Main types of questions addressed in LRP research

1. About **dynamics of information processing**, especially nature of transmission in the processing system. *e.g.,* Is partial information about a stimulus transmitted to the response system before stimulus is fully evaluated?

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3. About **processing locus of particular experimental effects or individual differences**, e.g., Given processing is delayed in an experimental condition or group, where in processing system does the delay occur?

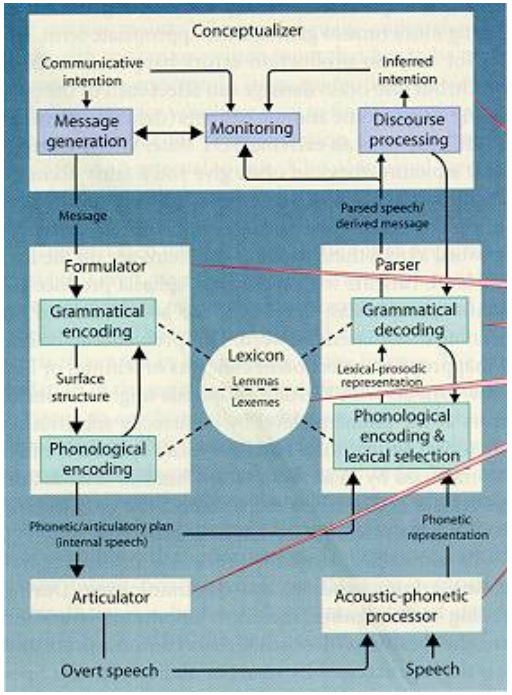
4. About **locus of inhibitory effects**

   e.g., at what level in processing system do inhibitory mechanisms act to stop a response?

LRP in language production

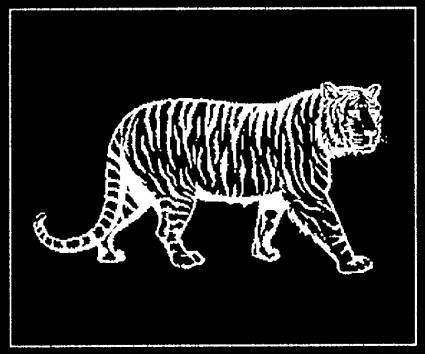
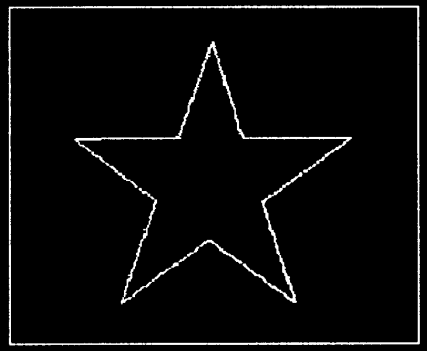
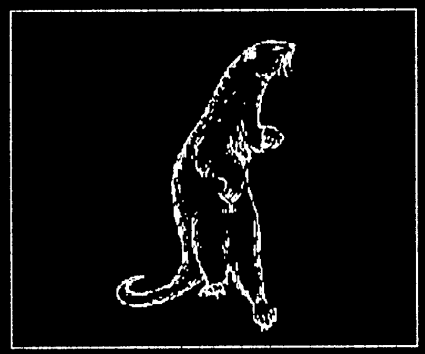
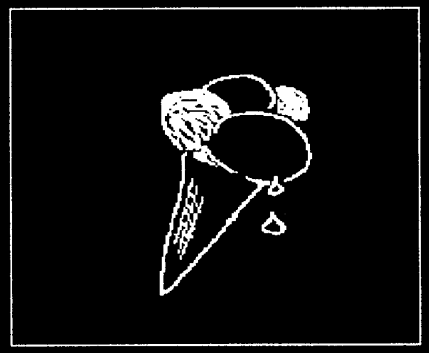
- LRP measures response preparation; central response activation; hand specific motor activation
- LRP after response selection before motor programming
- LRP indicates when specific information becomes available to make a response
- Suitable to measure time course of speech planning
- By comparing two information processes, e.g.,
  - one based on meaning
  - one based on phonology

(*Van Turennout et al., 1997; Schmitt, Muente, and Kutas, 2000)*



Stimuli/design

SEMANTICS

PHONOLOGY	**left hand** animal	**right hand** object
go word initial consonant		
no go word initial vowel		

Two main experimental conditions

- **hand = semantics**

  left/right hand response preparation on semantics
  go/nogo decision contingent on phonology

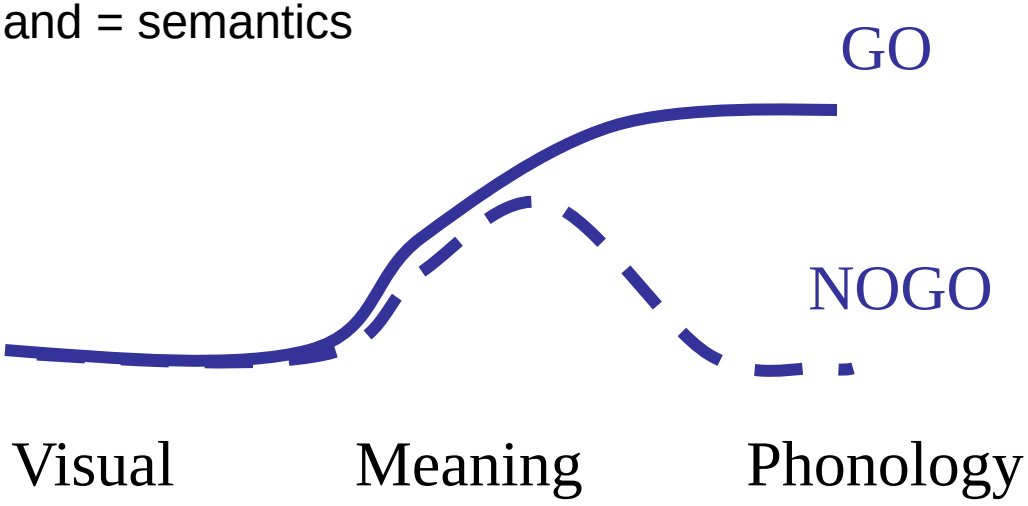
- ***critical to reverse the instruction***

- **hand = phonology**

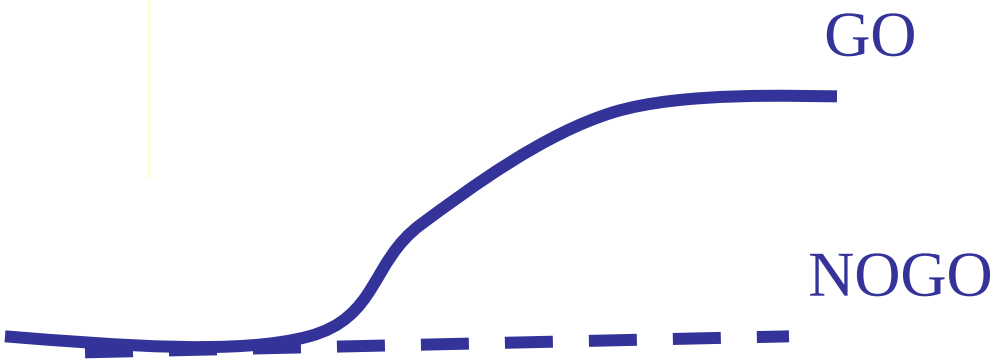
  left/right hand response preparation on phonology
  go/nogo decision contingent on semantics

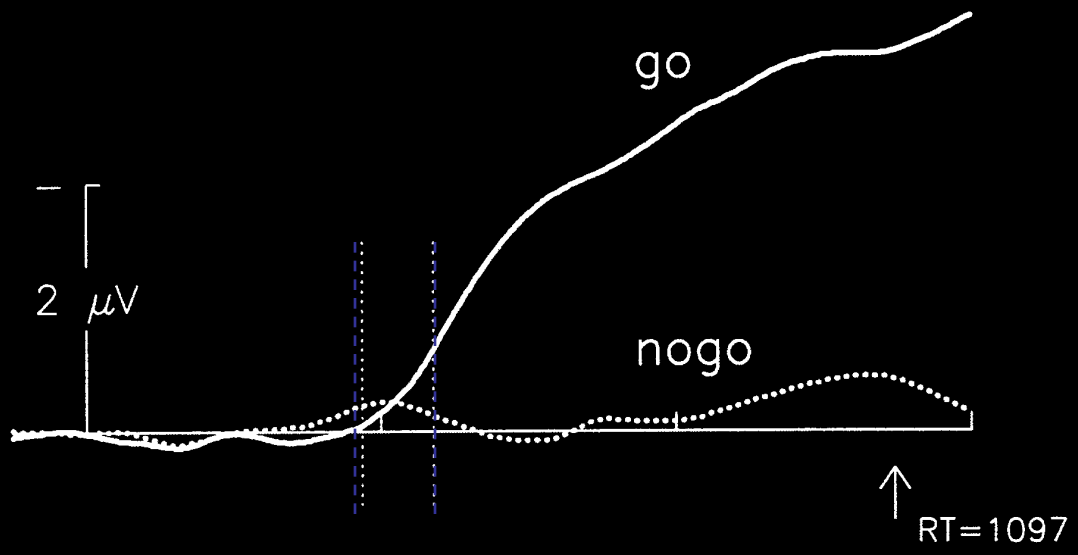
If semantics precedes phonology, and

hand = semantics

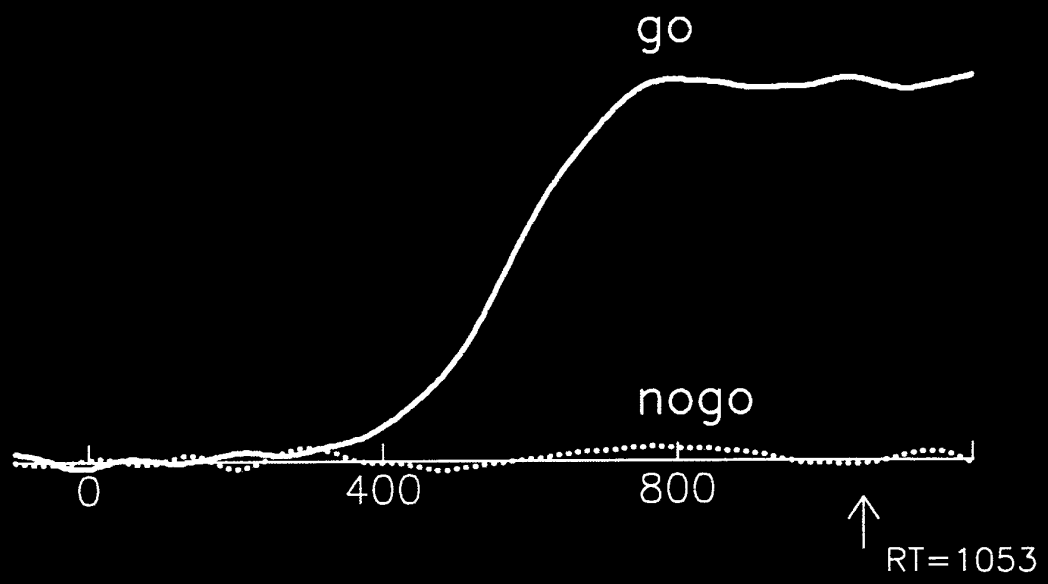


hand = phonology





hand=semantics
go/nogo=phonology



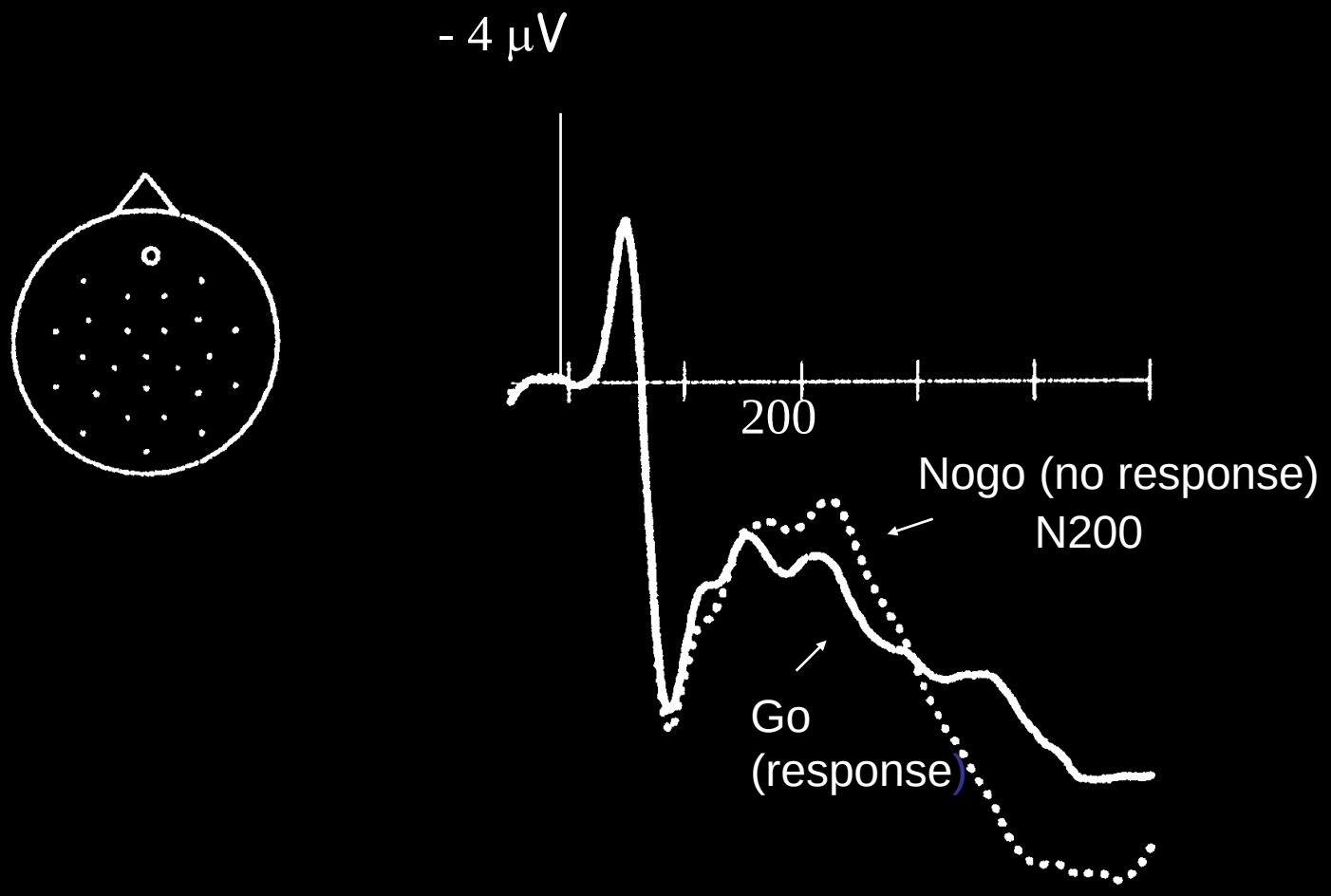
hand=phonology
go/nogo=semantics

LRP Conclusions

- nogo LRP, hand = semantics (380-460ms)
- no nogo LRP, hand = phonology
- data fit with semantics first hypothesis
- Conclusion: semantic encoding precedes phonological encoding by about ~80 ms

Go-Nogo paradigm: Nogo N200

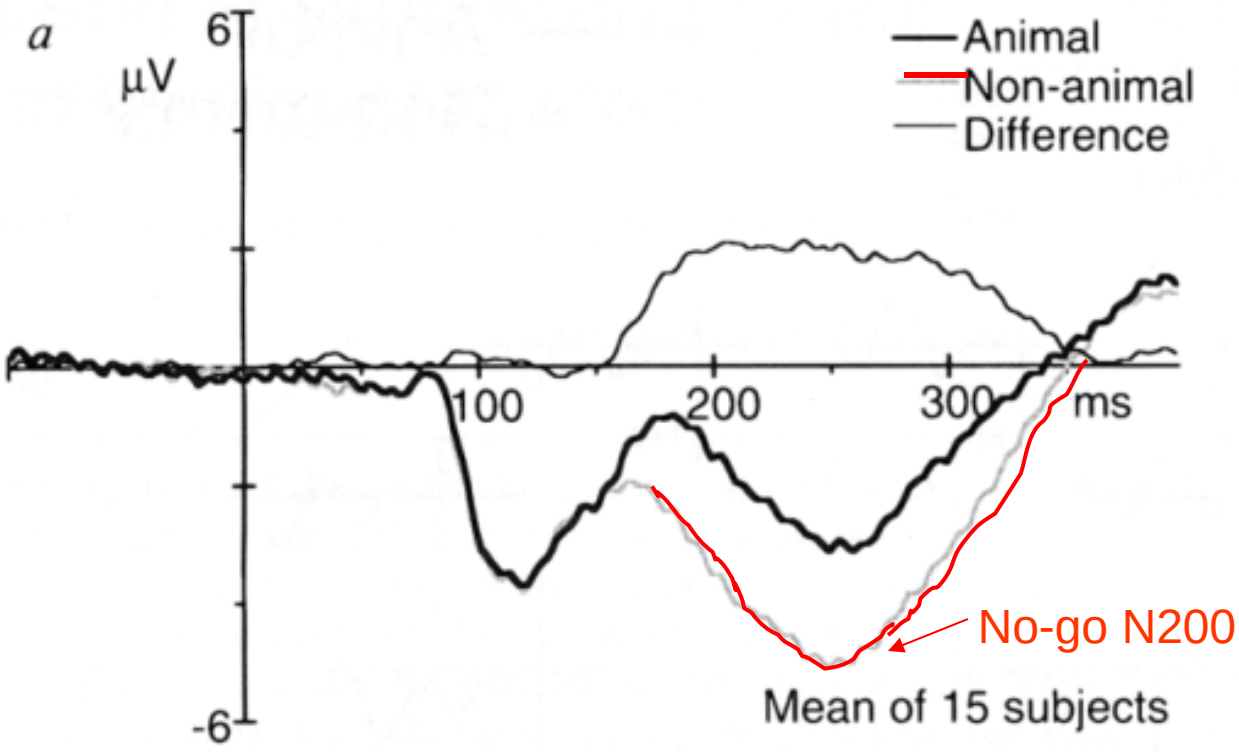
- go/nogo paradigm
- enhanced negativity (1-4 uV) for nogos compared to gos (N200 for withholding response; latency task dependent)
- maximum at fronto-central sites
- related to response inhibition; or response conflict
  - *Sasaki and Gemba, 1989, 1993*
  - *Single cell recordings in monkeys*


- 4 μV
200
Nogo (no response)
N200
Go
(response)

INFERENCES from NO-GO N200 LATENCIES

The ***onset latency of the N200 effect*** -- the moment in time when go and nogo trial ERPs first diverge from each other at the scalp - can be taken as the time at which information begins to become available to help the person decide whether or not to respond

The ***peak latency of the N200 effect*** can be interpreted as the moment in time when sufficient visual information is available for a person to decide whether or not to respond



Thorpe et al. 1996

People can withhold their response within 150 ms!

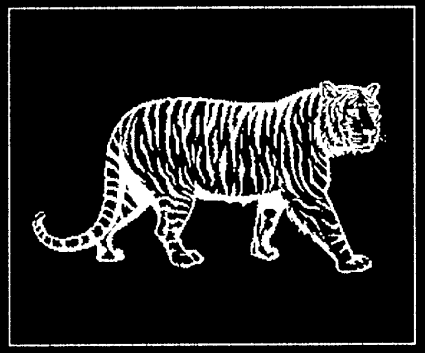
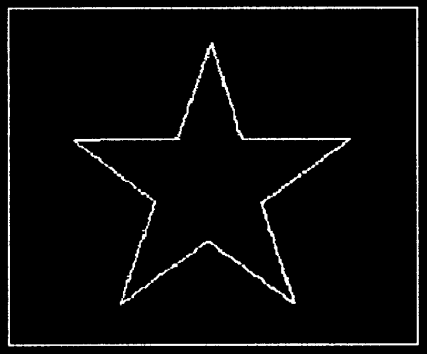
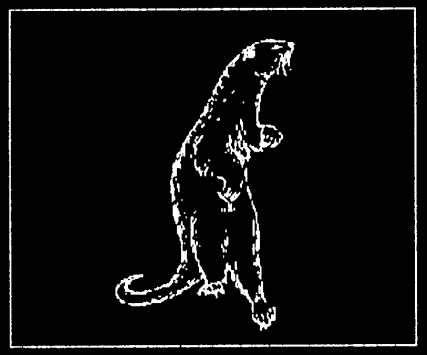
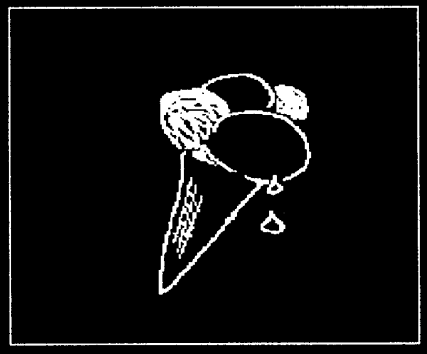
Nogo N200 effect

- nogo - go difference wave
- onset and peak of the nogo N200 effect
- moment in time when specific information is available (Schmitt, Muente, and Kutas, 2000)
- Can be recorded along with LRP derivation

Go/nogo phonology

PHONOLOGY

SEMANTICS

	left hand animal	**right hand** object
go word initial consonant		
no go word initial vowel		

Go/nogo phonology

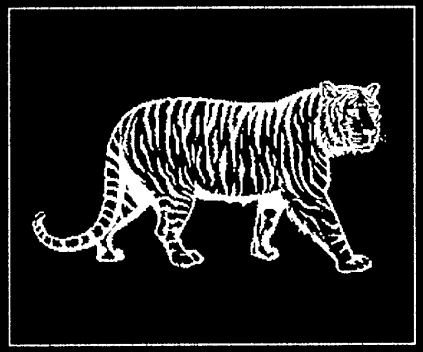
SEMANTICS

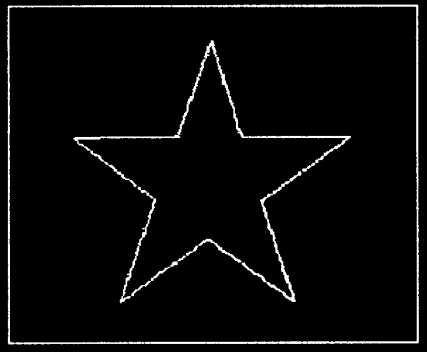
left hand
animal

right hand
object

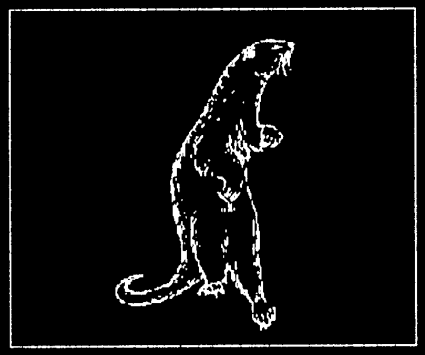
PHONOLOGY

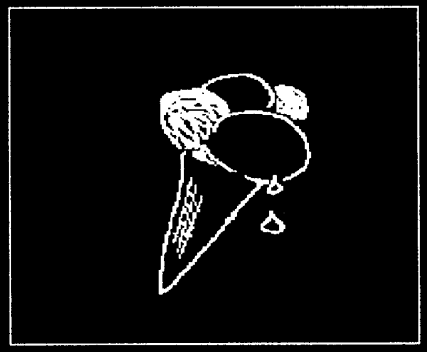
go
word initial
consonant





no go
word initial
vowel



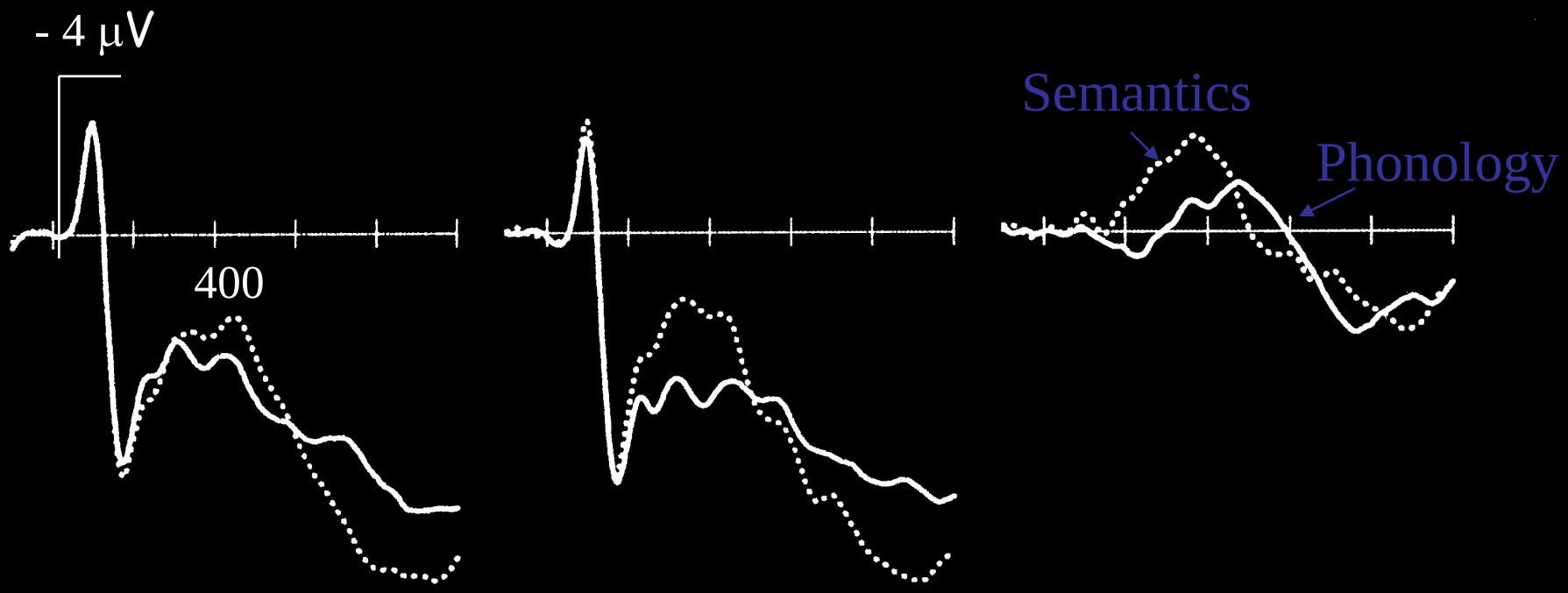


Reverse the mappings/instructions

GO/NOGO = PHONOLOGY

GO/NOGO = SEMANTICS

RESPONSE INHIBITION (NOGO – GO)



NOGO

GO

Difference

Conclusions: Semantics vs. Phonology

- N200 peak semantics at 380 ms
- N200 peak phonology at 470 ms
- peak latency difference = ~90 ms

- semantic information is available earlier than phonological information
- Similar comparisons for syntax vs phonology, or any two sources of information

Support for serial/cascading models of speech production

Main types of questions addressed in LRP research

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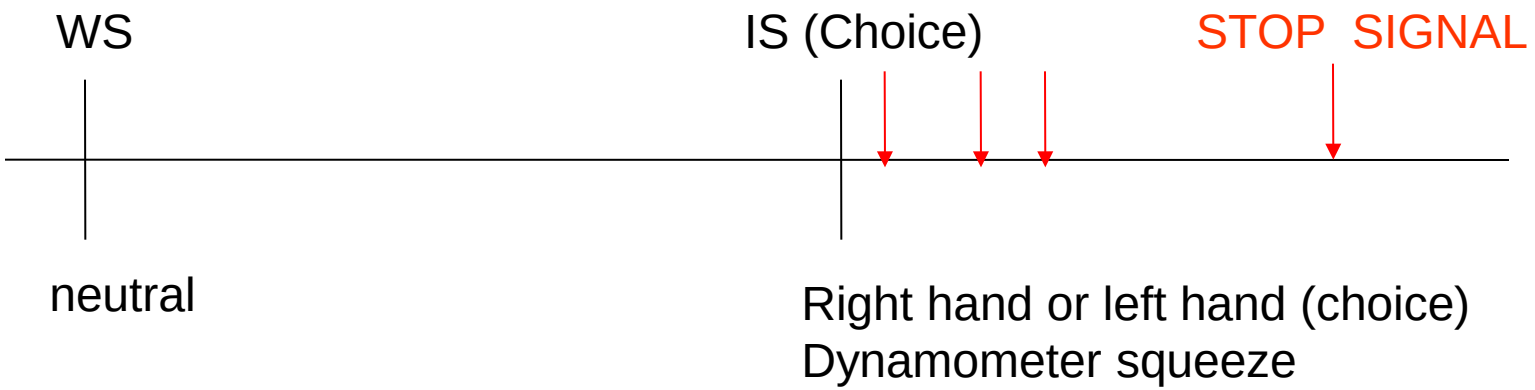
Is there a point of no return in the course of response execution?

STOP SIGNAL PARADIGM



Dependent measures: EMG, ERP, RT, dynamometer squeeze parameters

Response threshold: avg amp of LRP at response initiation

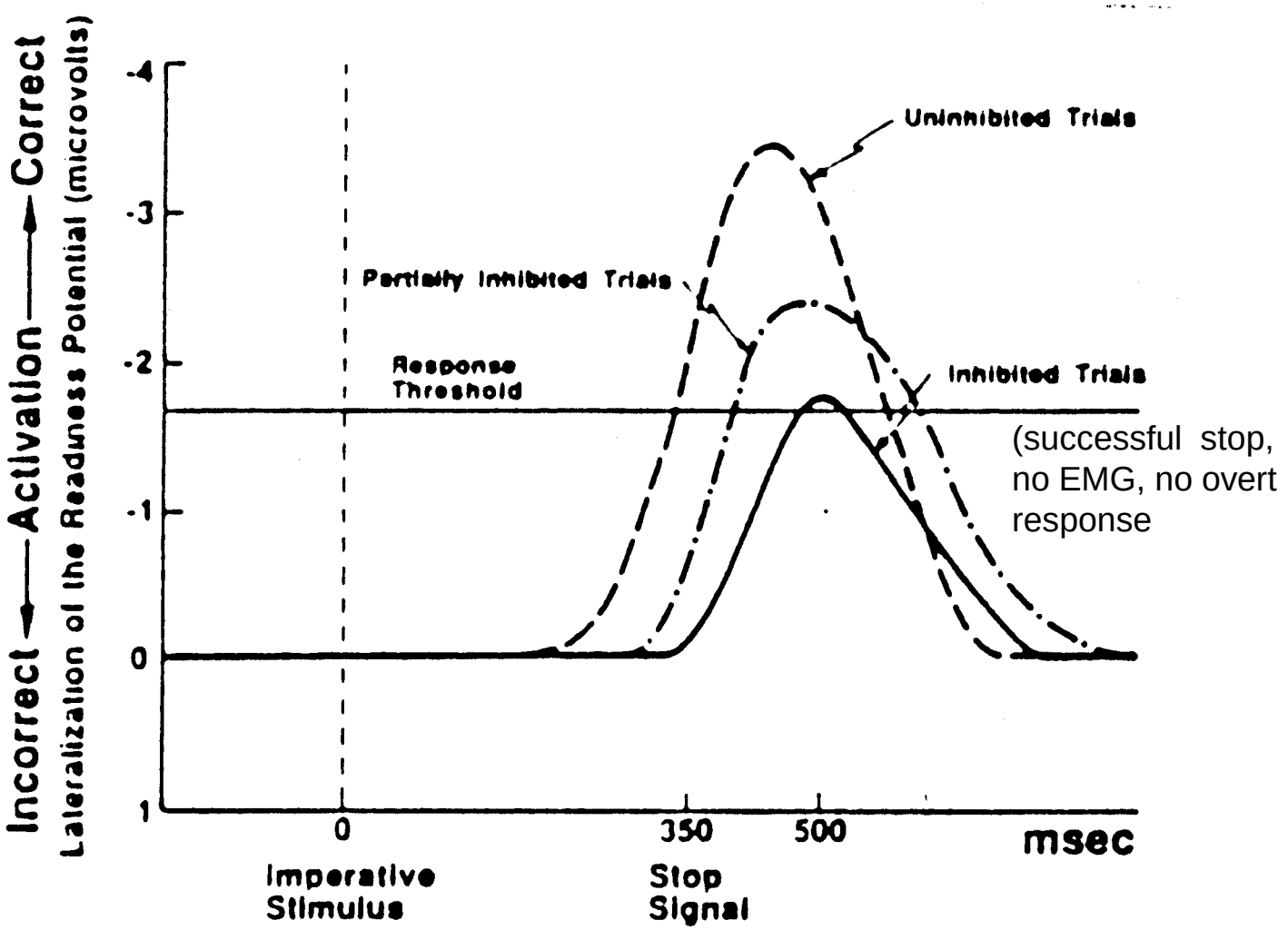
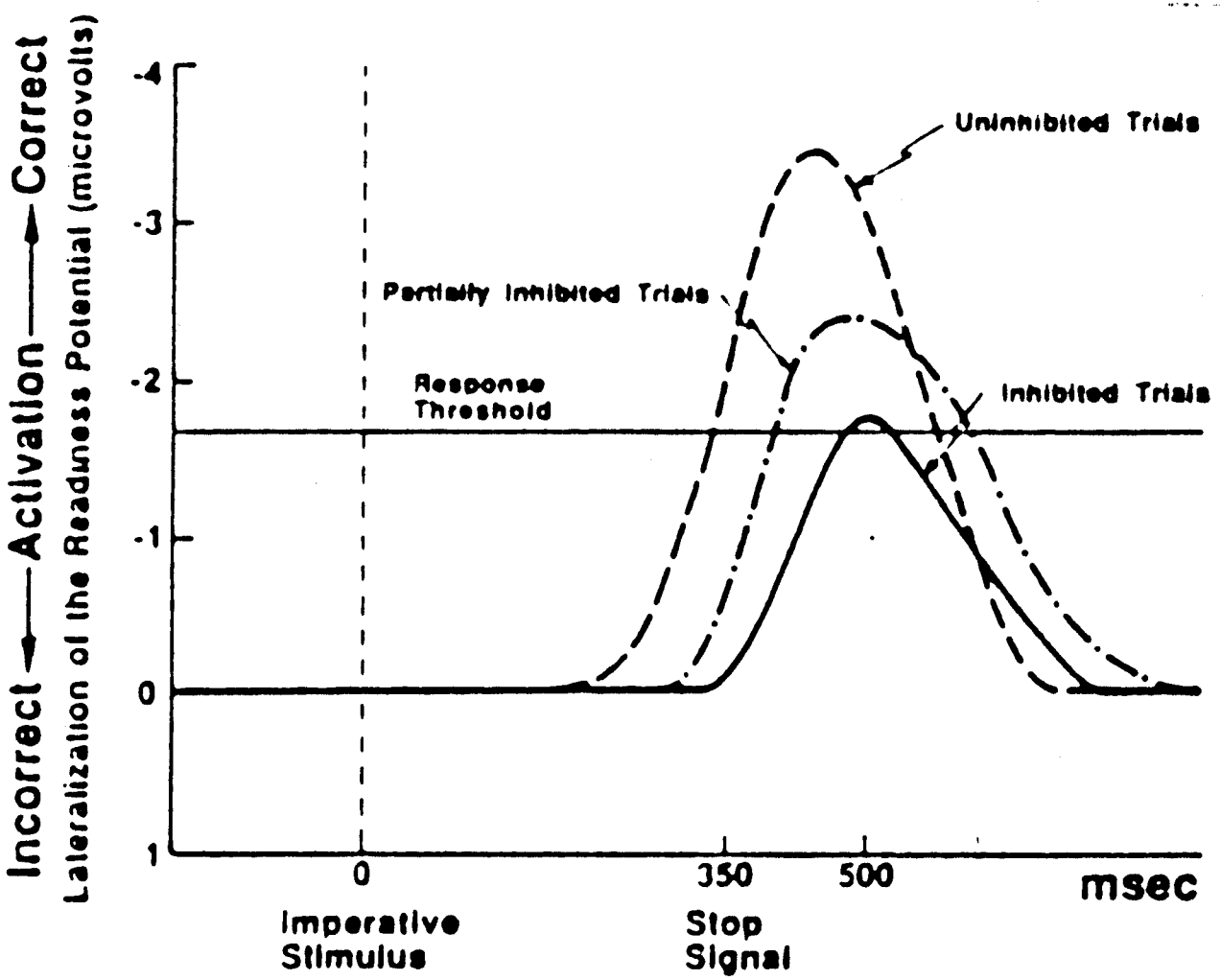


Figure 10. Lateralized readiness potential data from the stop-signal paradigm. Averages are shown separately for inhibited trials, partially inhibited trials (on which sub-threshold squeeze and EMG activity occurred), and un-

Point of no return is after response initiation as reflected in LRP



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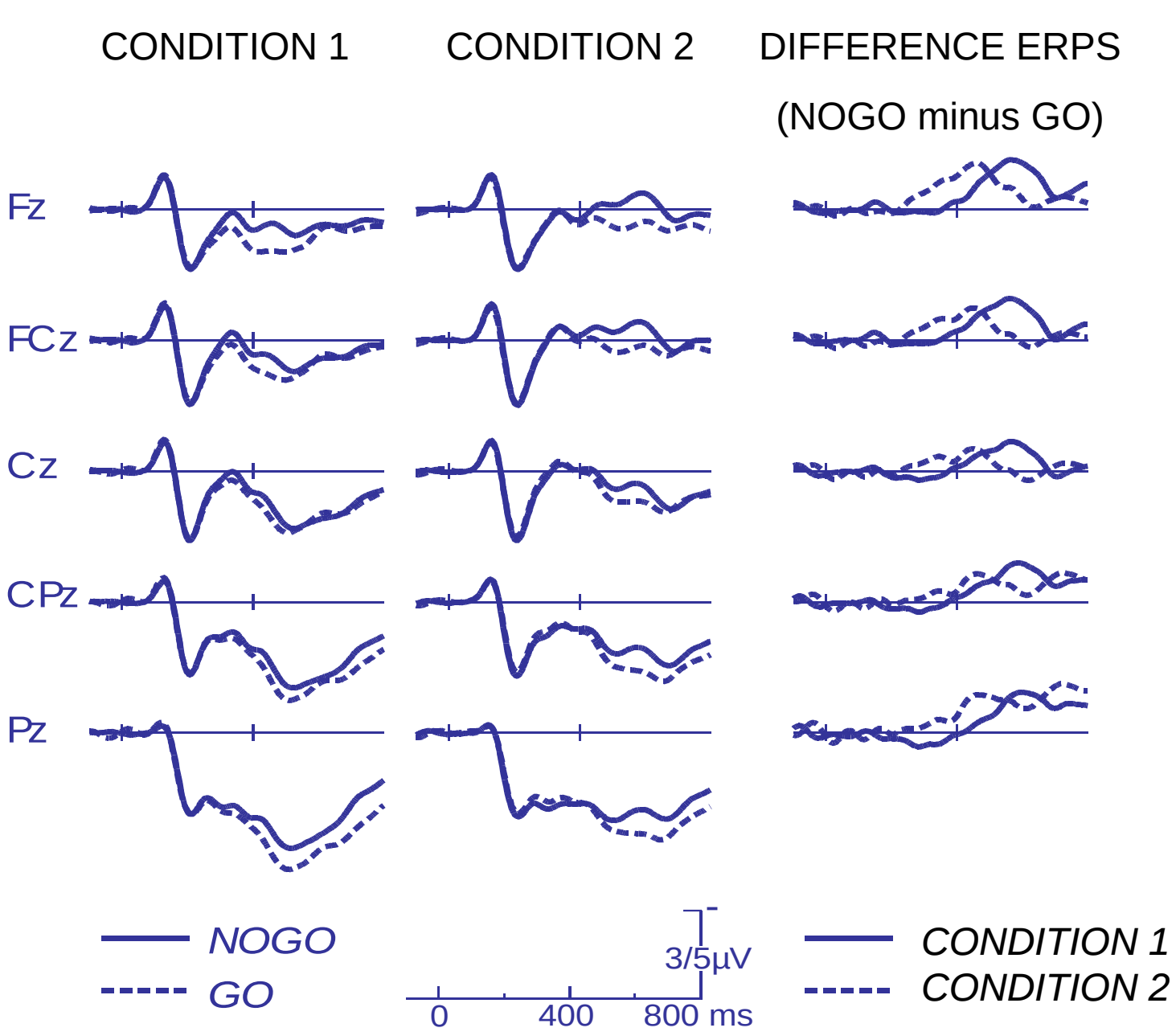
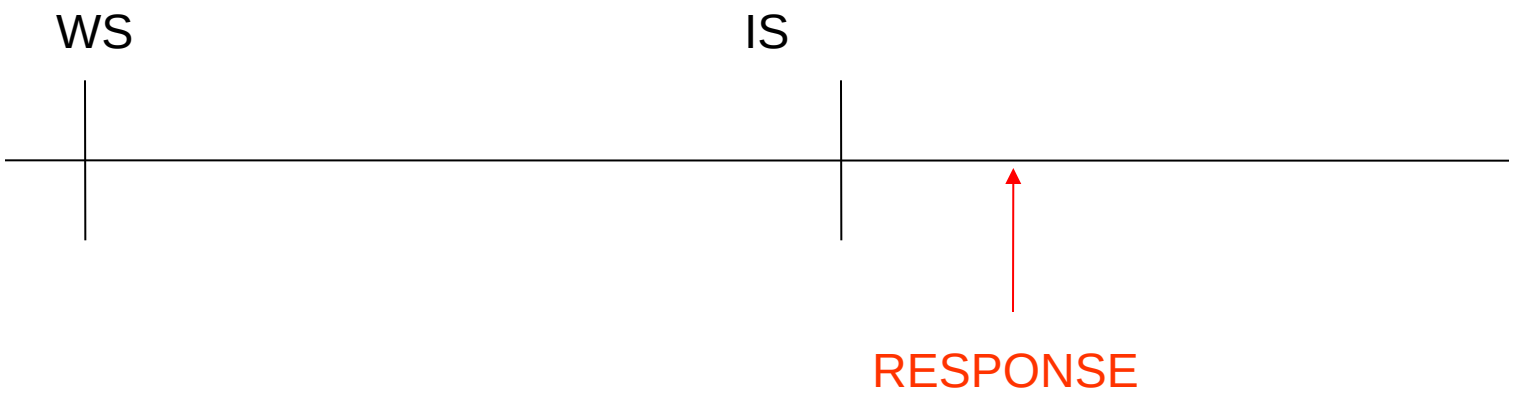
Final comment on LRP

If you can phrase question of interest in terms of question about relative activation of two response (L, R hands) then you can use the LRP procedure. For each condition, need to have one hand be correct and other correct (and vice versa) and overall to have probabilities of two hands being correct the same.

- Dynamics of information processing
- Locus of experimental effects and individual differences
- Order of information extraction

Current topic: Do stimuli below perceptual threshold (so-called subliminal perception) activate response system?


CONDITION 1
CONDITION 2
DIFFERENCE ERPS
(NOGO minus GO)
Fz
FCz
Cz
CPz
Pz
NOGO
GO
3/5µV
0
400
800 ms
CONDITION 1
CONDITION 2



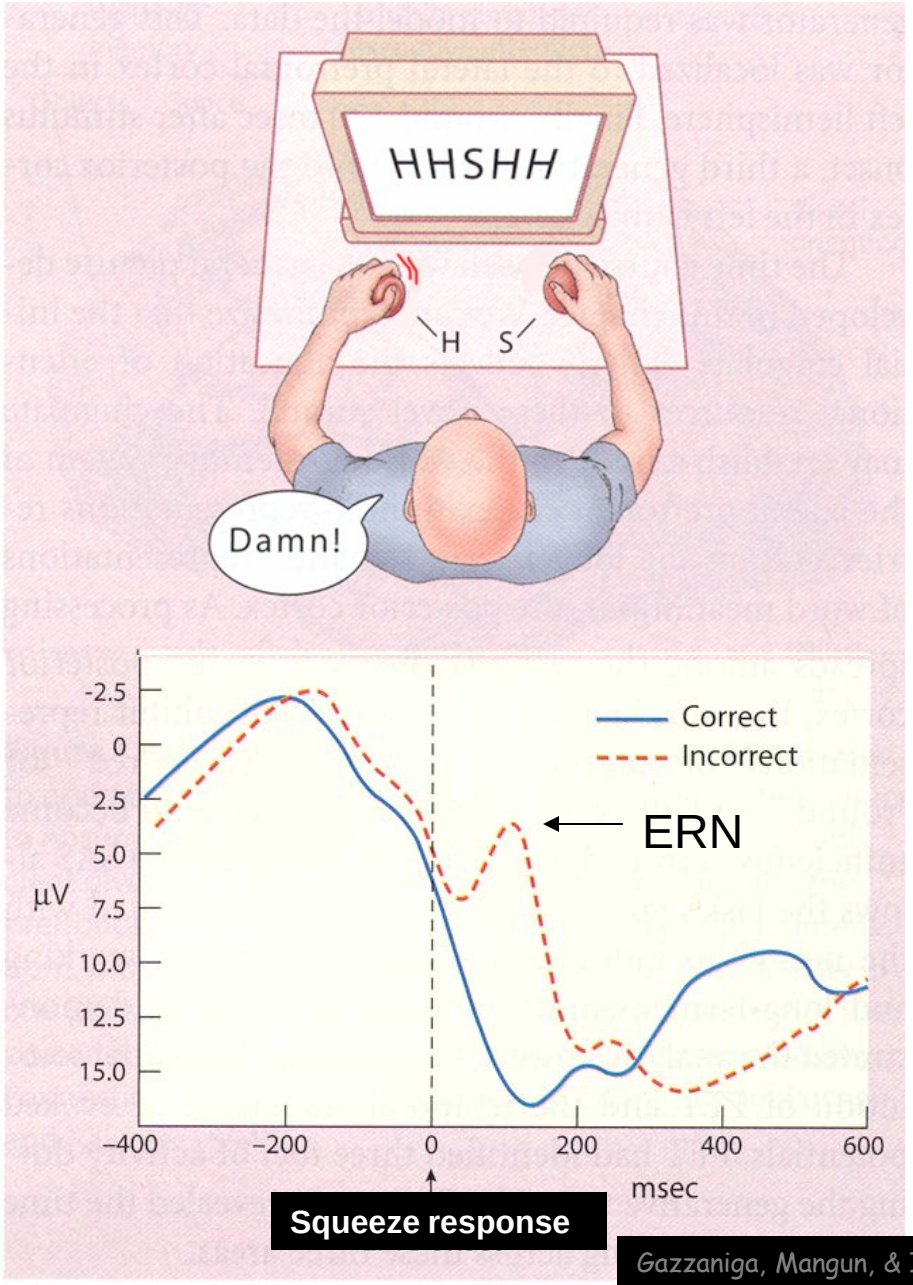
Response evaluation
Error monitoring
Error remediation

ERROR PROCESSING

The Error-Related Negativity (ERN), aka Ne

Coles

Falkenstein



Gazzaniga, Mangun, & Ivry, *Cognitive Neuroscience, 2nd. ed.*

ERN – error related negativity/Ne – error negativity

Negativity following response errors (hands, eyes, feet) in variety of tasks – called the ***response ERN***

- Fronto-central negative-going peak
- begins about time of error (EMG), in response-locked average
- peaks 80-120 ms after onset of error
- proposed Anterior cingulate cortex (ACC) generator

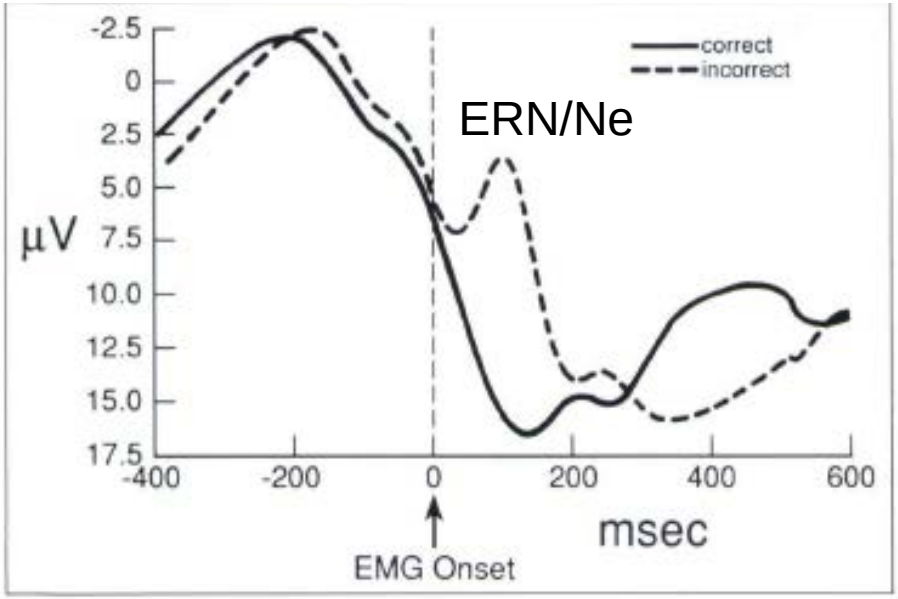


Fig. 1. Comparison of response-locked event-related potential activity, recorded at the C_z electrode, for correct and incorrect trials.

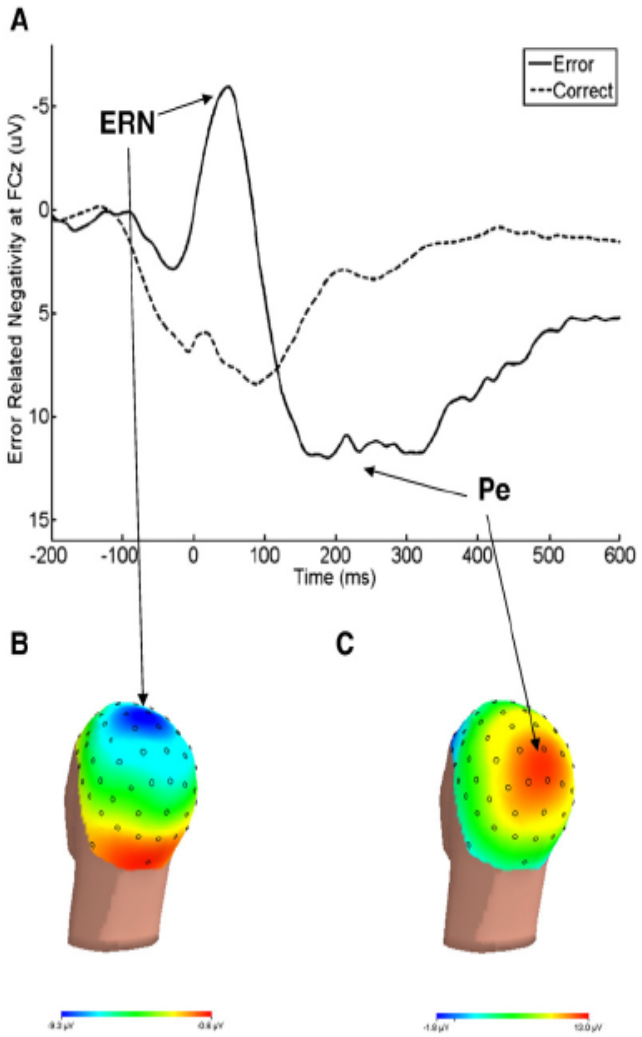


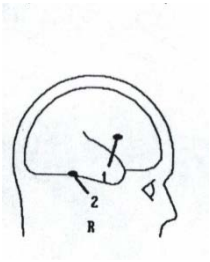
Fig. 1. The response locked ERPs for error and correct trials at FCz, where the ERN was maximal (A). The response onset occurred at 0 ms and negative is plotted up. Scalp topography of error-related brain activity from 0 to 100 ms post-response (B). Scalp topography of error positivity from 200 to 400 ms post-response (C).

fERN – error related negativity/Ne – error negativity

Negative ERP component following feedback about an error (negative feedback stimuli) – known as feedback ERN (e.g., FB about time estimation) (*Miltner, Braun, & Coles, 1997*)

Fronto-central negative-going peak 5-10 uV, 230-270 ms after feedback in stimulus-locked average
Modality independent: Auditory, visual, or somatosensory

Proposed generator, ACC



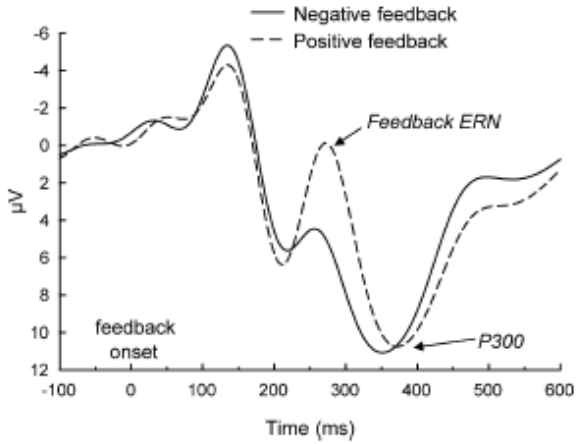


Fig. 1. Typical example of event-related brain potentials associated with negative and positive feedback (adapted from Ref. [25]). Negative is plotted up by convention. Waveforms were recorded from electrode Cz. Arrows indicate the peak of the feedback ERN and the P300 components in the waveform associated with negative feedback. Note that although the P300 reaches maximum amplitude over posterior parts of the scalp, the component is also visible over frontal regions as seen here.

Hypothesis: negativities following response errors (response ERN) and negative feedback (feedback ERN) are associated with the same neural and cognitive error-detection/monitoring process.

Response ERN = Feedback ERN

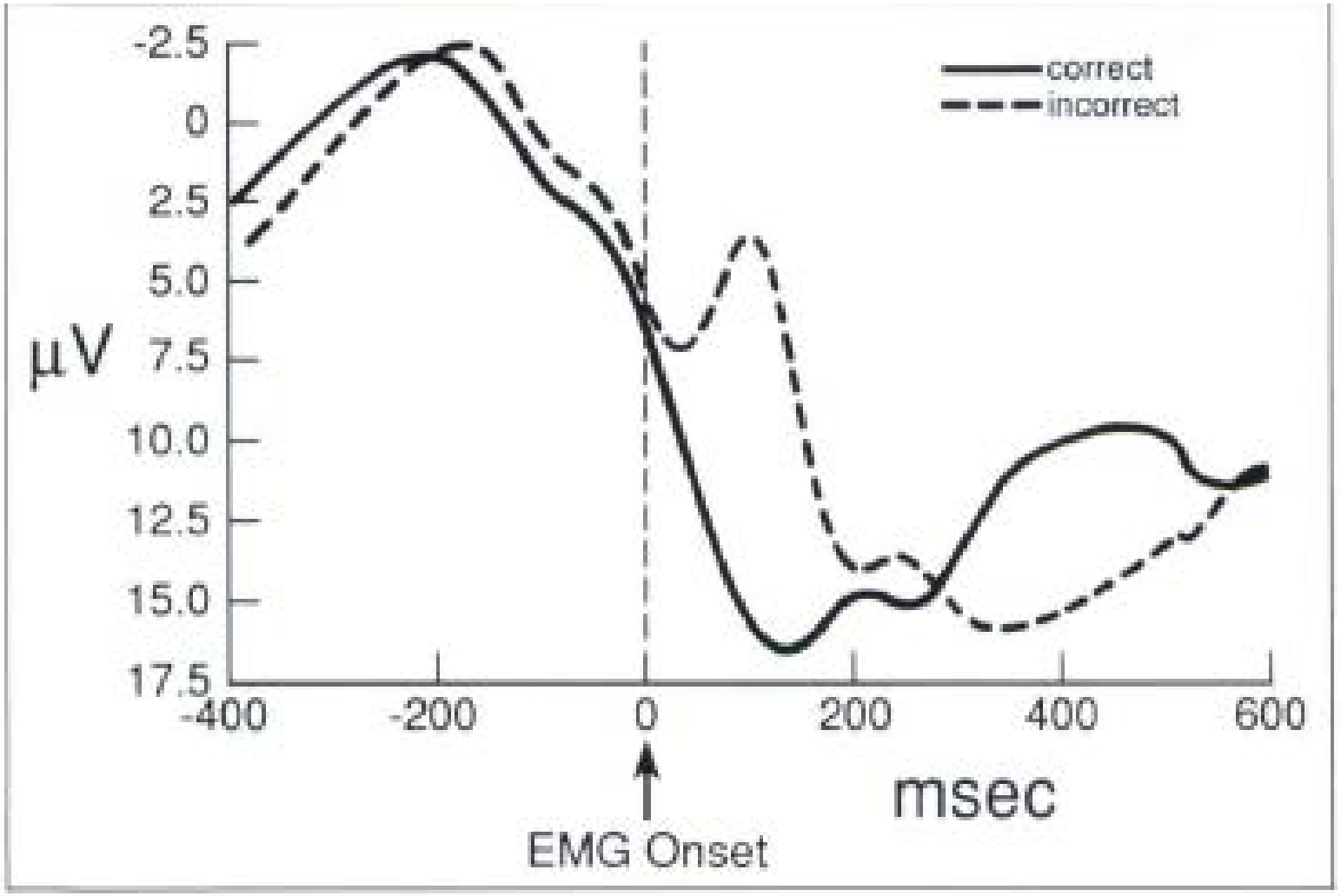


Fig. 1. Comparison of response-locked event-related potential activity, recorded at the C_z electrode, for correct and incorrect trials.

ERROR RELATED HYPOTHESIS: activity of system associated with error monitoring; related to accuracy of response, perhap also error compensation

Speed vs Accuracy Instructions

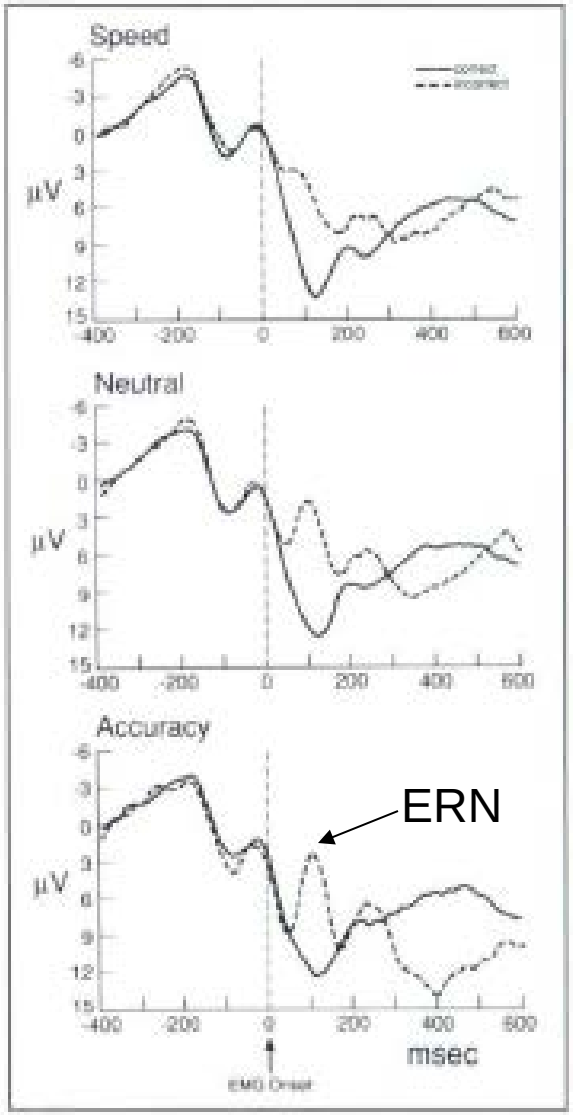


Fig. 2. The effects of different speed-accuracy instructions on the error-related negativity recorded at C_z. For each of the three conditions, trials with the same reaction time were used (see text).

Note positive up

ERN amplitude and degree of error

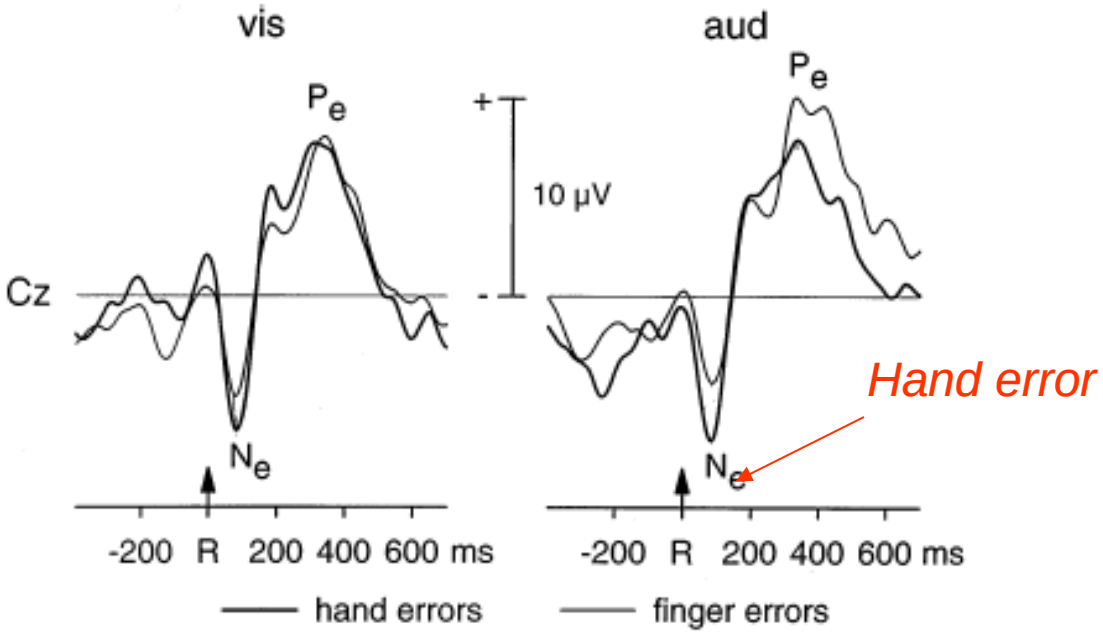


Fig. 6. Grand averages (Experiment 4; $n = 12$) of the RTA for hand errors (wrong hand; heavy lines) and finger errors (correct hand, wrong finger; light lines) in a four-way choice task with the fore- and middle fingers of both hands. The Ne is smaller for finger errors than for hand errors.

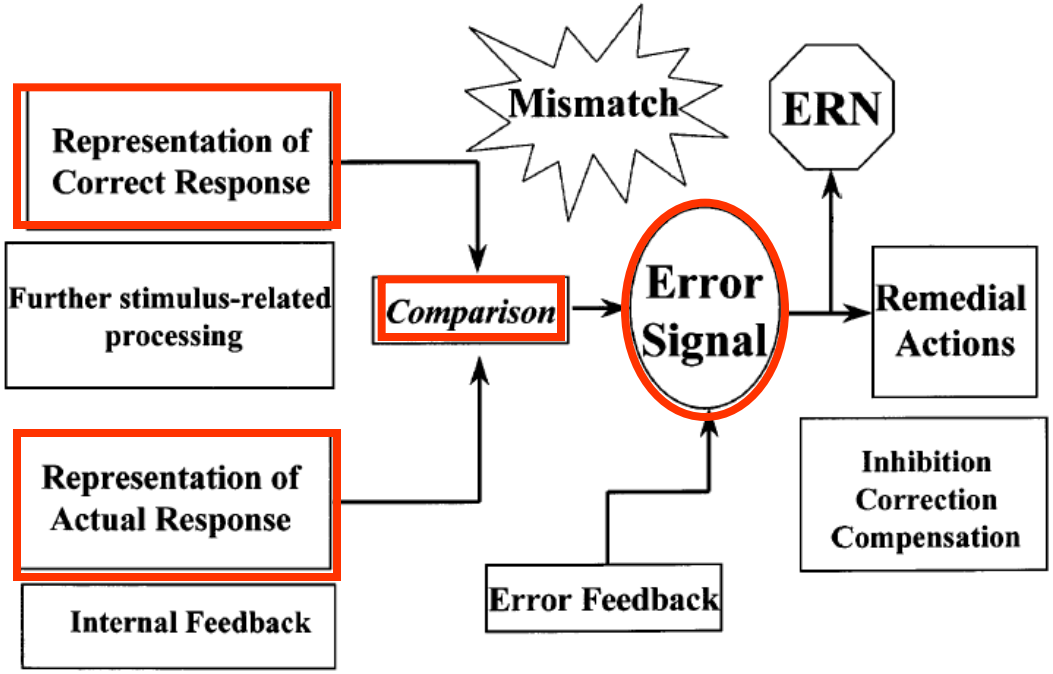
ERN amplitude is directly related to degree of mismatch between correct and erroneous response; the more dissimilar the correct response and the error, the larger the ERN. Supports idea that ERN is related to error detection, via comparison of response representations

Factors influencing ERN/Ne amplitude

- Larger ERN when participants strive for accuracy rather than speed
- Larger ERN when incorrect response differs from correct one on two versus one parameter (i.e., is more incorrect)
- ERN elicitation is not dependent on ability to correct error (e.g., no go error also yields ERN, though no chance of correction via response)
- ERN is sometimes related to remedial actions taken to compensate for error being made or already committed (e.g., attempts to inhibit the error, correct the error, or slow down so that the system).

Falkenstein: "ERN is affected by strength, and hence detectability of error"

ERROR DETECTION/MONITORING VIEWS of ERN



ERN reflects a monitoring process that signals errors whenever it detects a ***mismatch between the response produced and the correct, or intended, response – compare what it is doing vs what it thinks it should have been doing,*** as determined by the state of the response system after the response is executed. Some views emphasize comparison, others the error signal, but several groups emphasize some aspect of error detection/monitoring process as functional significance of ERN.

Main views on functional significance of ERN

1. Error monitoring, detection and correction, system

2. Response conflict detection/monitoring system

3. Response-comparison process

3. Detection of motivationally or emotionally salient events, especially negative ones

Perhaps ERN is not just for ERROR detection

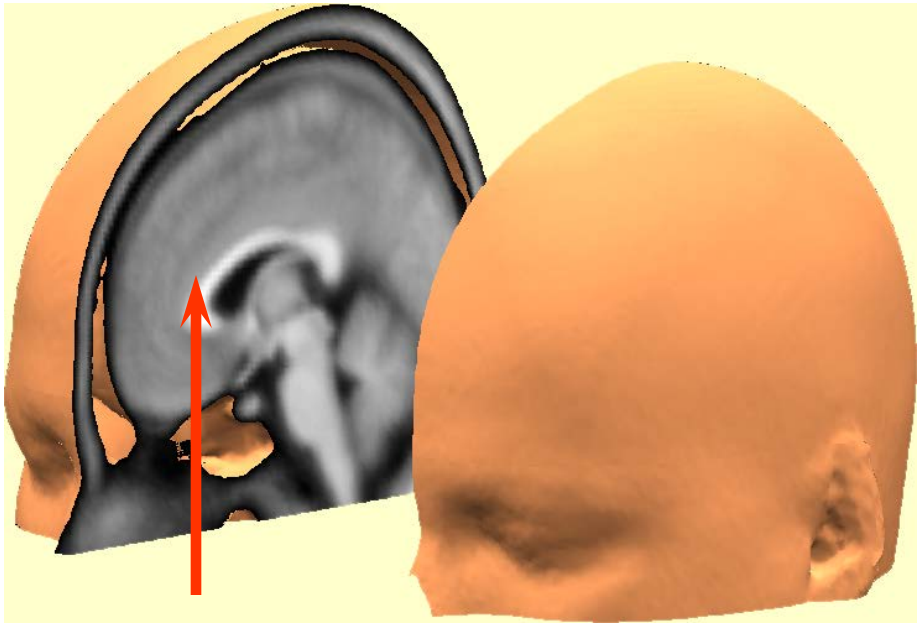
- ERN is not limited to outright errors
  e.g., Stroop paradigm

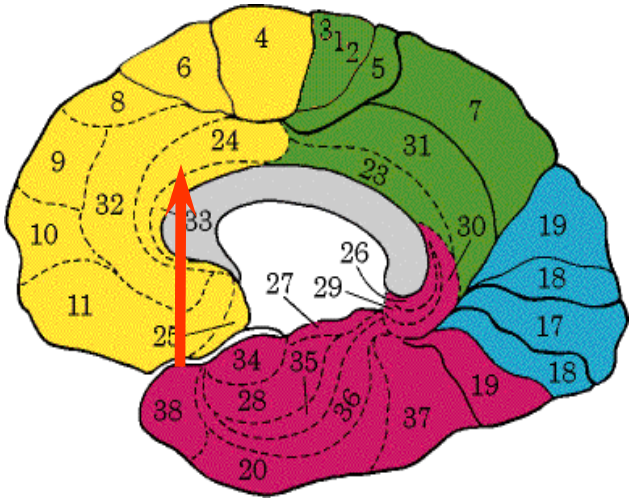
RED vs RED

- ACC activation not limited to error processing

Slower RT and ERN to RED in blue ink – when ink color and word meaning conflict, even though there is no overt error! Likewise, ACC activation is not limited to errors

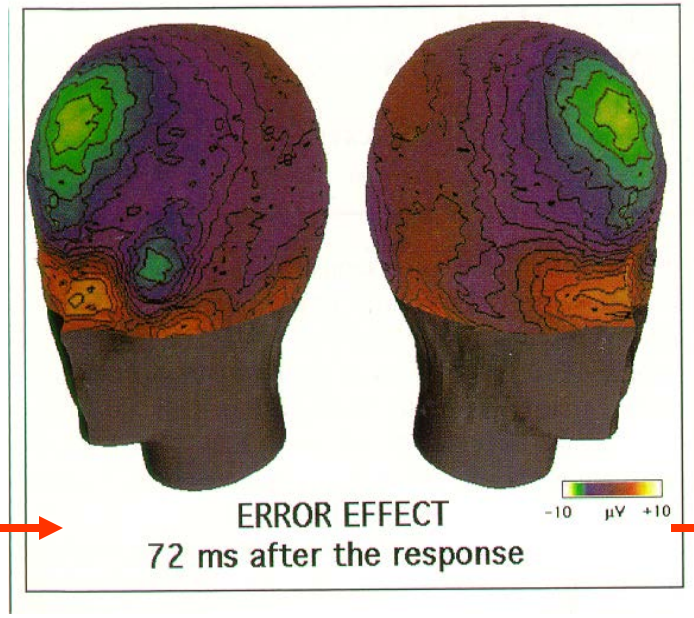
Hypothesis: Anterior Cingulate Cortex (ACC) (24, 32) is generator of rERN

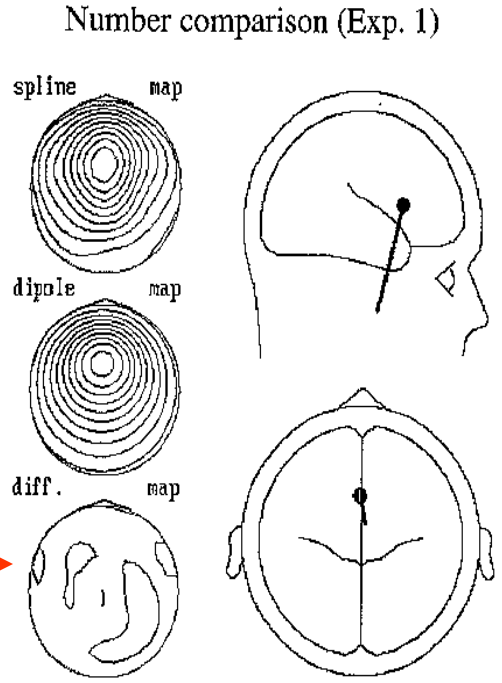




Anterior Cingulate Locus of the ERN

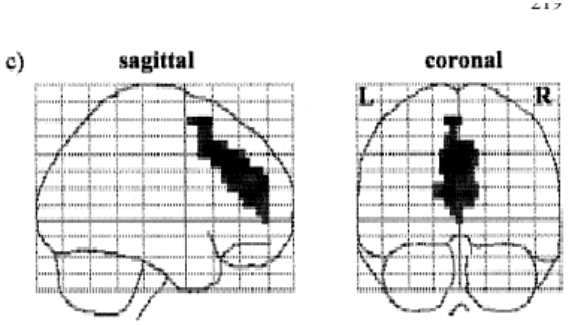
(Dehaene, Posner, & Tucker (1994))



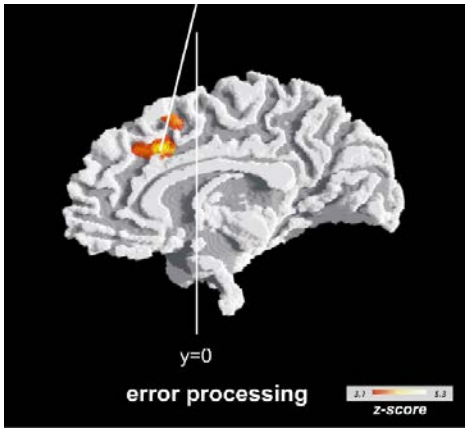


High density mapping and source modelling suggest ACC locus of rERN

fMRI-based error-related activity in the ACC

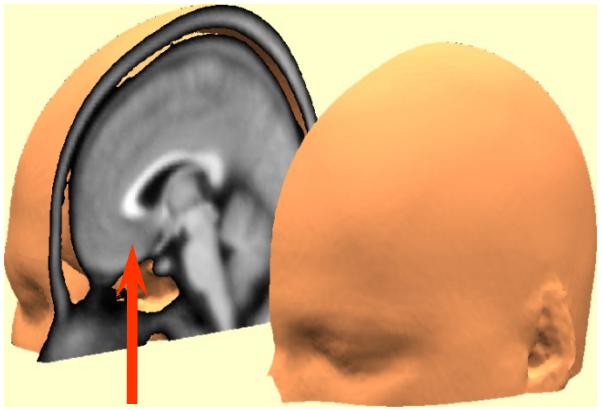


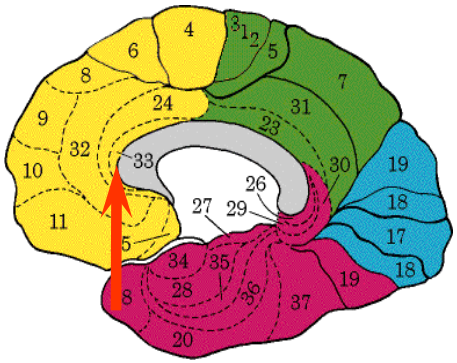
Kiehl et al. 2000 *Psychophysiology*

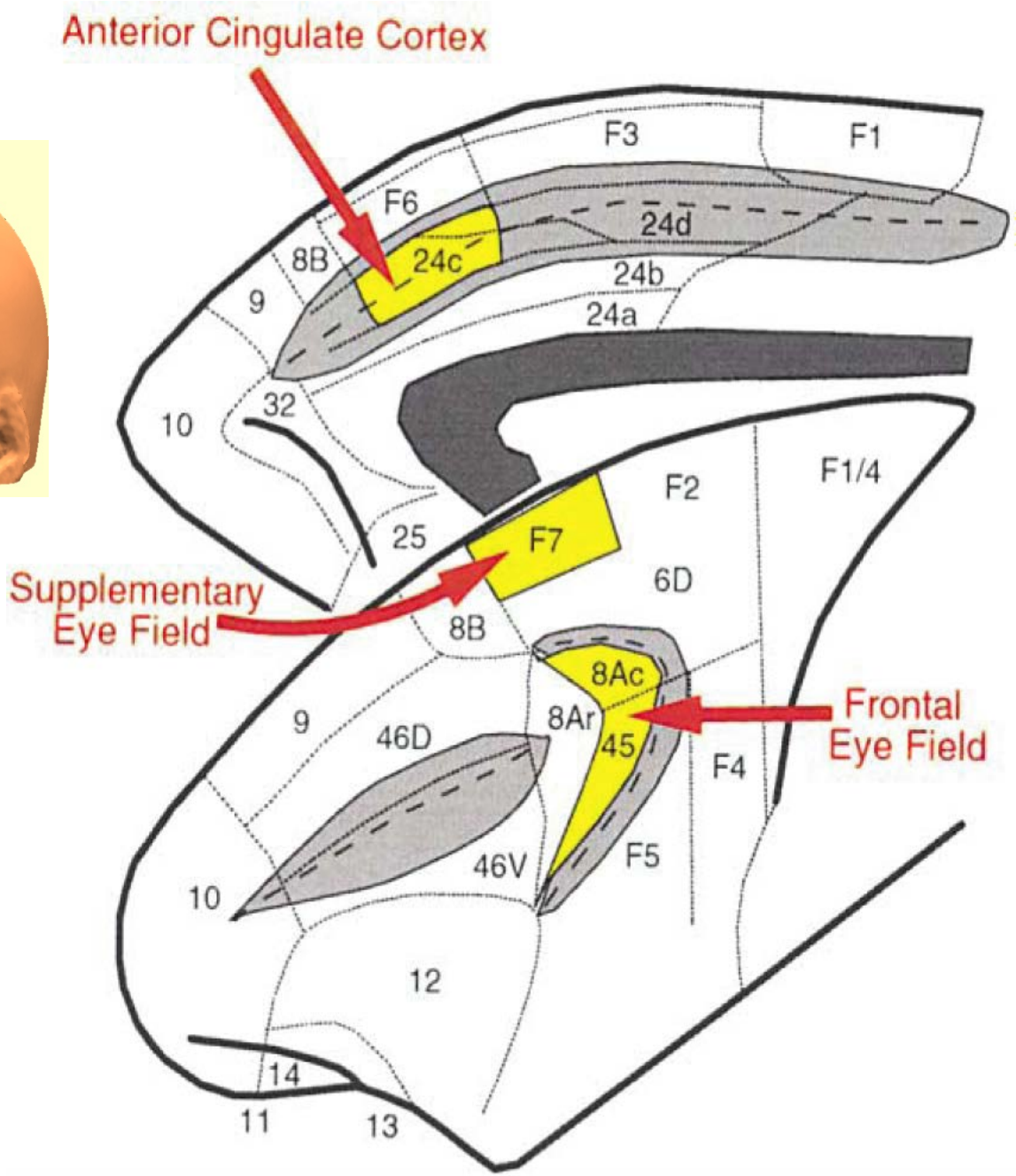


Ullsperger & von Cramon (2001) *Neuroimage*

Menon et al. (2001) *Human Brain Mapping*

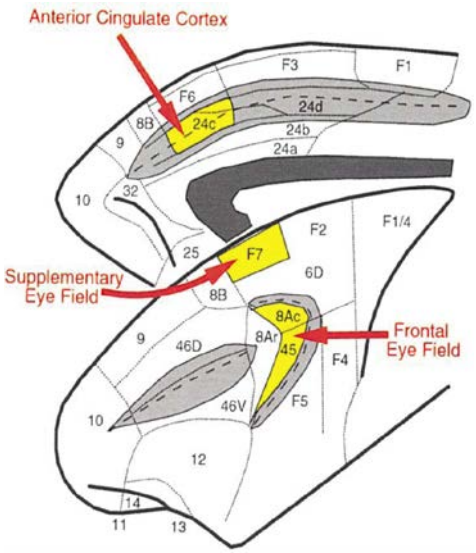






fMRI activity in ACC is not only seen with errors but with response conflict!

Anterior Cingulate Cortex (ACC)



Very heterogeneous area based on gross morphology and cytoarchitecture

Dense connections with motor cortex and DLPFC

- Implies a integration of cognition and action
- Allows DLPFC to influence motor output

Inputs from thalamus, VTA & indirect input from amygdala

ACC has dense reciprocal connectivity with SEF

Lesions:

- Inability to initiate movement
- Suppress externally triggered motor subroutines.

Single unit activity:

- Error
- Rewards
- Action Initiation
- Combinations

FMRI activity:

- Monetary gains/losses
- Emotional decision
- Conflict

Stimulation:

- Causes movement (eyes)
- Monkey calls.

We can use what is known about the functions, inputs, outputs, computations of a brain area to generate hypotheses about ERP components that it generates.

Main views on functional significance of ERN

1. Error monitoring, detection and correction, system

2. Response conflict detection/monitoring system
   - role of ACC is to monitor conflict!

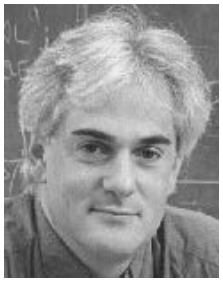
3. Response-comparison process

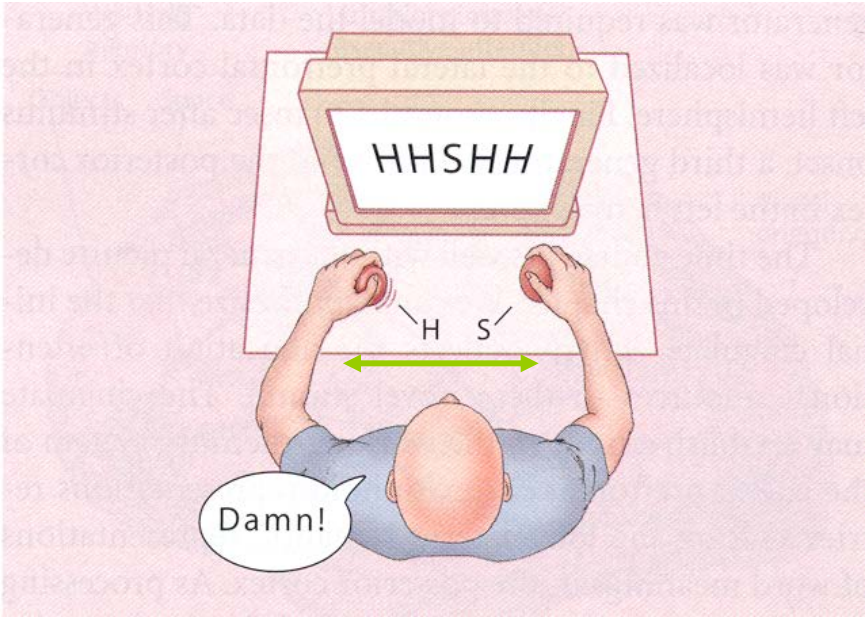
3. Detection of motivationally or emotionally salient events, especially negative ones

Conflict Detection Theory

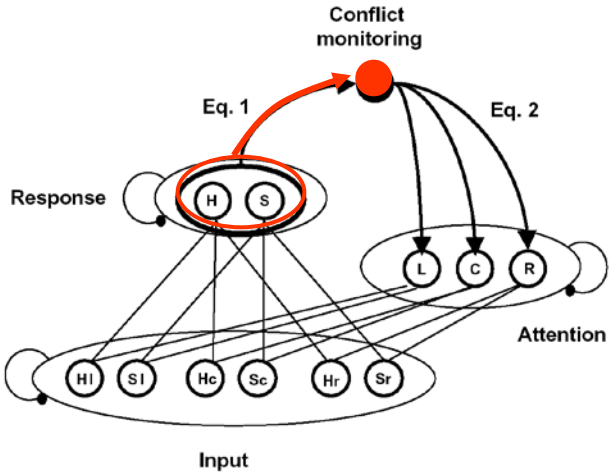
(Cohen, Carter, Botvinick, et al.)

- Detects need for control, when errors are likely
- Signal reflects degree of conflict





Computational model



ERN reflects conflict detection

Incorrect response is given before stimulus evaluation is complete.

When stimulus evaluation is complete, then correct response is activated.

As a consequence, the two responses – correct and incorrect – are in conflict.
The conflict is reflected in the ERN!

Note: positive up

Potential problem for error-related view?

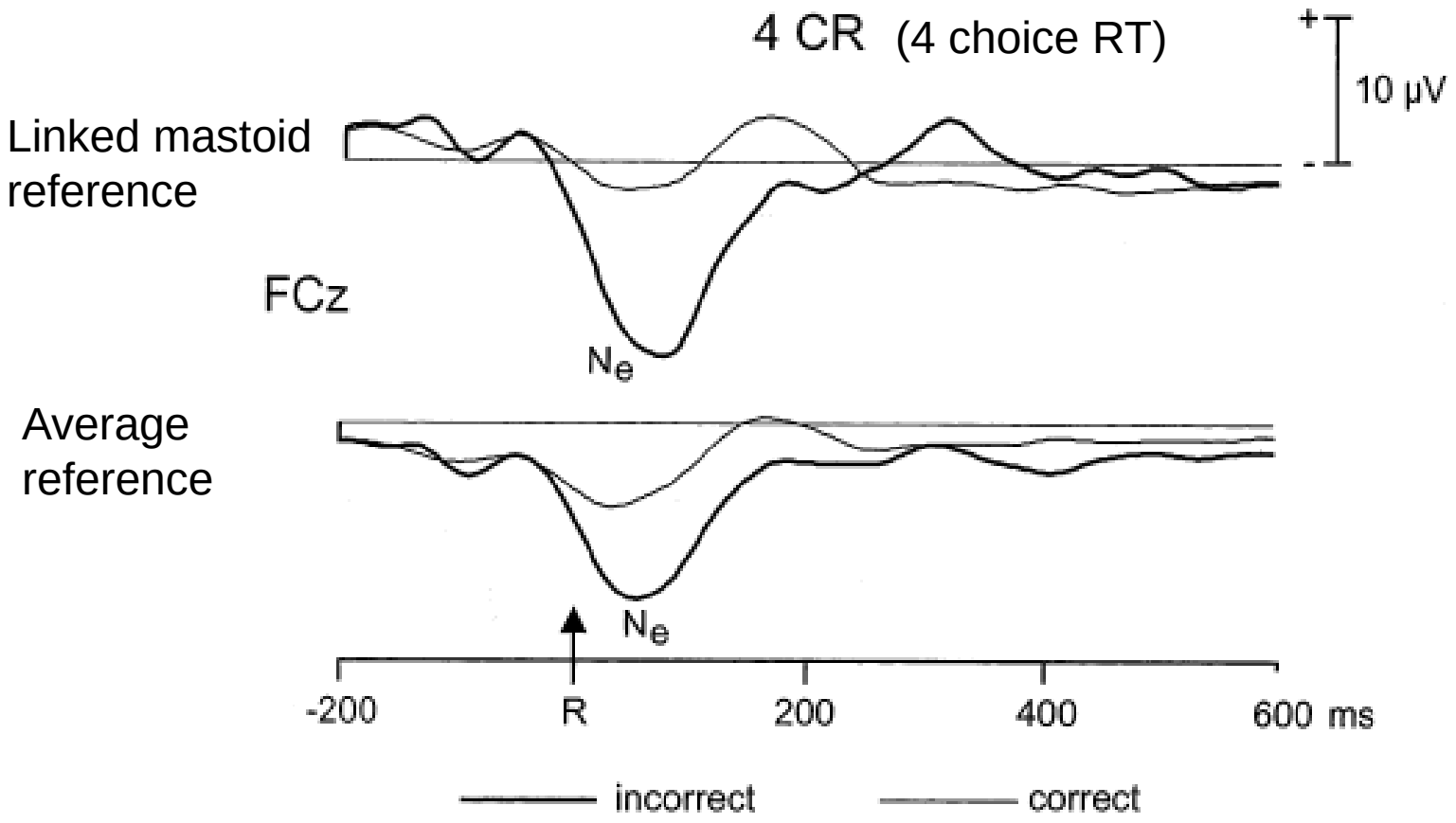
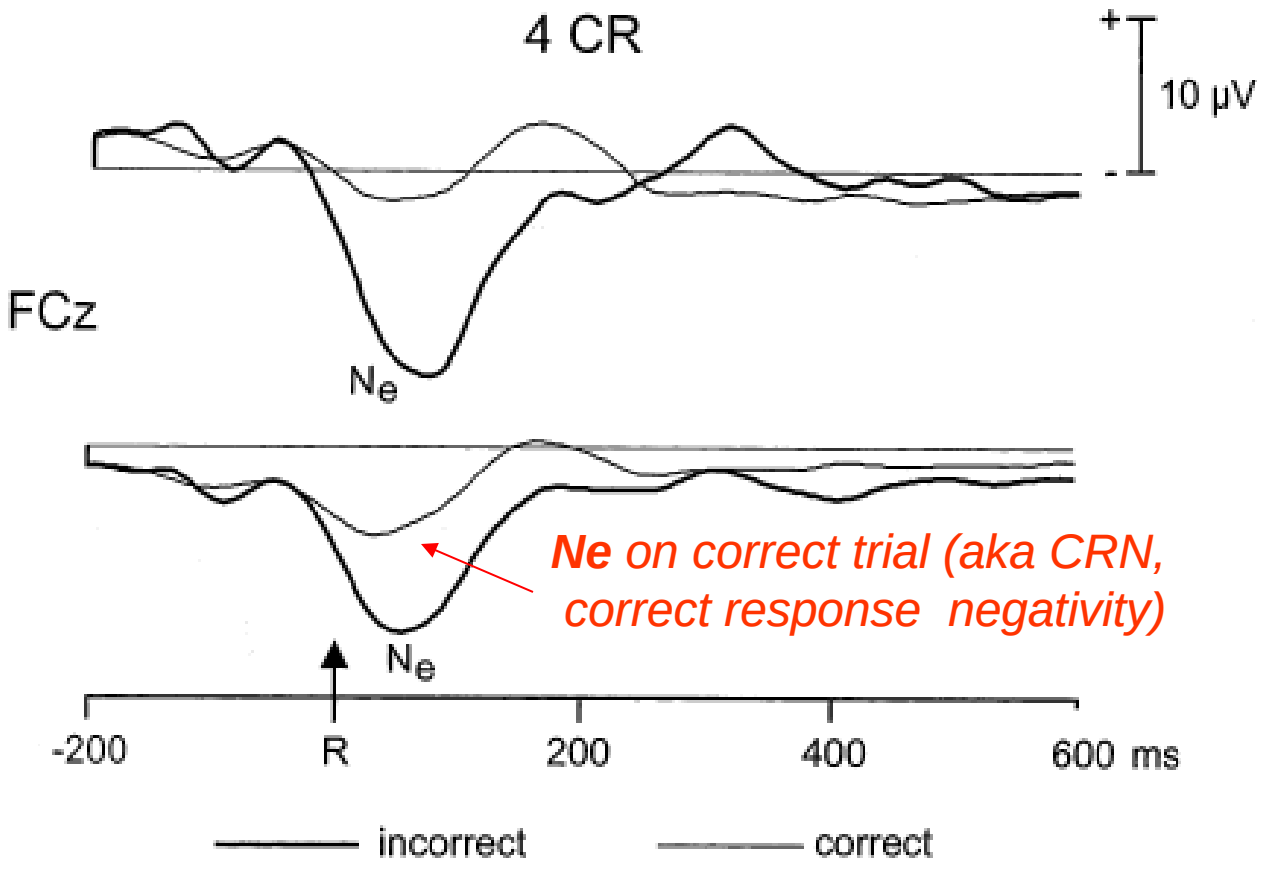


Fig. 9. Grand averages (Experiment 5; $n = 12$ young subjects) of the RTA in a 4-CR. Upper panel: linked mastoid reference, lower panel: average reference. The Ne is clearly seen after errors; after correct responses a similar (though smaller) negativity is seen (cf. text).

CRN – correct response negativity



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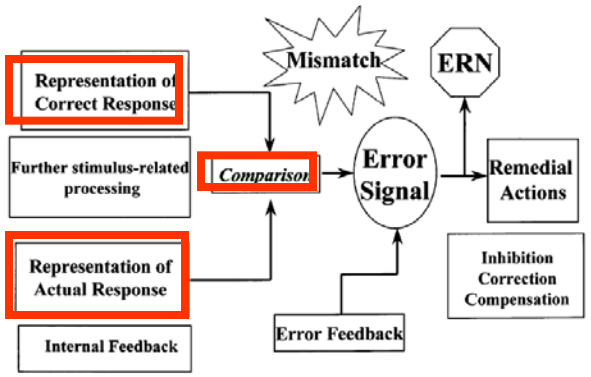
Main views on functional significance of ERN

1. Error monitoring, detection and correction, system

2. Response conflict detection/monitoring system

3. Response-comparison process

3. Detection of motivationally or
   especially negative ones



ERN might reflect appraisal of the motivational or affective impact of the error

ERN amplitude increases with negative emotionality/affect, so perhaps it reflects degree of affective distress (Tucker & Luu)

Main views on functional significance of ERN

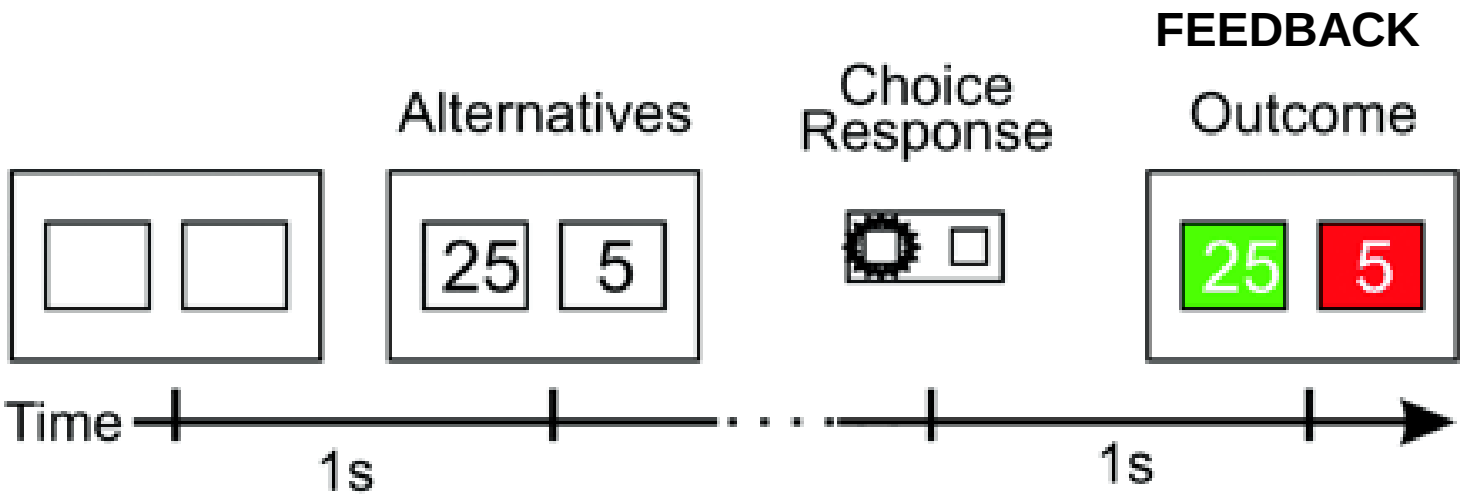
1. Error monitoring, detection and correction, system

2. Response conflict detection/monitoring system

3. Response-comparison process

3. Detection of motivationally or emotionally salient events, especially negative ones

GAMBLING TASK



Green = gain
Red = loss

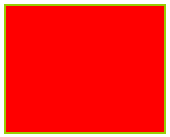
= gain

= loss

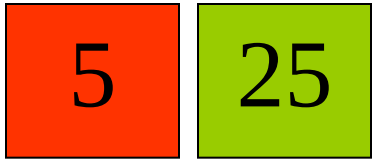
Gehring & Willoughby, 2002

“Gambling” Task

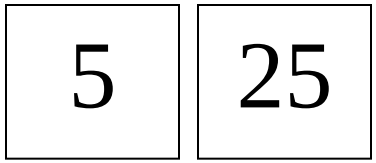
= gain



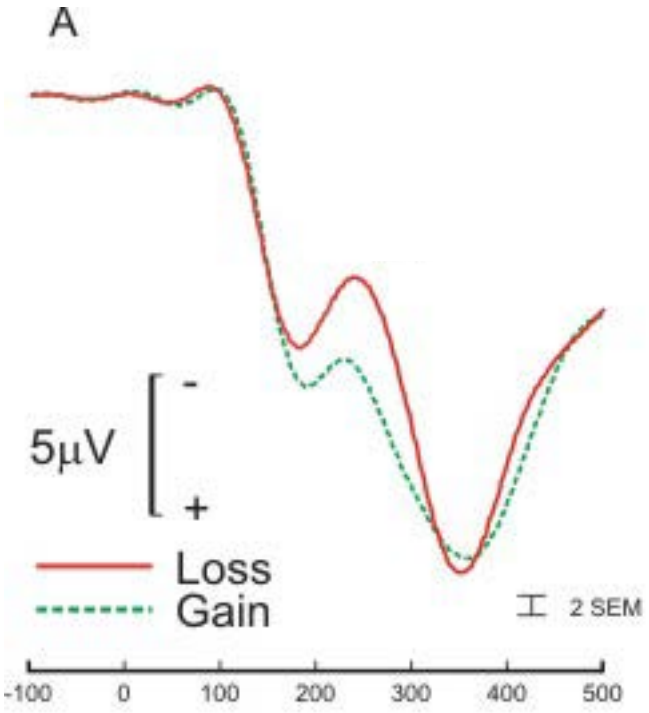
= loss



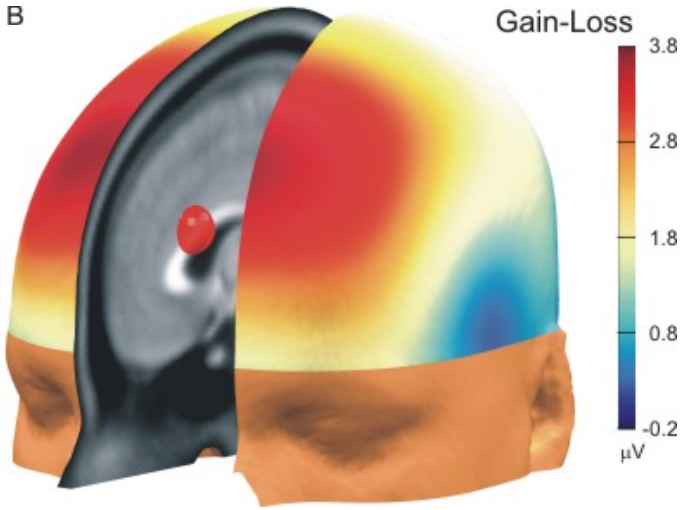
Choose left or right



Frontal site

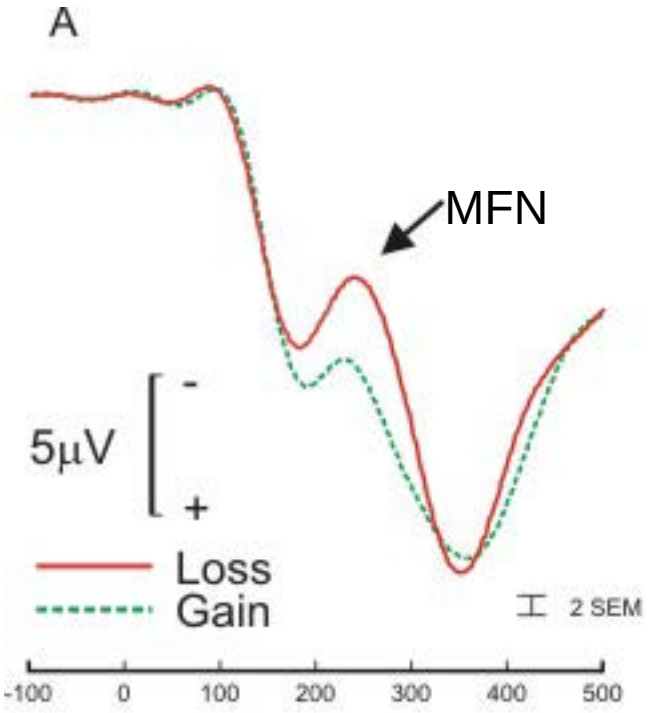


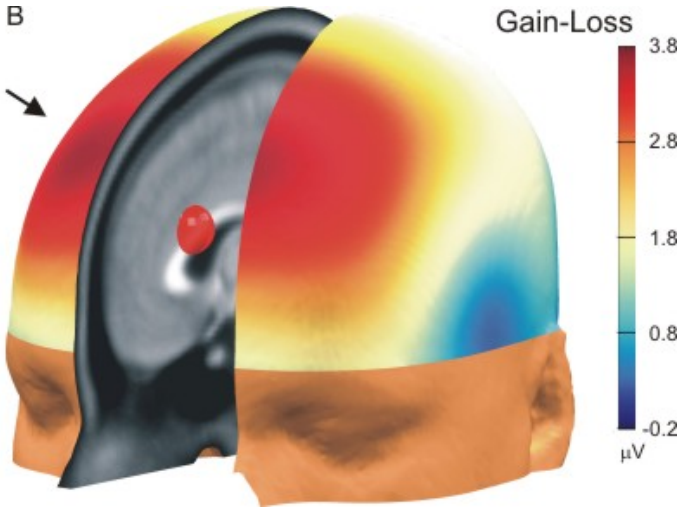
Dipole modelling localization



Gehring & Willoughby (2002)

Medial-frontal negativity (MFN)

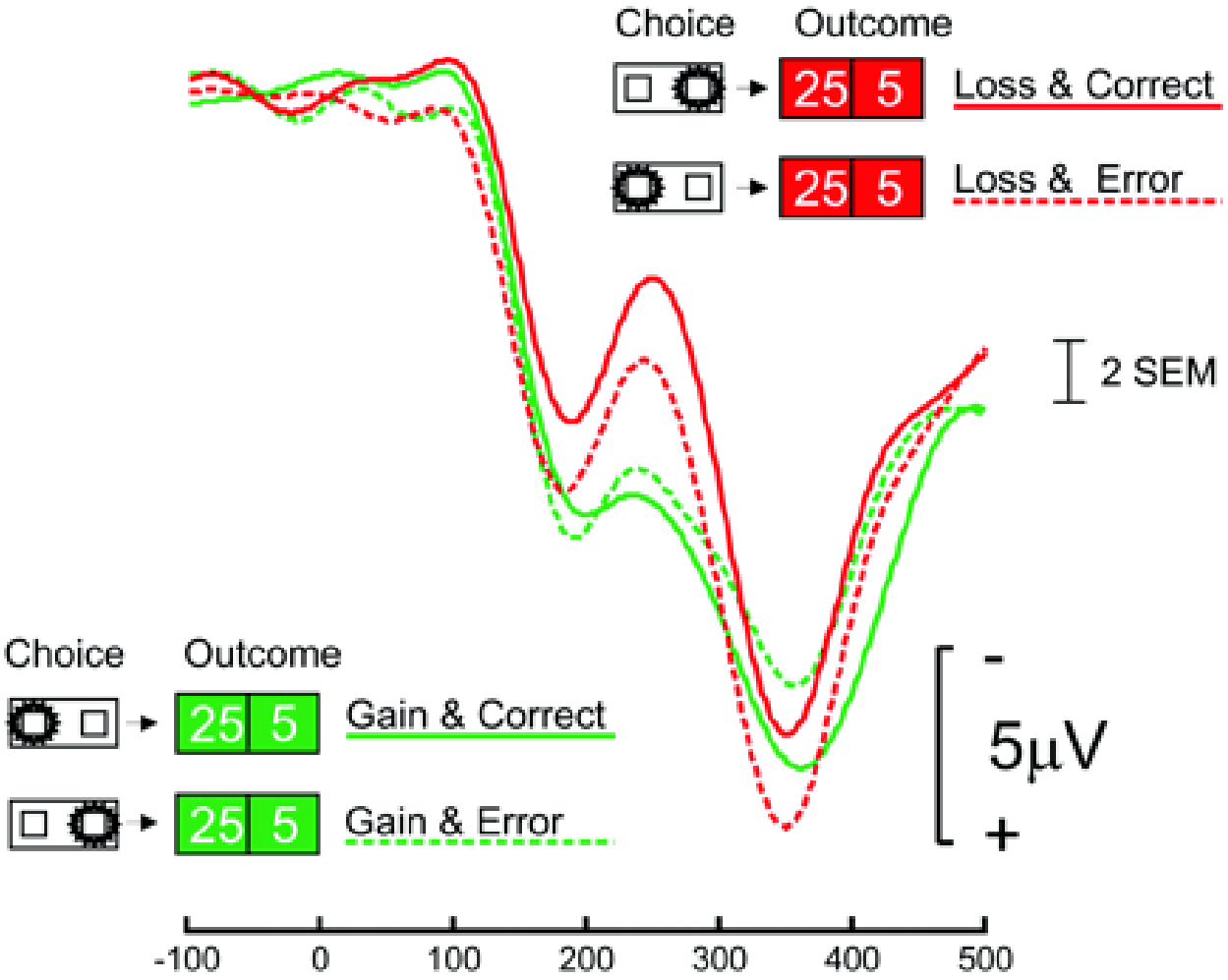




MFN is sensitive to the value of outcome in gambling task; Coles and Holroyd call this fERN

Gehring & Willoughby (2002)

EFFECT of RESPONSE ACCURACY



Gain = gained money; Loss = lost money
Correct = better choice among the alternatives; error = worse choice

MFN is sensitive to the “utilitarian” (gain or loss) value of feedback, rather than to the “performance” (correct or incorrect) value of feedback.

GAMBLING TASK

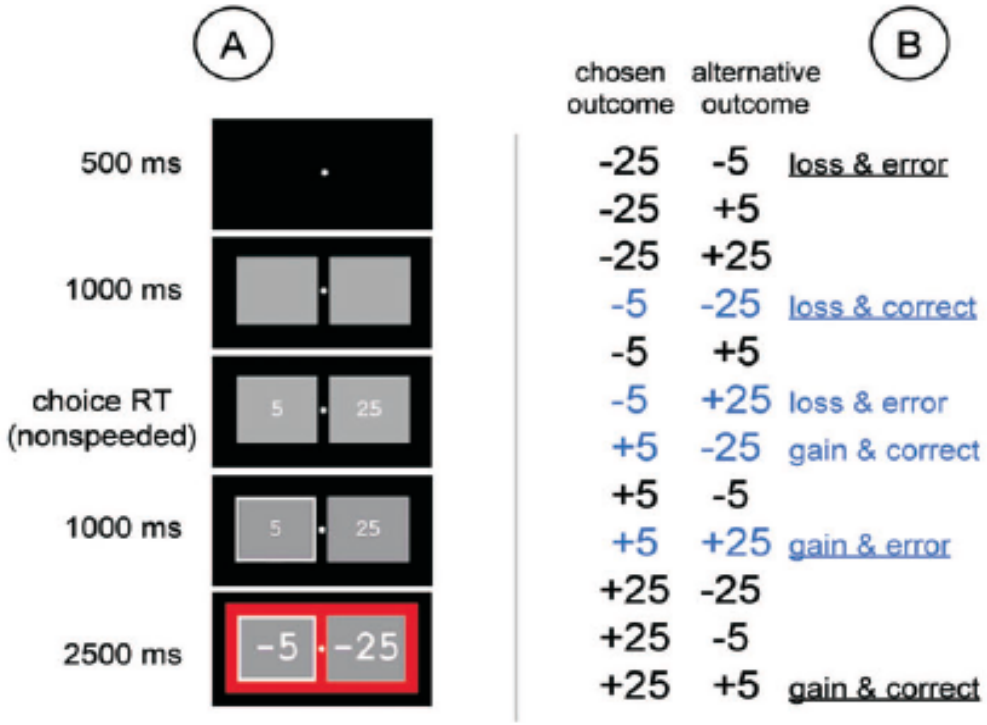
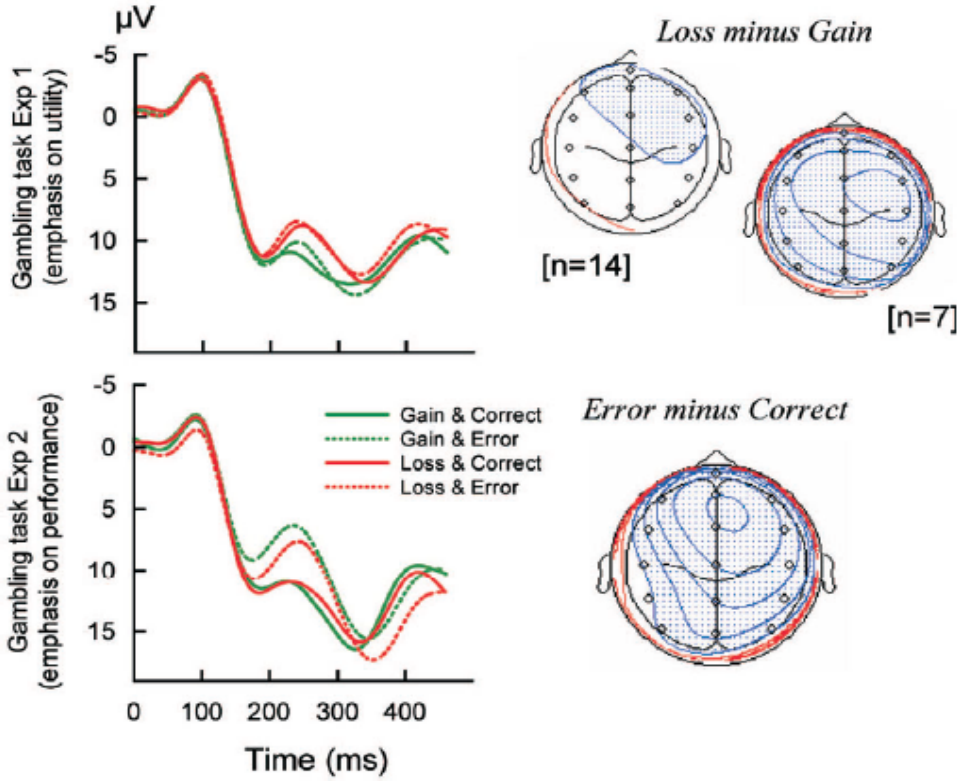


Figure 1. (*A*) Example of stimulus events in the gambling task. The duration of each stimulus event is indicated. See text for details. (*B*) List of possible combinations of chosen outcome and alternative outcome. The blue conditions indicate the four conditions chosen here to analyze the effects of gain versus loss and correct versus error. The underlined conditions indicate the four conditions chosen by Gehring and Willoughby (2002a). 'Loss' and 'gain' indicate that the chosen outcome yielded a financial penalty or reward, respectively. 'Error' indicates that the alternative outcome would have yielded a larger reward or a smaller penalty, relative to the chosen outcome. 'Correct' indicates that the alternative outcome would have yielded a smaller reward or a larger penalty, relative to the chosen outcome.

Gambling Task

Emphasize gain/loss

Emphasize correctness



Medial Frontal Negativity, MFN=FB-ERN?

RL(reinforcement learning)-ERN

...a learning signal generated when the consequences of an action are ***worse than expected*** ...***used to modify performance on the task at hand*** (*Holroyd and Coles, 2002*)

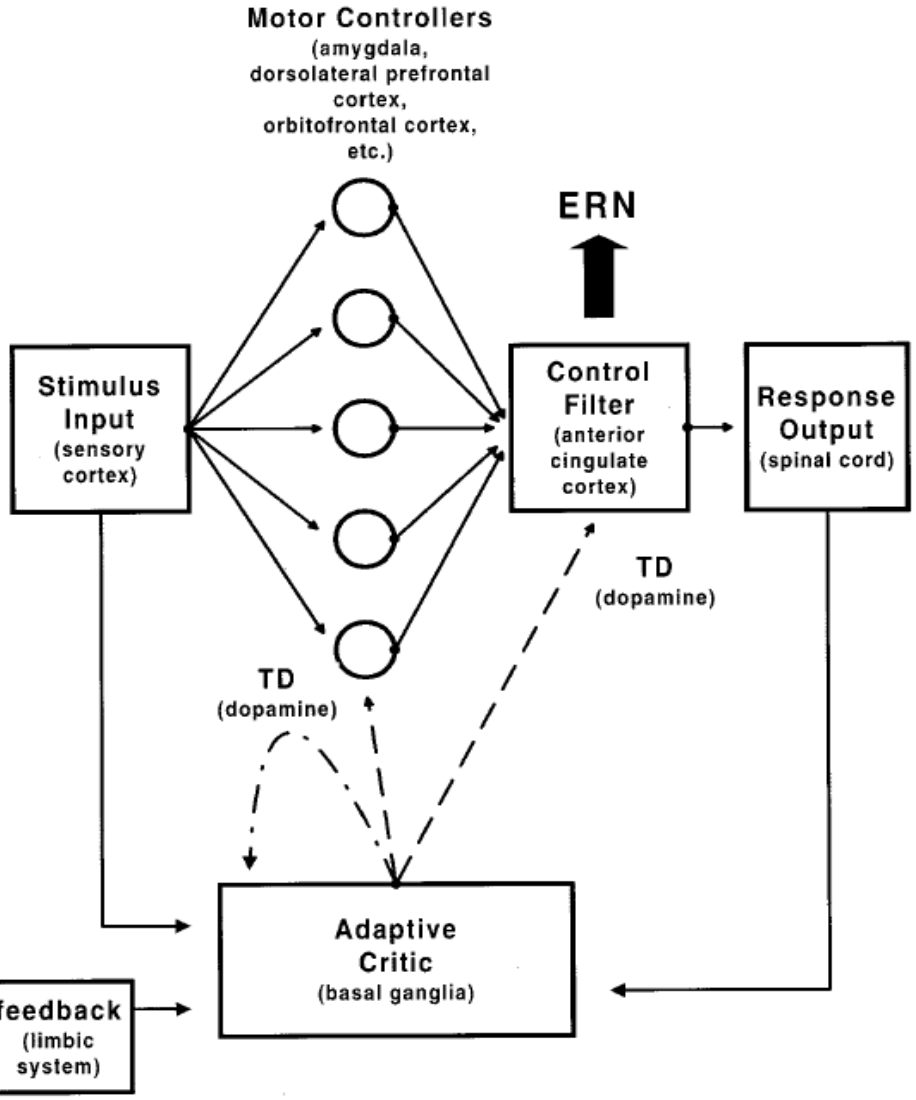


Figure 1. A schematic of the model. The corresponding neural substrate is given in parentheses below each component label. See text for details. ERN = error-related negativity; TD = temporal difference error.

ERN is generated when a negative TD error is carried by the mesencephalic dopamine system to the anterior cingulate motor areas, during or after response generation. ERN is produced when the system first detects that the consequences of an action are worse than expected.

Reinforcement learning theory of ERN

(a) ERN reflects the transmission of a reinforcement learning signal to the anterior cingulate cortex;

(b) this error signal is carried by the mesencephalic dopamine system;

(c) Signal is used to train the anterior cingulate motor cortex to optimize performance on the task at hand.

ERN is generated when a negative TD error is carried by the mesencephalic dopamine system to the anterior cingulate motor areas, during or after response generation. ERN is produced when the system first detects that the consequences of an action are worse than expected.

Reinforcement theory predicts what's important is whether situation is better or worse than expected.

3 possible, equiprobable outcomes:
Win condition: +5, +2.5, 0 (objective expected outcome = 2.5)
Lose condition: -5, -2.5, 0 (objective expected outcome = -2.5)

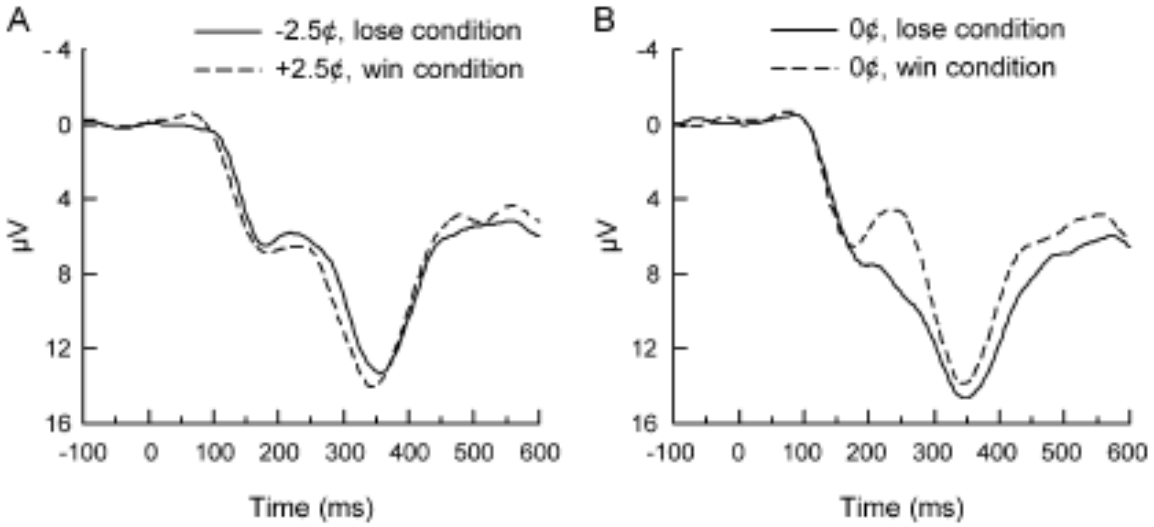


Fig. 2. Illustration of context sensitivity of the feedback ERN (adapted from Ref. [7]). Waveforms were recorded from electrode FCz. Time = 0 ms indicates the onset of the feedback stimulus. See text for details.

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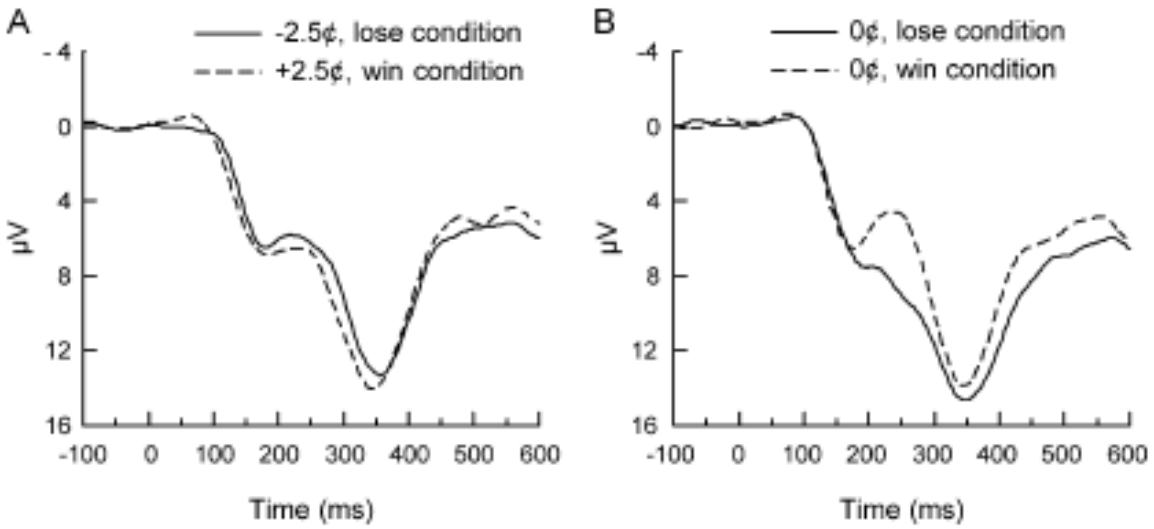

Fig. 2. Illustration of context sensitivity of the feedback ERN (adapted from Ref. [7]). Waveforms were recorded from electrode FCz. Time = 0 ms indicates the onset of the feedback stimulus. See text for details.

Feedback ERN is sensitive not to the absolute magnitude of the reward, but rather to deviations from the expected value of the reward. Feedback ERN behaves as if it is reflects a reward prediction error

According to RL-ERN theory, ERN reflects a negative reward prediction error – a signal elicited when the monitoring system has to revise its reward expectations for the worse. The amplitude of the ERN is proportional to the size of the prediction error; the amplitude of the ERN depends on the difference between the actual outcome of a trial and the expected outcome of the trial.

Error related positivity, Pe

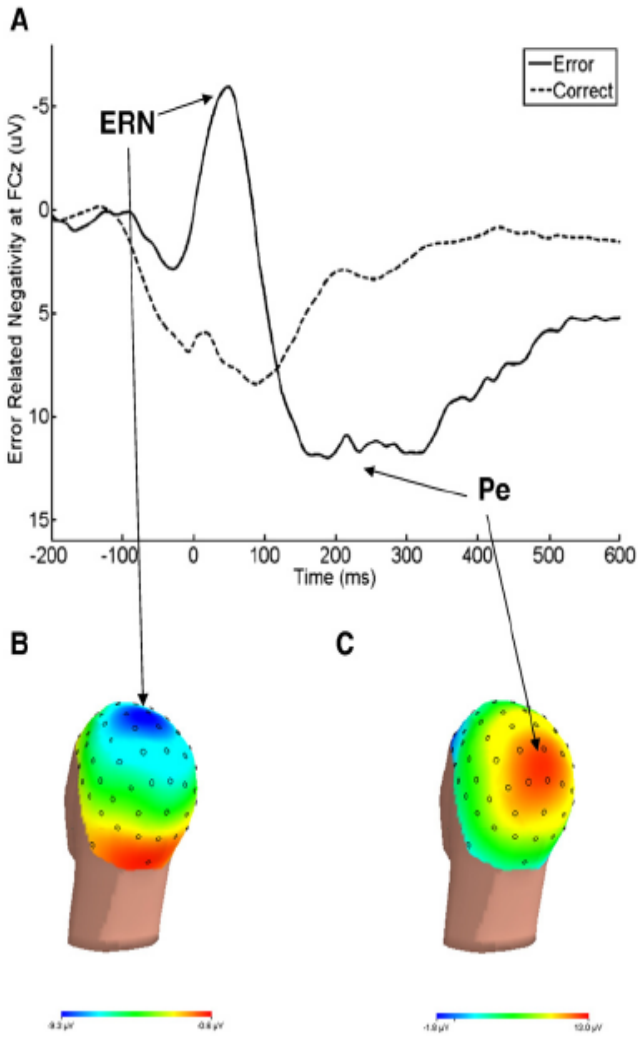

Fig. 1. The response locked ERPs for error and correct trials at FCz, where the ERN was maximal (A). The response onset occurred at 0 ms and negative is plotted up. Scalp topography of error-related brain activity from 0 to 100 ms post-response (B). Scalp topography of error positivity from 200 to 400 ms post-response (C).

Pe – error positivity

Note positive up

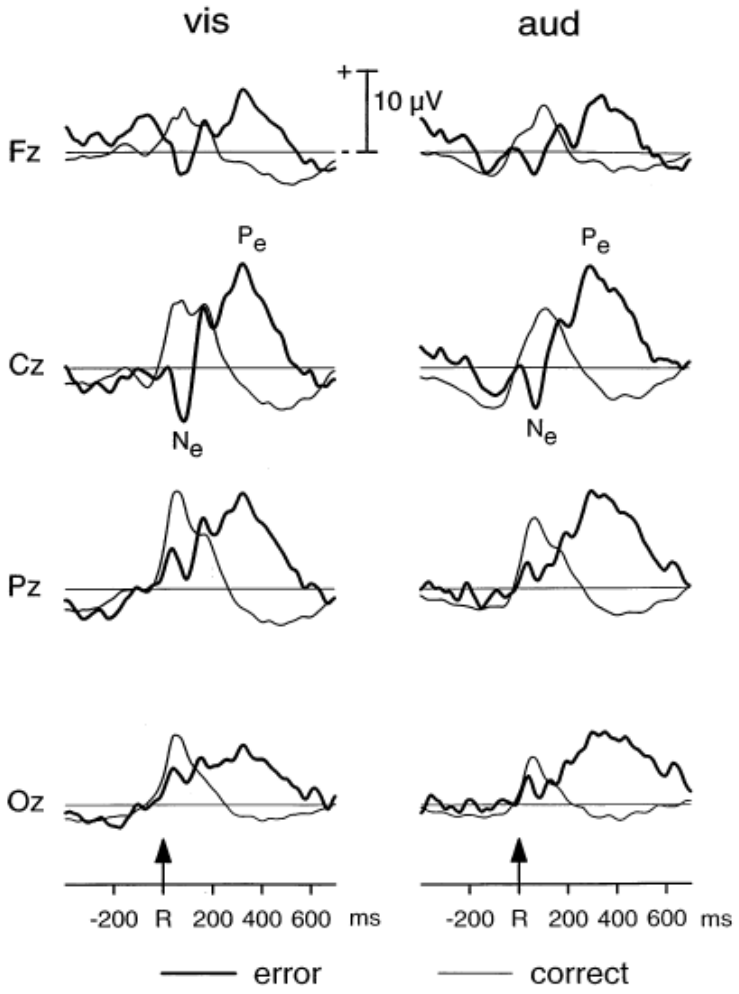

Fig. 1. Grand averages (Experiment 4; $n = 12$) of the RTA for errors (heavy lines) and correct trials (light lines) after visual (vis) and auditory letter stimuli (aud) in a 2-CR task. The error negativity ('Ne') is seen as a sharp negative deflection with central maximum peaking at about 80 ms after the incorrect key press (R). The error positivity ('Pe') is seen as a late parietal positivity with Cz maximum peaking at about 300 ms after the incorrect key press. On correct trials a positive complex with Pz maximum is seen.

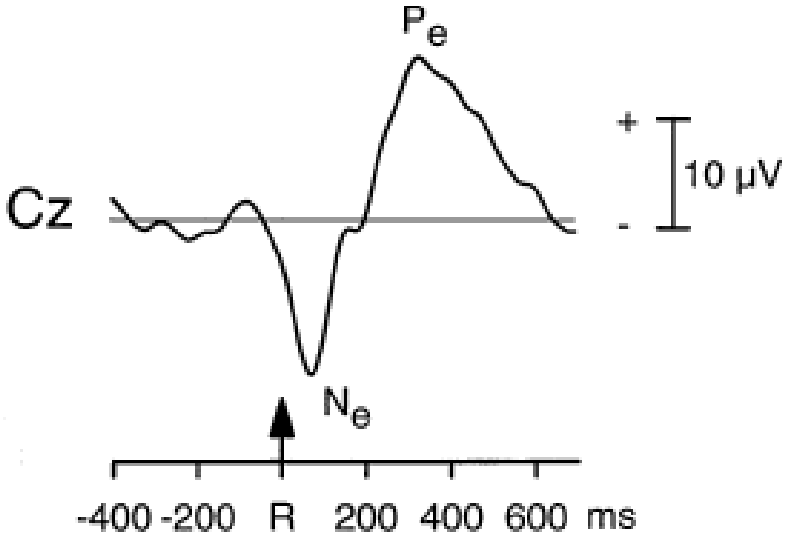

Fig. 2. Grand average of the response-triggered difference waveshapes (error minus correct RTAs) from Fig. 1 (visual stimuli; Cz electrode). The Ne and the Pe are highlighted as large negative and positive deflections.

Pe – error positivity

- Pe similar across all age groups (unlike Ne which is smaller in children)
- Unaffected by SDAT, Parkinson's, schizophrenia, all of which reduce Ne
- Unaffected by OCD (which increases Ne)
- Like Ne, smaller or absent in individuals with frontolateral or basal ganglia lesions; neither are affected by frontopolar or temporal lesions
- Seems to covary with degree of awareness of error or salience of error-inducing stimulus

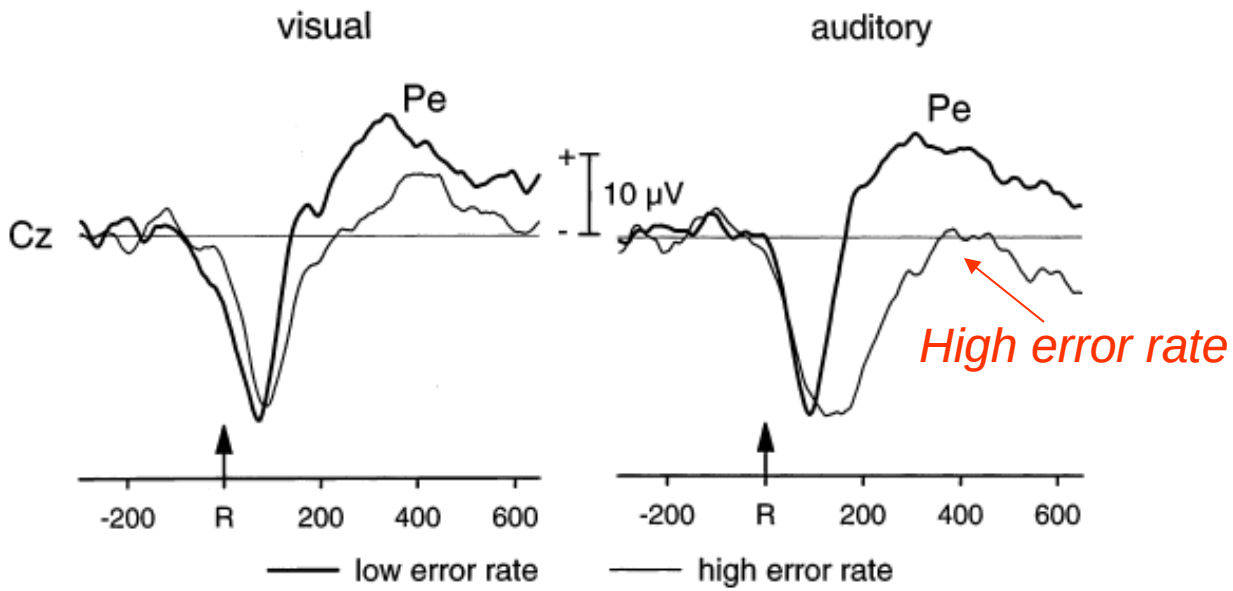

Fig. 11. Grand averages (Experiment 2; $n = 10$) of the response-triggered difference waveshapes (error minus correct) for subjects with low error rate (heavy lines) and subjects with high error rate (light lines) in a Go/Nogo task. While the Ne has the same amplitude for both groups, the Pe is very small for subjects with high error rate.

Functional significance of Pe

Error awareness

Affective processing

Post processing of error/remediation
- Ne: fast automatic correction
- Pe: slower, more conscious correction system

Just a P3

Who knows???

Psychophysiology, 38 (2001), 752–760. Cambridge University Press. Printed in the USA.

Error-related brain potentials are differentially related to awareness of response errors: Evidence from an antisaccade task

SANDER NIEUWENHUIS,[a] K. RICHARD RIDDERINKHOF,[a] JOS BLOM,[a]
GUIDO P.H. BAND,[b] AND ALBERT KOK[a]

[a]Department of Psychonomics, University of Amsterdam, The Netherlands
[b]Experimental and Theoretical Psychology Unit, Leiden University, The Netherlands

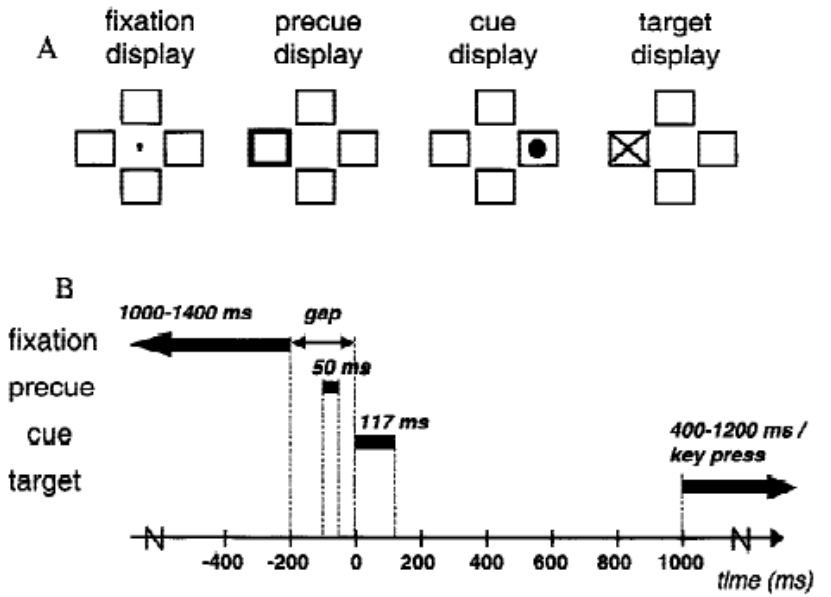

Figure 1. A: Example of stimulus displays in the present experiment. See text for actual size. B: Relative timing and presentation duration of stimulus events in the present experiment. Time $t = 0$ ms corresponds to the moment of cue onset. Note that the probability of a precue being presented was 50%.

Nieuwenhuis et al. 2001

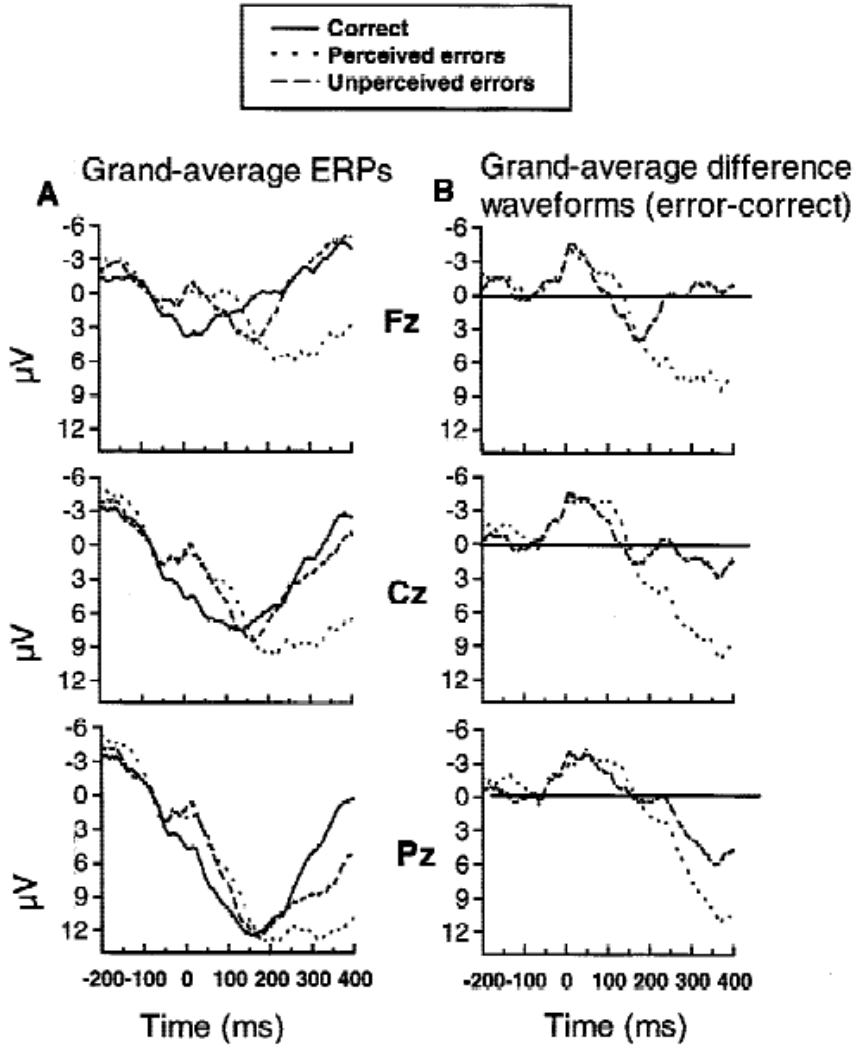

Figure 4. A: Original, grand-average response-locked ERP waveforms for each trial type. B: Grand-average response-locked ERP difference waveforms for (perceived errors minus correct) and (unperceived errors minus correct).

Nieuwenhuis et al. 2001

CNV, PINV, RP, LRP (CMA), nogo N200, ERN/Ne (response ERN, Feedback ERN, Pe, CRN, MFN