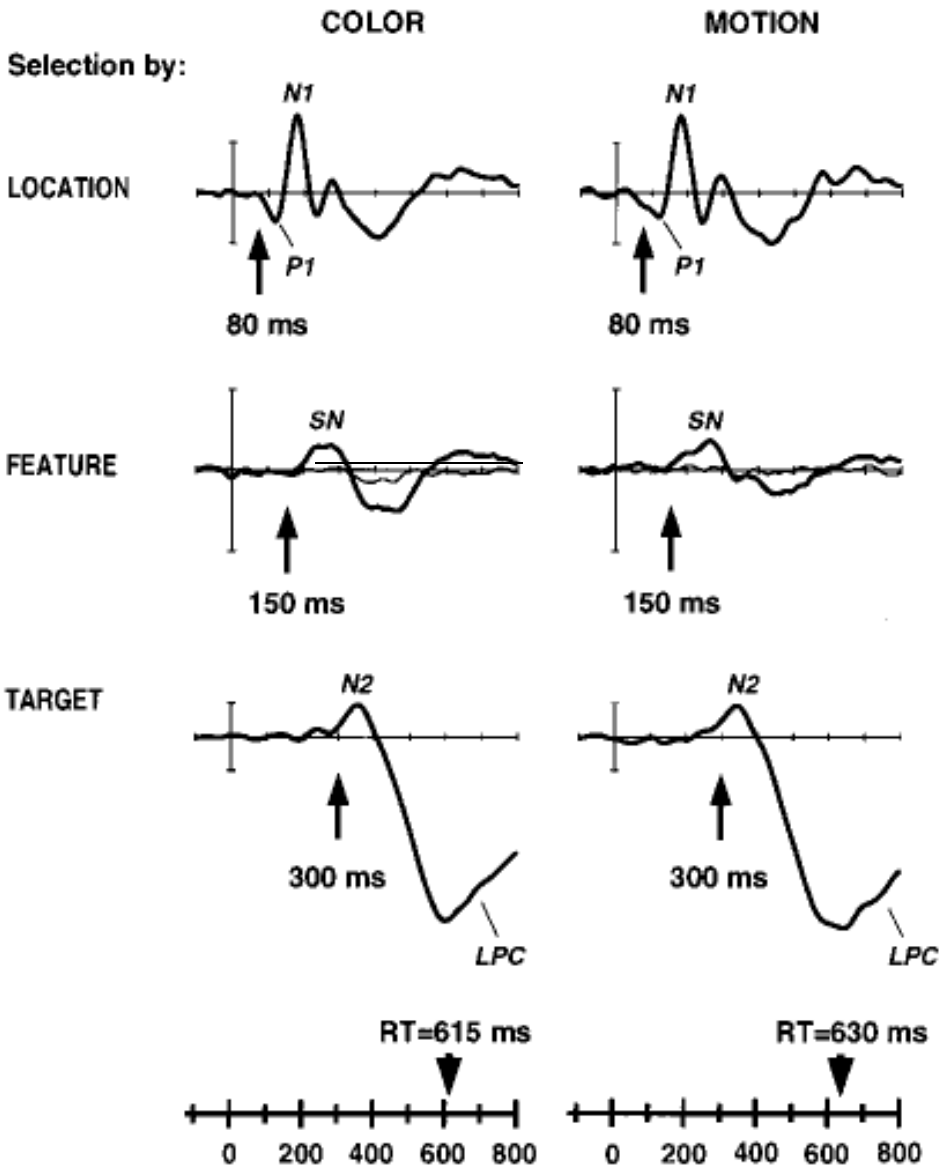
Anllo-Vento and Hillyard, 1996
Perception & Psychophysics



Anllo-Vento and Hillyard, 1996
Perception & Psychophysics



ATTEND



Unattended location

Attended location

More color selection
ERP effects

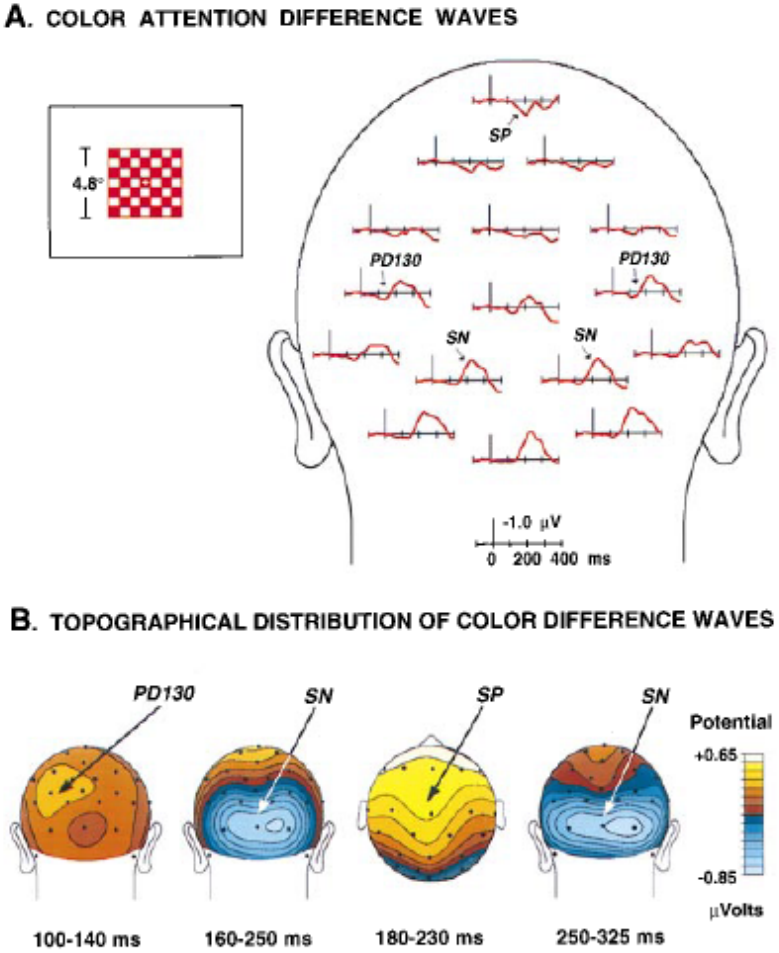


FIG. 3. (*A*) Grand average ERP difference waves in a color task (43) in which red and blue flashed checkerboards were presented in a rapid, randomized sequence at the center of the screen. Stimulus durations were 100 ms, and stimulus onset asynchronies ranged from 150 to 450 ms. Either the red or blue checks were attended on separate runs. Difference waves were formed by subtracting ERPs to the unattended color from those to the attended color, collapsed over red and blue stimuli. Attention-related components include a posterior selection negativity (SN), an anterior selection positivity (SP), and an early positive difference (PD130). (*B*) Scalp voltage distributions of attention-related ERP difference components at different latency ranges.

Conclusions

- Stimuli at attended locations elicit enhanced early P1 and N1 components over occipital brain regions. P1 amplitudes are enhanced for all stimuli occurring at an attended location, whether those stimuli are the relevant events being discriminated or task-irrelevant probes.

- In contrast, attending to non-spatial features (e.g. ***color, spatial frequency, orientation, shape, and direction of motion***) is associated with a late negative ERP (***selection negativity or SN*****)** between 125+ ms, or sometimes ***selection positivity*****.** Scalp topography of SNs differs as function of feature being selected.

- At unattended locations, the processing of stimulus features (indexed by selection negativity, positivity) is suppressed.

- Spatial attention has a unique, early selection mechanism and dominates the selection of other features. At the earliest stage, spatial attention seems to modulate inputs solely according to their location without regard to their identity. As Anne Treisman says “Space is special”.

1. In which particular visual-cortical areas is sensory input from attended locations amplified, i.e., how early (retina, LGN, Superior colliculus, V1, V2, etc.) in stimulus processing stream is attentional selection?

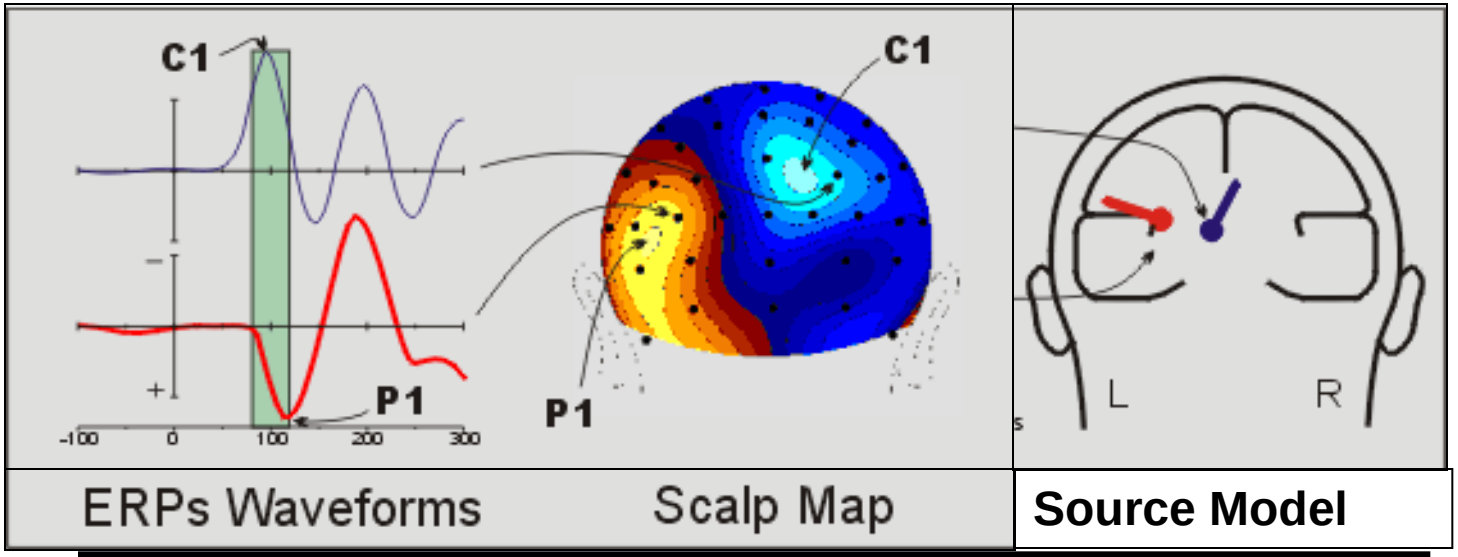
2. In particular, does spatial attention modulate visual input at the level of the primary visual cortex (area V1), as numerous neuroimaging studies have suggested?

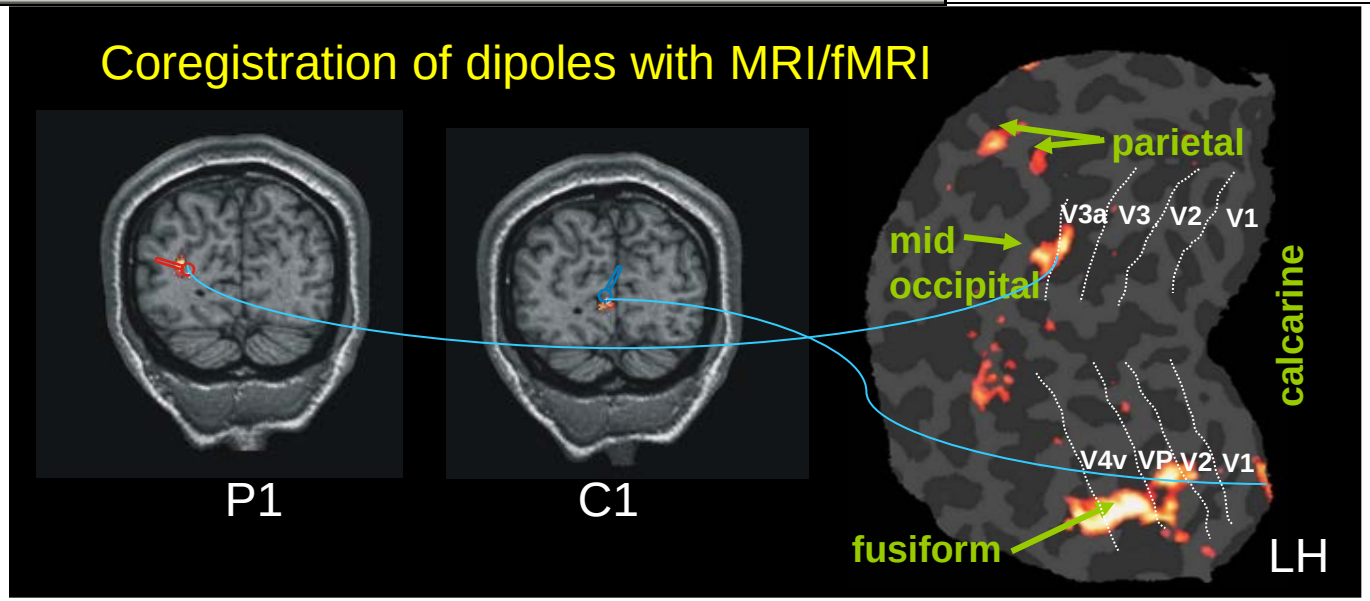
Studies by Steve Hillyard and colleagues over the years have provided strong evidence that the earliest evoked component (C1), which onsets at 50 ms originates primarily from the primary visual cortex (V1).

C1 (can be positive or negative depending on location of stimulus in visual field

Spatio-Temporal Analysis of Brain Activity

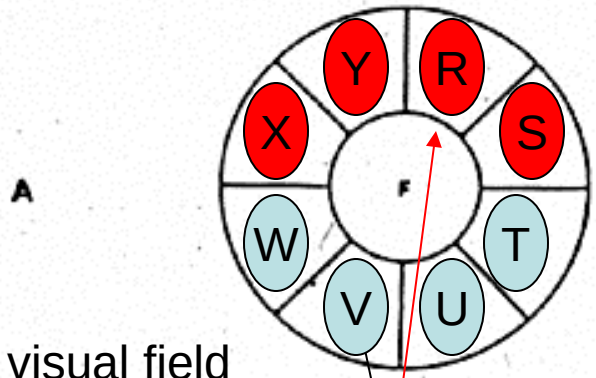
Right field stimulus



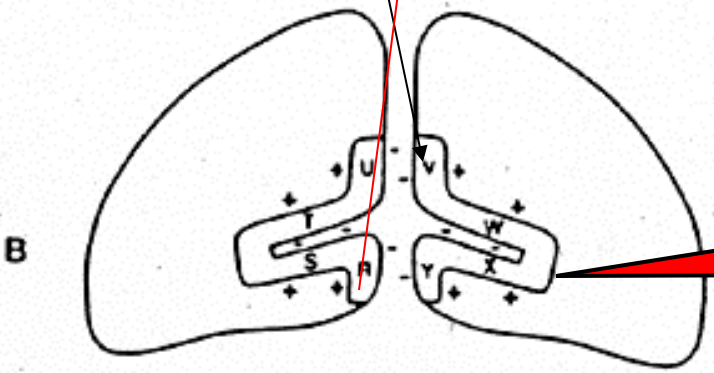


V1 TOPOGRAPHY

Upper visual field
lower bank of calcarine fissure



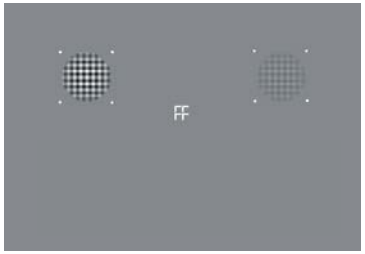
Lower visual field
upper bank of calcarine



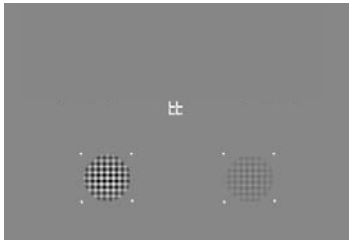
cortical magnification
of the representation
of the fovea

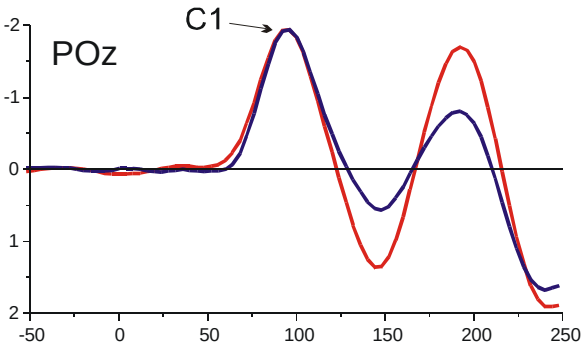
approximate cancellation
of dipoles in periphery

Upper Left Stimulus

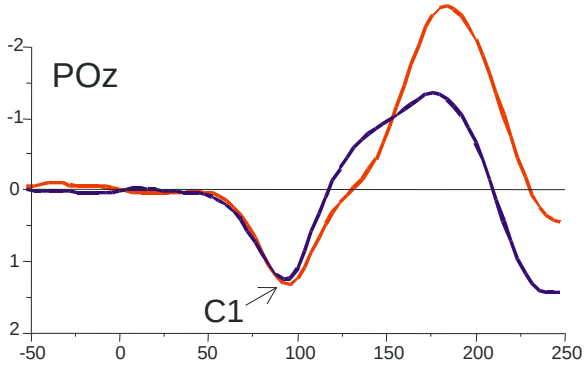


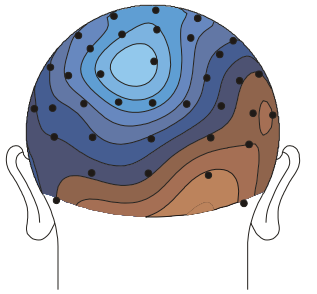
Lower Left Stimulus

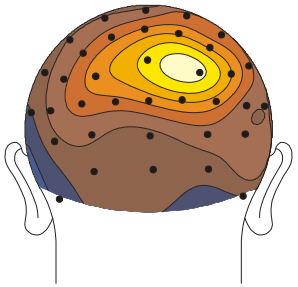


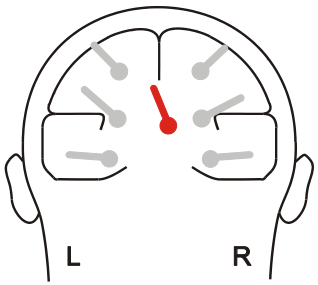


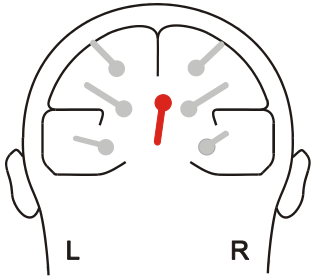
Attended
Unattended



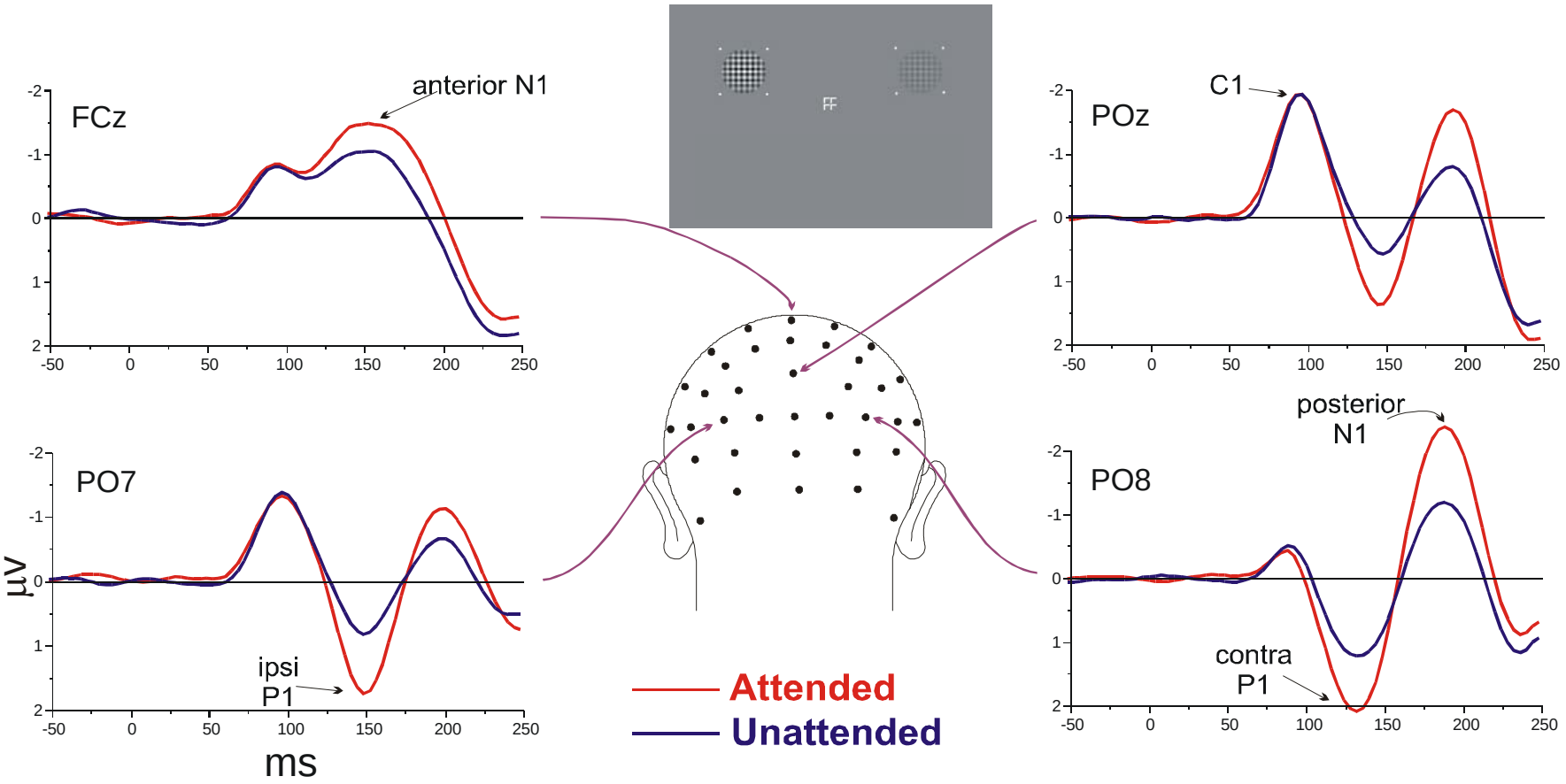




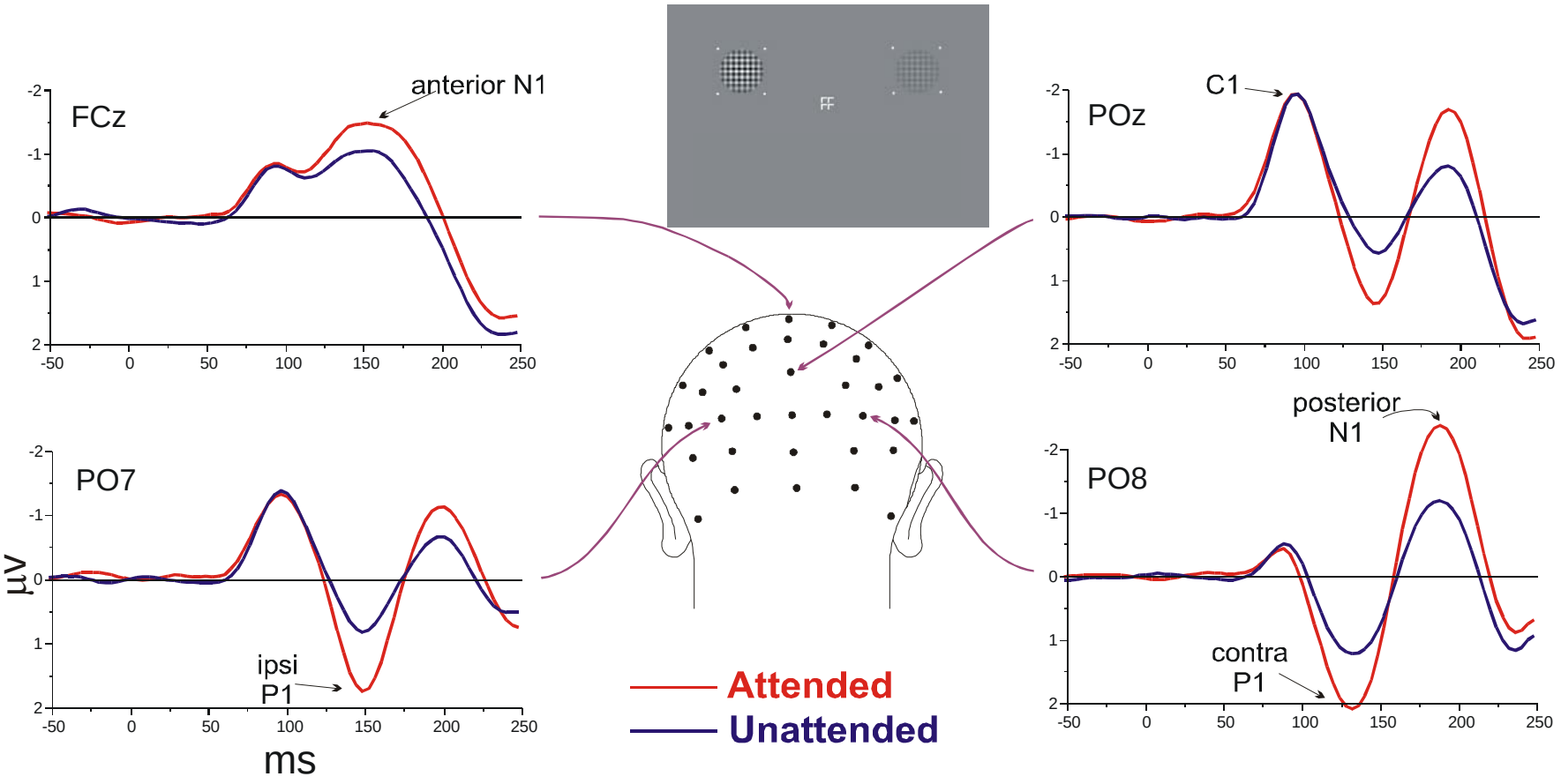




ERPs to Upper Left Stimuli

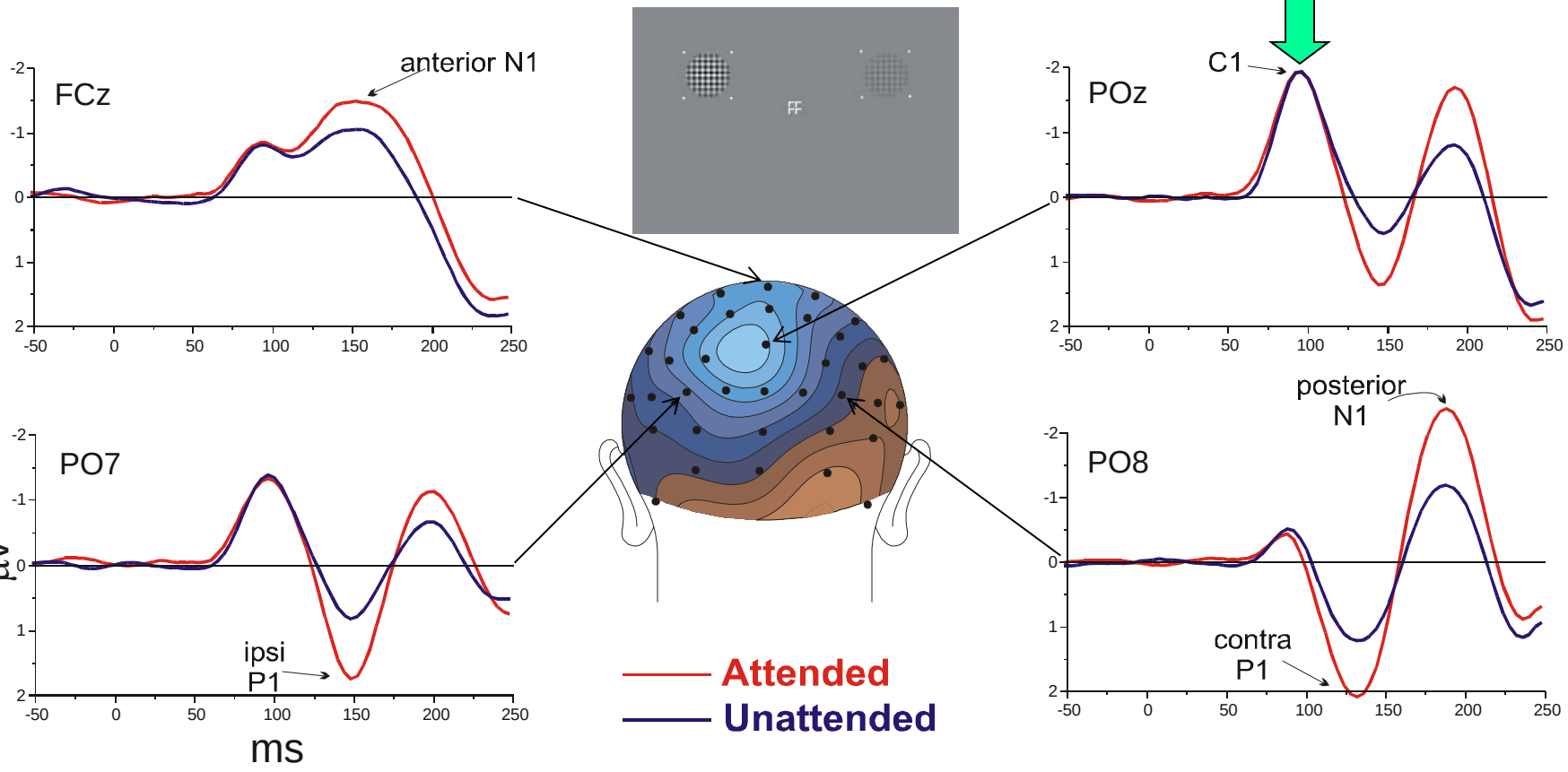


ERPs to Upper Left Stimuli

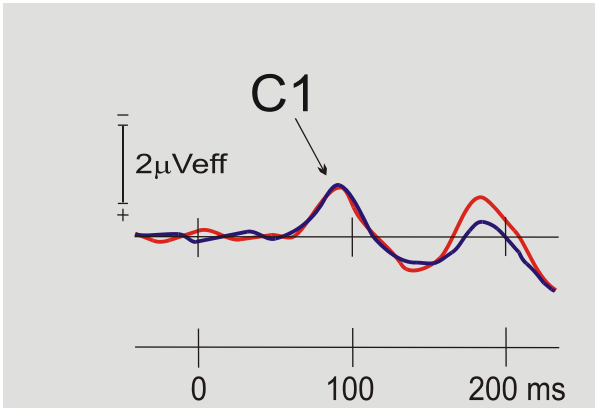


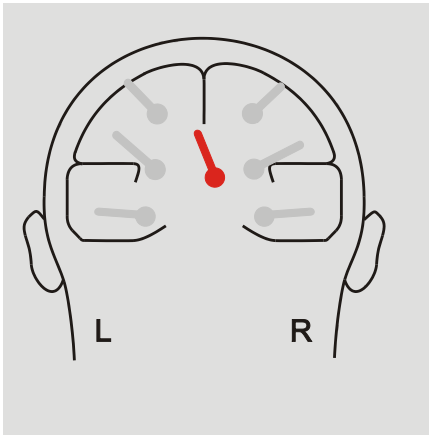
Attended-location stimuli elicit larger P1 and N1 components

But the earlier C1 component is not modulated by spatial attention

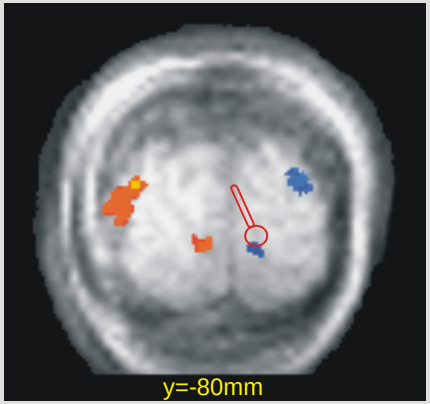


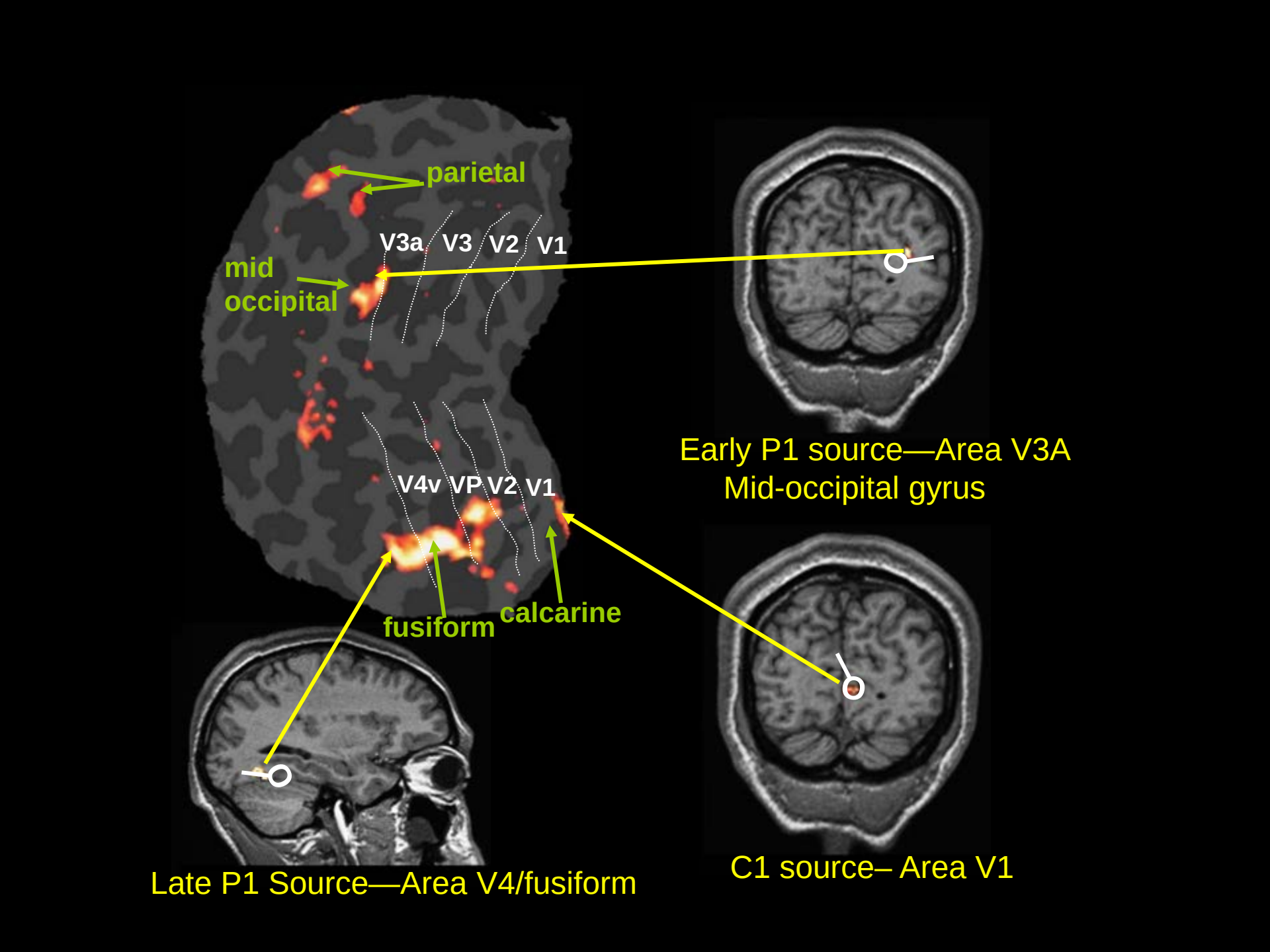
Dipole Model



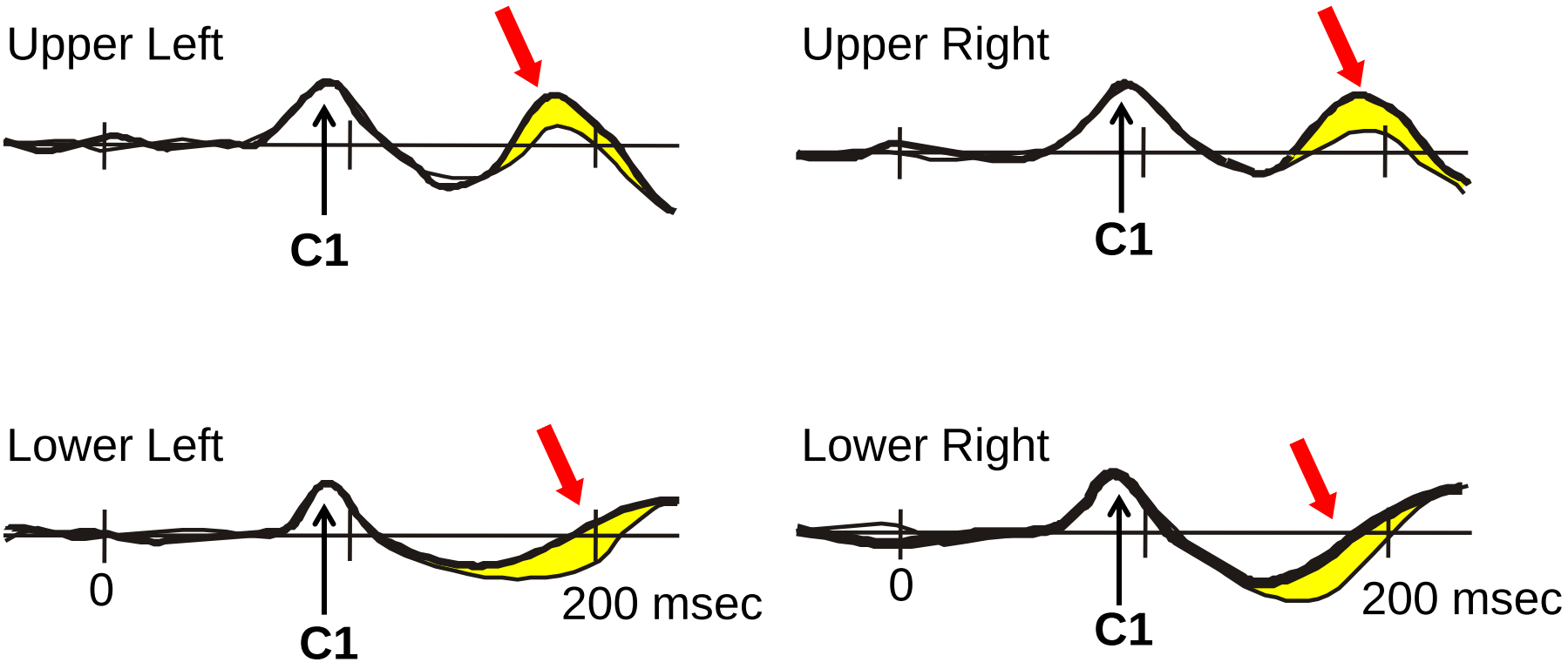


fMRI Co-registration




parietal
V3a
V3
V2
V1
mid
occipital
V4v
VP
V2
V1
fusiform
calcarine
Early P1 source—Area V3A
Mid-occipital gyrus
Late P1 Source—Area V4/fusiform
C1 source– Area V1

Late Activity of V1 Source is Modulated by Attention for Stimuli in All Quadrants



Visuospatial selective attention: P1 and N1 neural generators

(Based on dipole source modelling and co-registration with PET and fMRI)

P1 generators

(a) *initial phase (80-100 ms)*
mid-occipital, in/near V3/V3a & immediately anterior middle occipital gyrus

(b) *later phase (100-130 ms)*
ventral occipital cortex near V4, and adjacent fusiform gyrus

Posterior N1 generators (attention-sensitive): 3 subcomponents

(a) *early frontal (140 ms) and posterior parietal phases (140-160)*

(b) *later ventral occipital-temporal phase (160-200)*

Early modulations of visual evoked neural activity by the spatial focussing of attention occur at multiple sites along the extrastriate visual pathways.

Conclusions

- Earliest ERP attention effect is amplitude modulation of the P1 component generated in region of V3a/mid-occipital gyrus in dorsal stream (~80 msec) and in region of V4/fusiform gyrus in ventral stream (~100 msec)

- This ERP amplitude modulation appears to reflect a mechanism of sensory gain control. Visual information is amplified at attended locations and suppressed at unattended locations.

- This amplified information is fed forward to higher visual areas for further analysis and is also fed back to area V1. Net effect is to increase perceptual salience of stimuli in the spotlight of spatial attention.

Conclusions

1. Spatial attention does not affect initial evoked response (C1) in striate cortex (V1) at 50-80 msec.

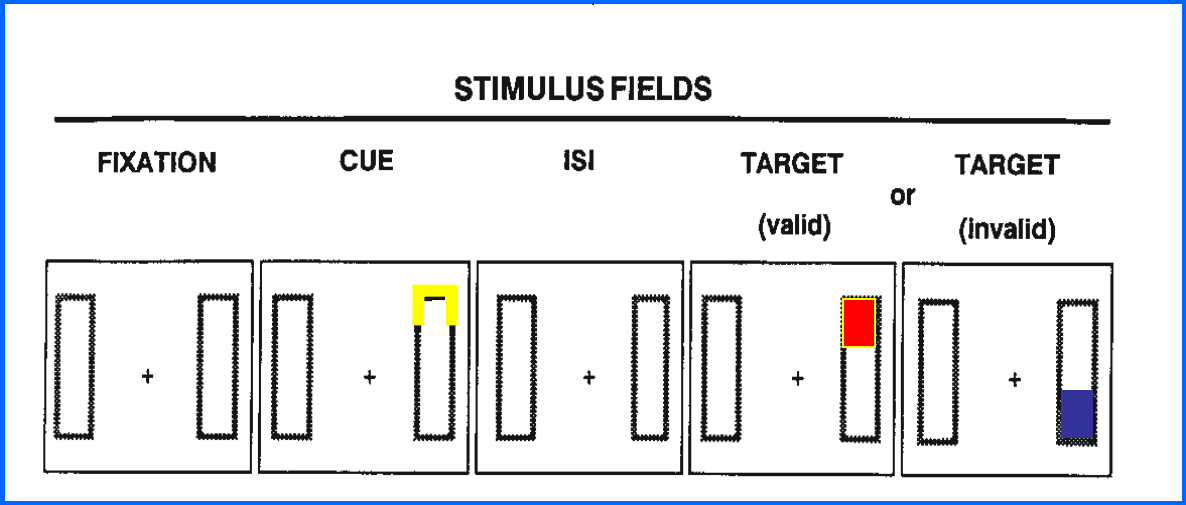
2. Argues against an early selection or “gate-keeping” at level of V1 or LGN.

3. Delayed attention effect (seen in fMRI) in area V1(130-150 msec) most likely due to feedback from higher areas.

Spatial vs. Object-Based Attention

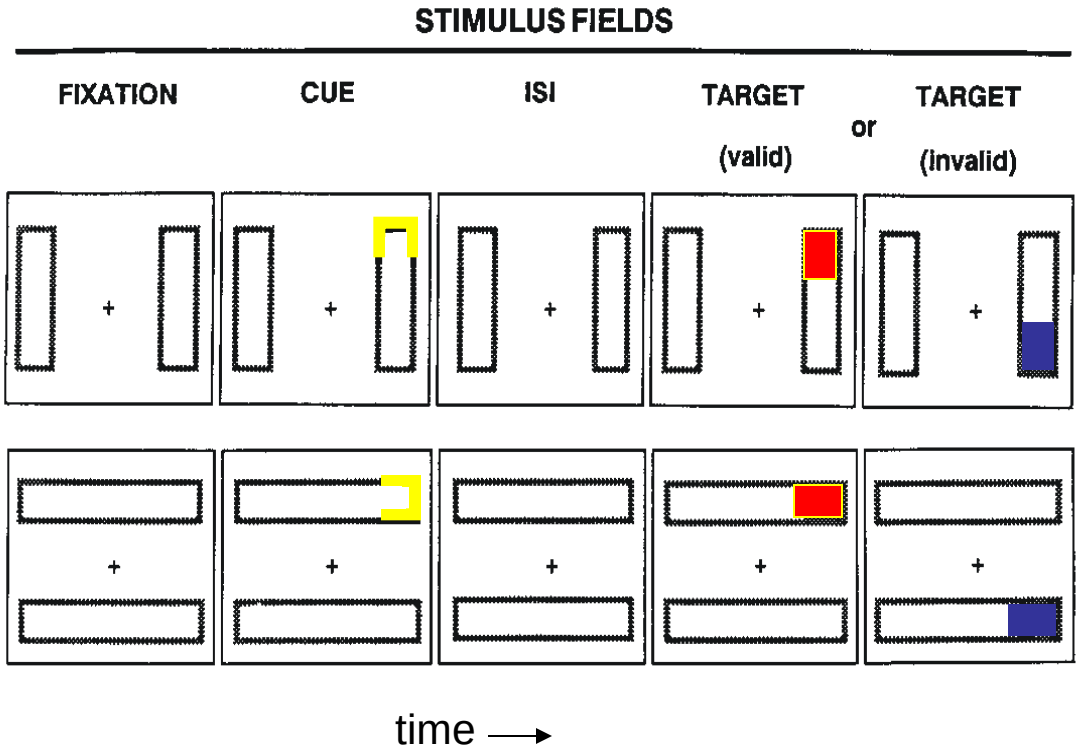
- Spatial attention selects all stimuli at attended location (within the “spotlight”).
- Attention can also be directed towards objects, selecting the entire object and all of its properties together.
- Key evidence for object-based attention: Paying attention to one part of an object improves processing of its other parts (*Egly et al. 1994*).

Experimental Design: *Egly et al. (1994)*



time ⟶

Experimental Design: *Egly et al. (1994)*



Egly, Driver & Rafal 1994

Egly et al. (1994)

- Both space-based and object-based effects were observed.

  - Valid (attended) targets were responded to faster than invalid (unattended).

  - however, invalid targets were responded to faster when they appeared at the other end of the attended object (known as ***same object advantage***).

We have a behavioral phenomenon. We need an explanatory mechanism.

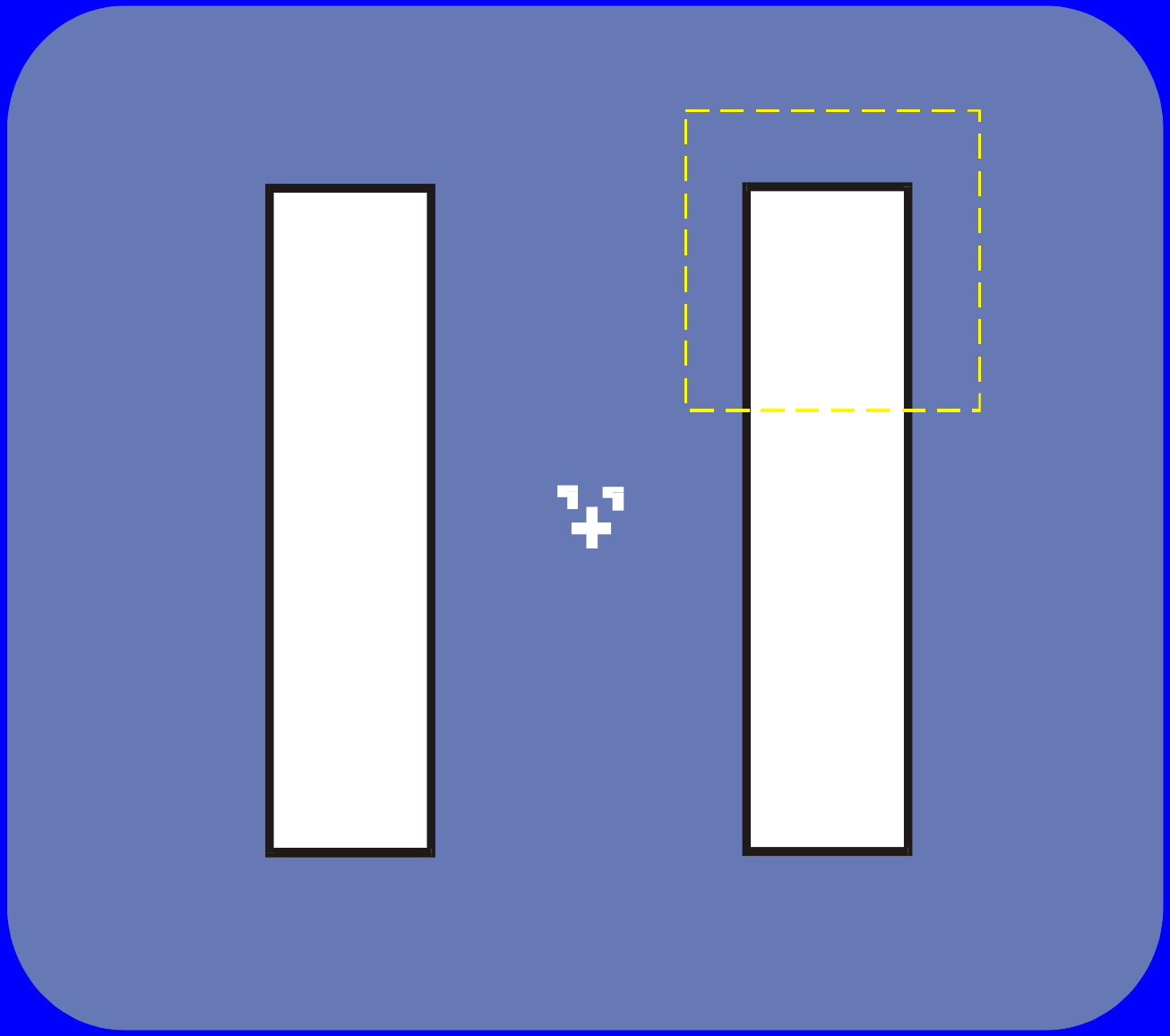
Can ERPs be helpful in finding mechanism?
Find precise question, then appropriate paradigm and design, then use hypothesis to generate predicted outcome (along with other potential outcomes) and inferences

Some open questions to test

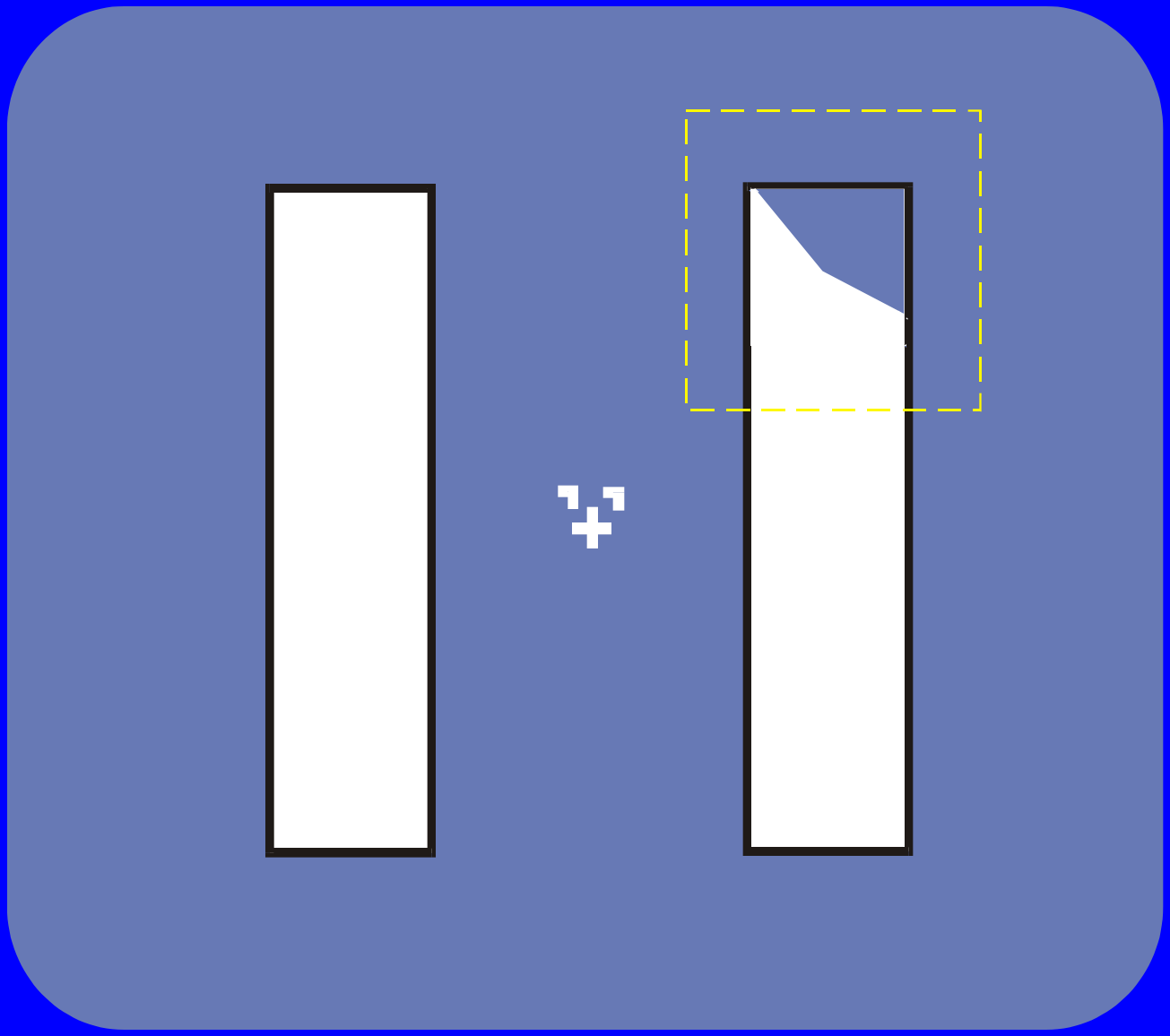
1. Do spatial and object-based attention use fundamentally different selection mechanisms at different levels of the visual pathways?

2. Or, does spatial attention tend to “spread” within object boundaries, selecting the entire object including all its parts?

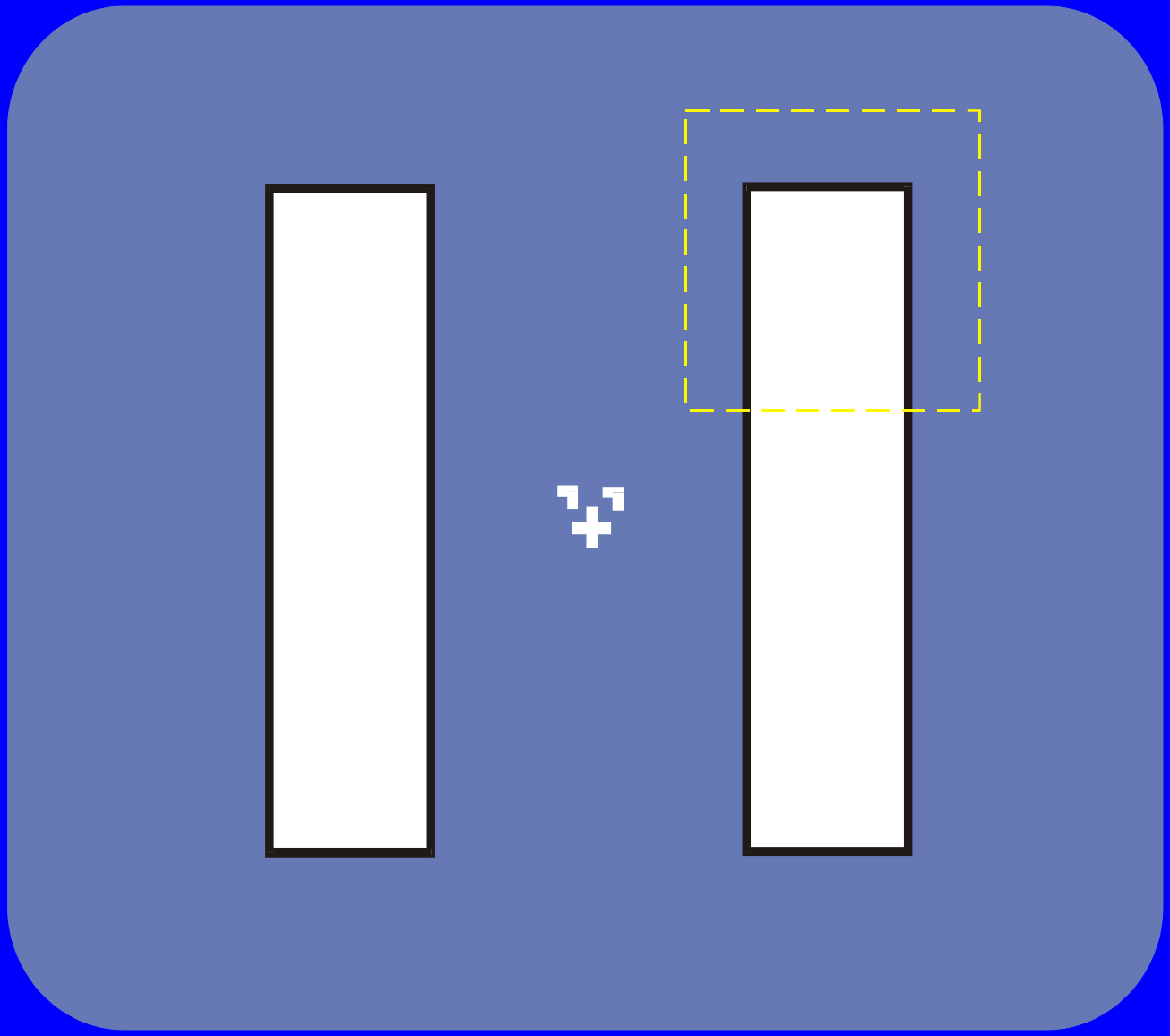
Experimental Design



Experimental Design



Experimental Design



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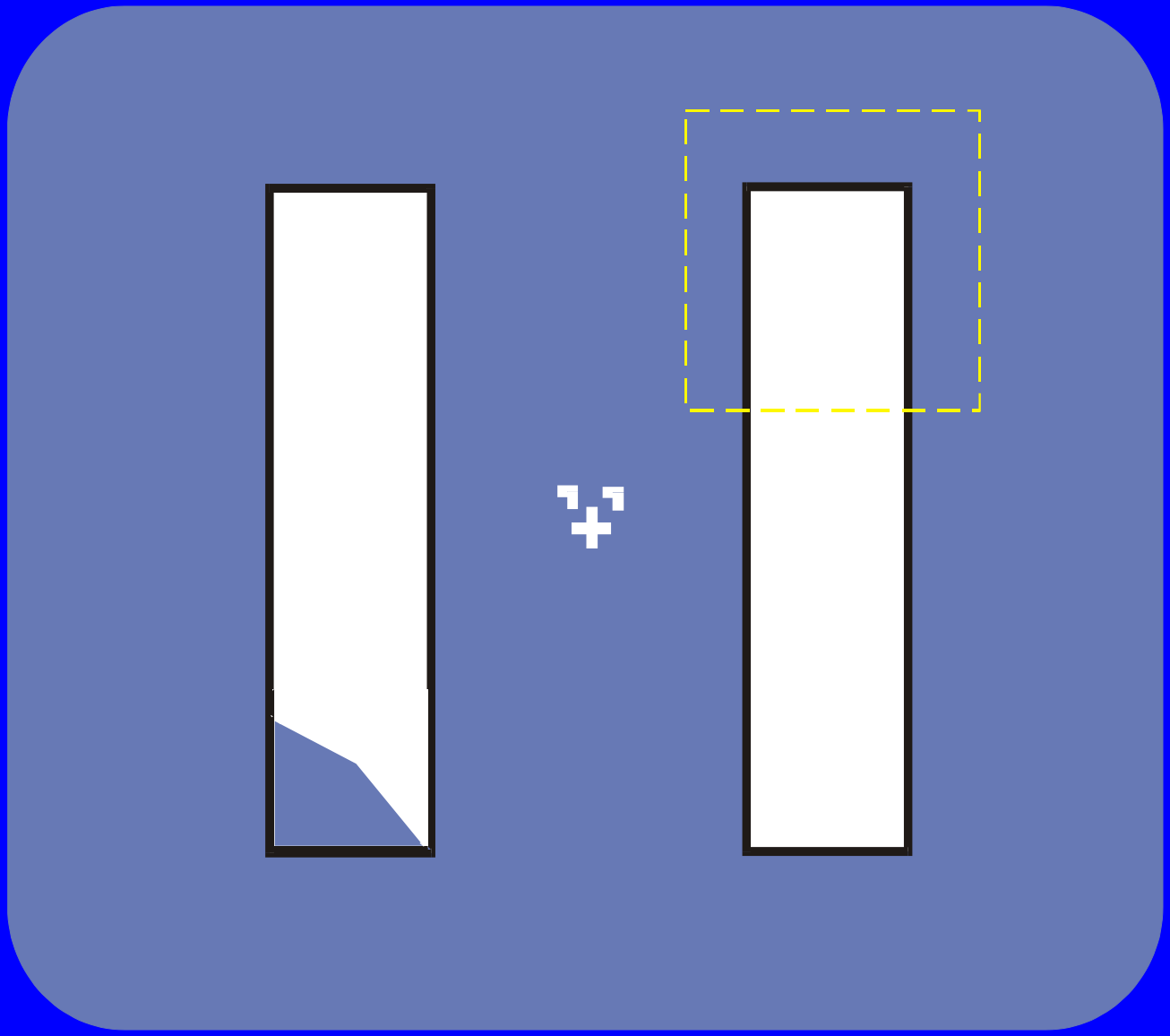

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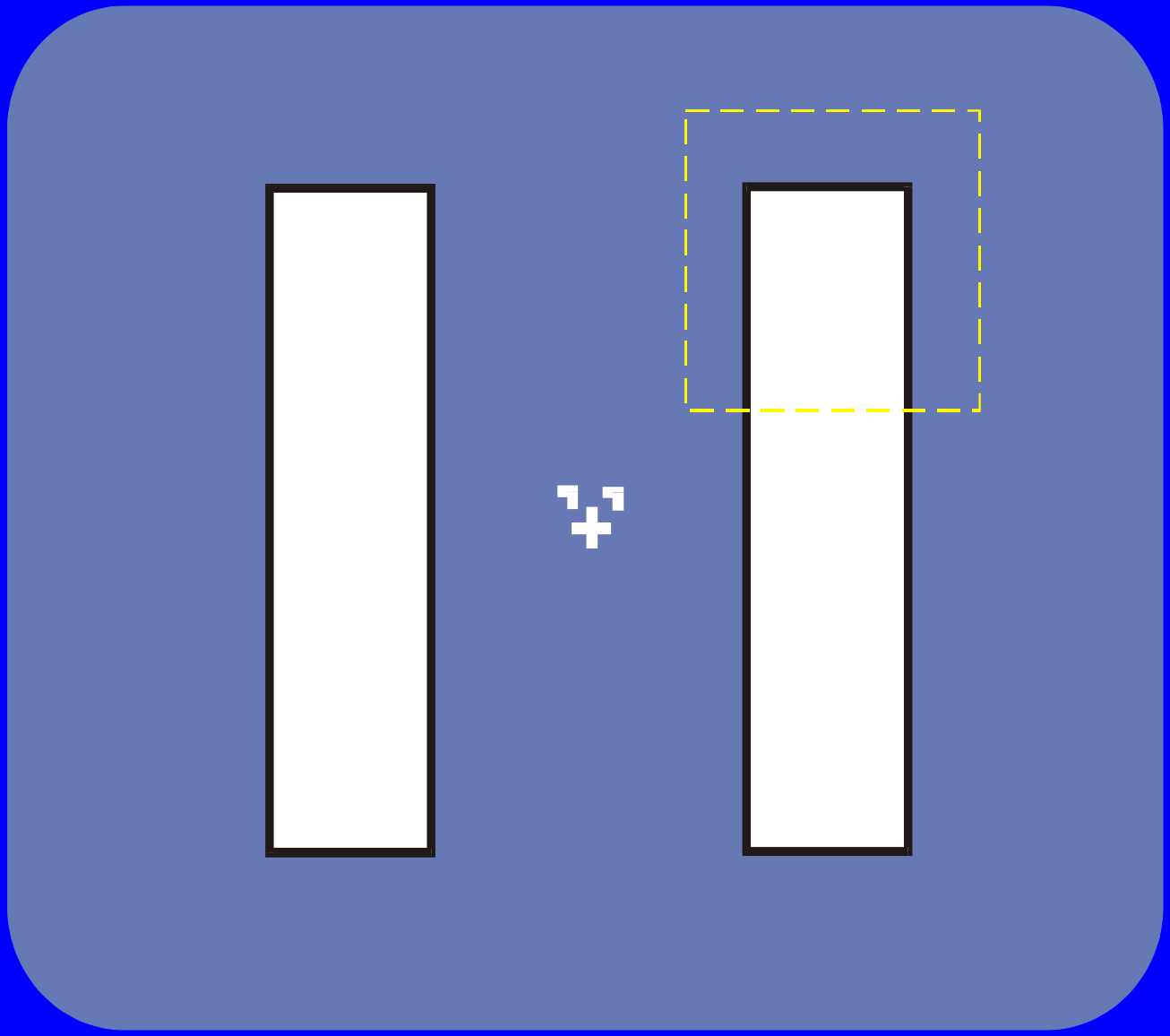

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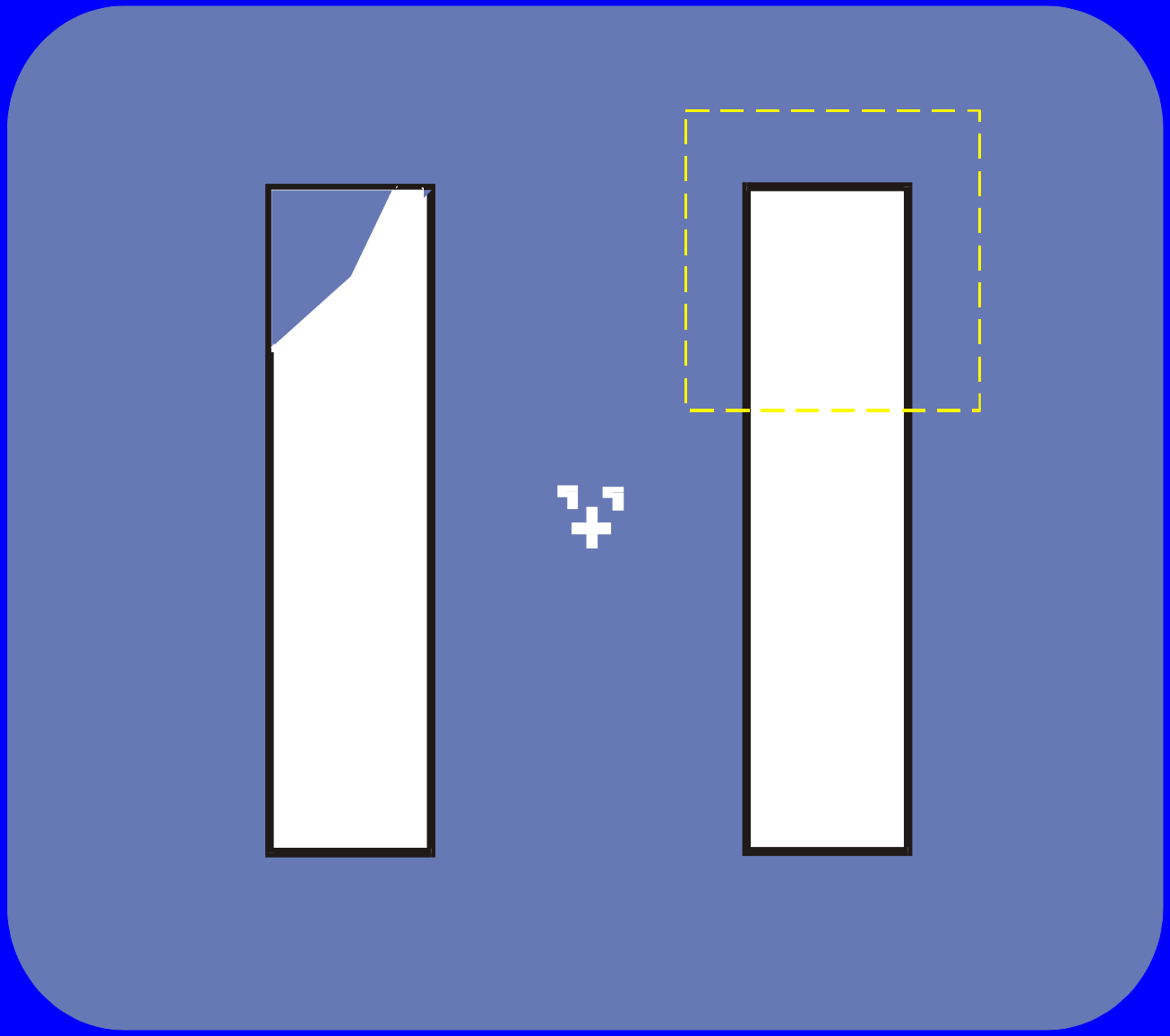

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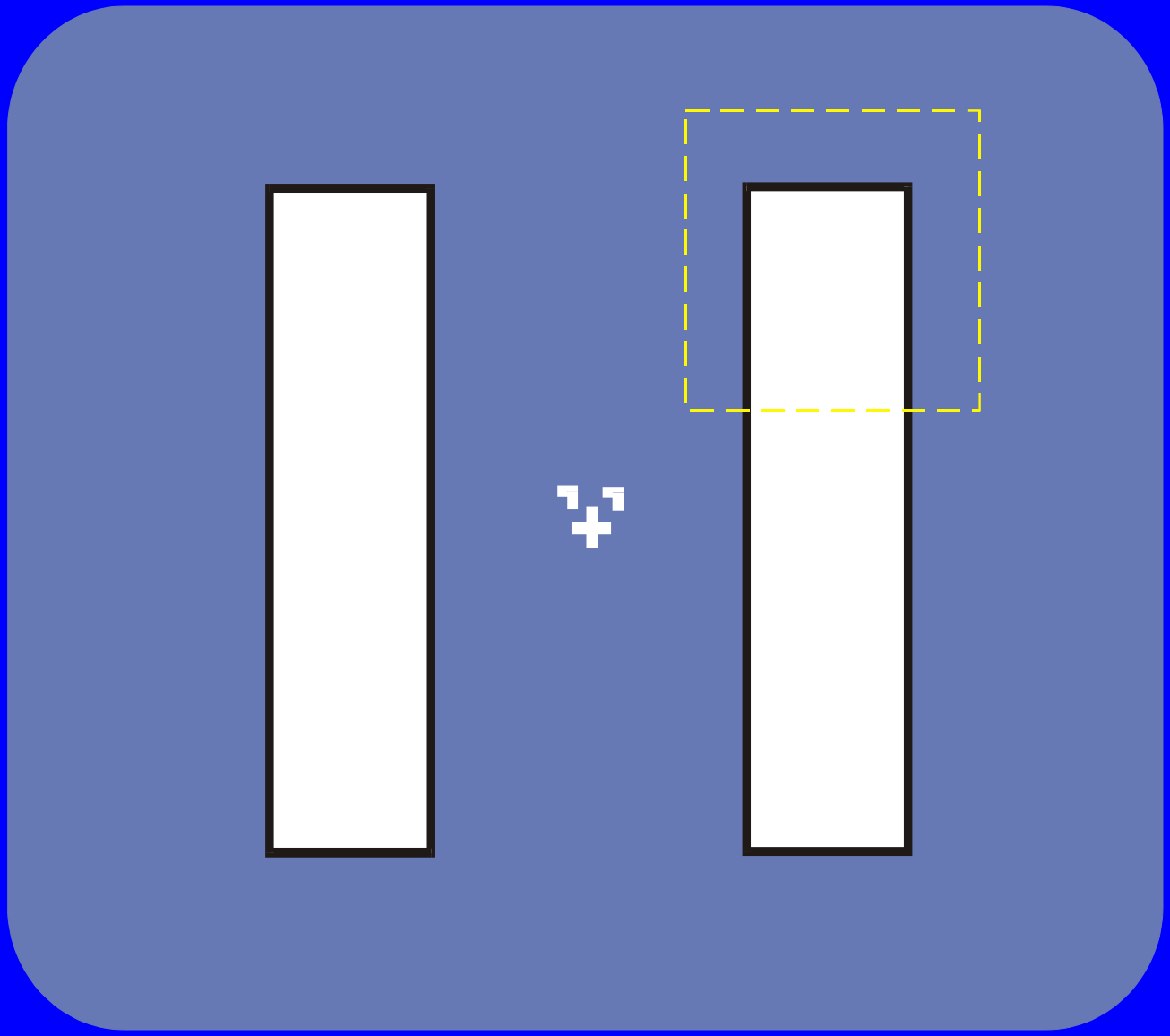

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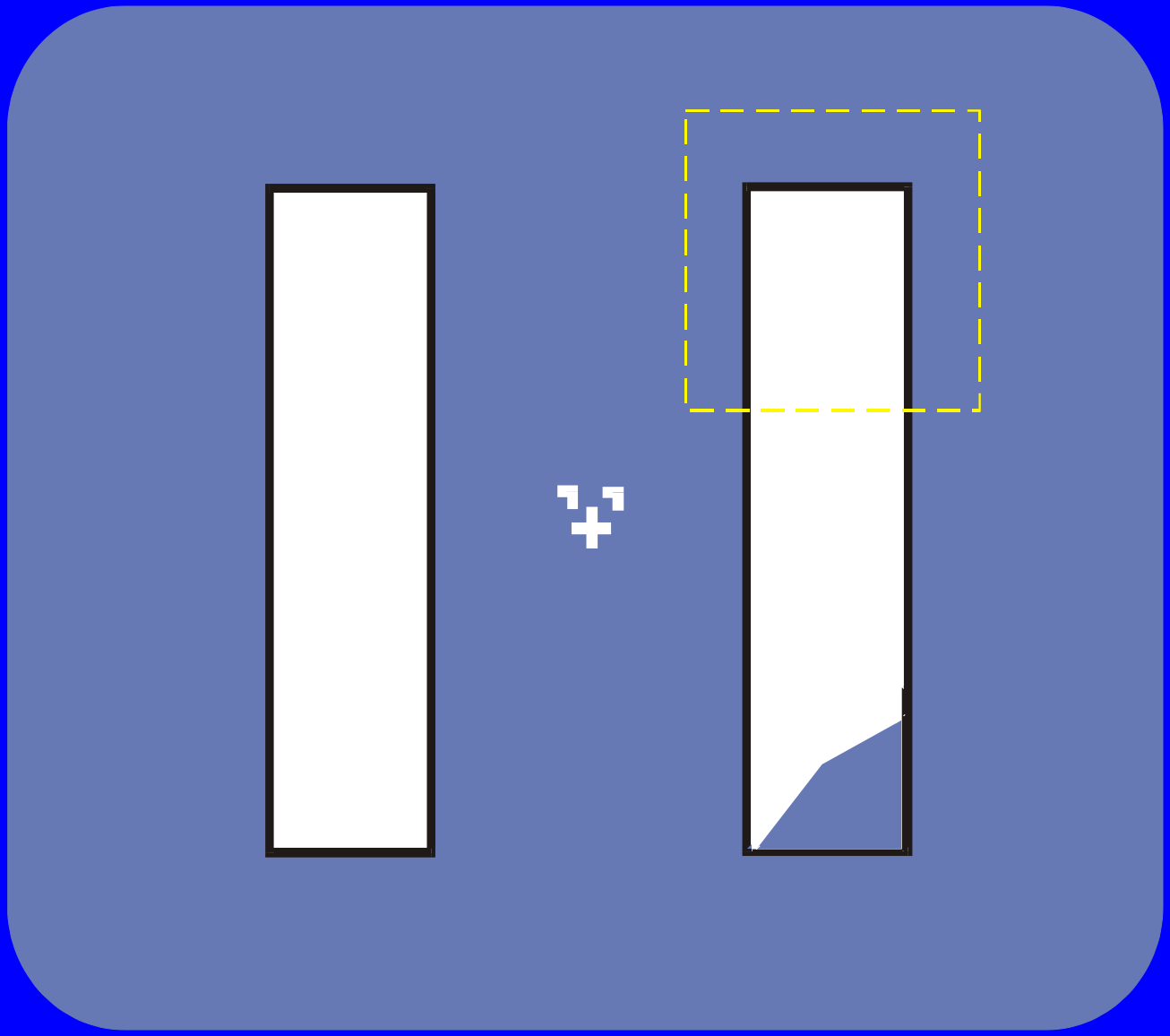

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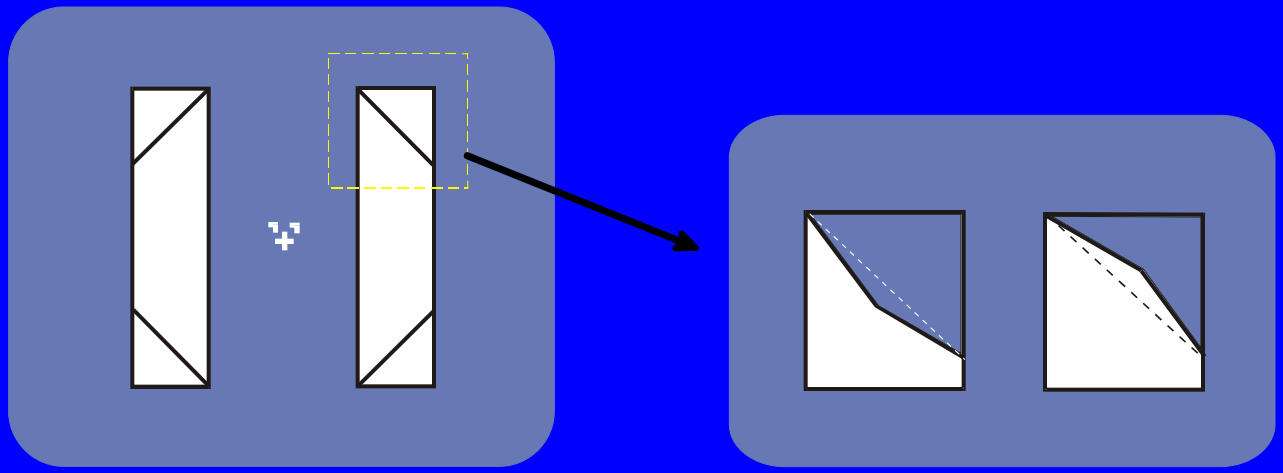
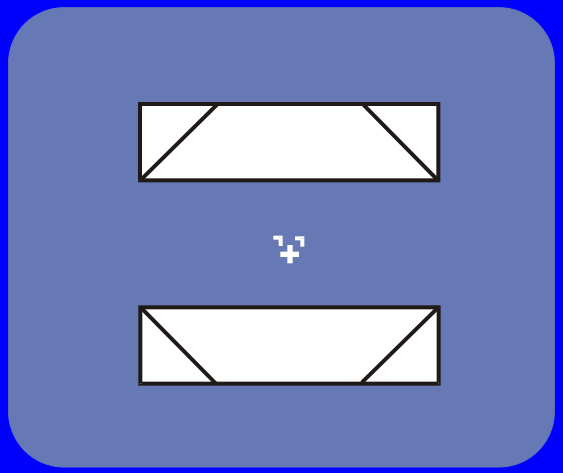


Vertical Bars

Standard Target



Horizontal Bars

Stimuli

--50 ms corner offsets
--Randomized sequence
--ISI's 300-500 ms

Conditions

--Bars either horizontal or vertical
--Subject attends to one quadrant at a time, detecting occasional targets
--20 sec runs, attend UL/UR, LL/LR