Brain-electrical correlates of negative location priming under sustained and transient attentional context conditions

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Running Title: Negative Priming and Attentional Context

Abstract

In the present study event-related potentials (ERPs) and event-related lateralizations (ERLs) were analyzed to investigate mechanisms of attentional inhibition engaged when a target stimulus has to be located within a simultaneous target-distractor display. The putative aftereffects of inhibition were examined with a prime-probe technique by comparing a 'DT' condition (the prime Distractor location becomes the probe Target location) with a control condition (the probe target appears at a previously empty position). The specific aim was to dissociate more 'automatic' aspects from more 'controlled' aspects associated with the inhibition of distractor locations. To do so, we compared physically identical prime-probe pairs under a sustained attention context (same target throughout a block) and a transient attention context (trial-by-trial target specification). Three early ERP/ERL components showed differential effects for DT compared to control: a) the posterior N1 with a diminished amplitude contra-lateral to the visual half-field side of target presentation, b) the N2pc with an enhanced amplitude contralateral to the visual half-field side of target presentation, and c) the posteriorly distributed N2 with a non-lateralized enhancement for DT compared to control. These effects were differently affected by the context manipulation. While the N2pc effect was observed exclusively under sustained attention, the N1 lateralization effect and the N2 effect were not differentially modulated. The N1 lateralization effect seems consistent with an inhibition-of-return explanation. The N2pc and N2 effects are supposed to be reflecting different aspects of a biasedcompetition model of distractor inhibition.

Keywords: Negative priming, Sustained attention, Transient attention, ERP, N2pc, Inhibition, Selective attention, Associative attentional learning, Biased competition

Introduction

In everyday life we are usually surrounded by many different objects located at separate spatial positions. If behavior requires to make use of one specific object, a mechanism is needed to precisely locate one relevant object among the numerous irrelevant objects (e. g., to be able to reach for this object). An assumption that has been expressed in theoretical accounts of selective attention is that both excitatory and inhibitory processes are co-operatively engaged to enable the perceptual segregation of relevant and irrelevant information (Desimone, Wessinger, Thomas, & Schneider, 1990; Houghton & Tipper, 1994; Luck, Girelli, McDermott, & Ford, 1997).

The present study focused on the inhibitory aspect of selective attention, specifically when a target stimulus has to be <u>located</u> among distractor stimuli. To study the underlying mechanisms, we employed the negative location priming (NLP) procedure which is a variant of the negative priming paradigm as an established tool for the investigation of attentional inhibition in behavioral experimental psychology (Fox, 1995; Kok, 1999; May, Kane, & Hasher, 1995).

In the NLP procedure (Tipper & McLaren, 1990; Tipper, Weaver, Cameron, Brehaut, & Bastedo, 1991) a target stimulus has to be selected by some non-spatial feature (e.g. letter 'X') while another simultaneously presented non-matching distractor stimulus (e.g. letter 'O') has to be ignored. The subjects' task is to indicate the spatial position of the target by pressing a spatially compatible response button. When the current target position is identical to the position of the previous distractor as compared to a previously empty position, performance is usually impaired. This so called NLP effect suggests that target selection among distractors includes an act of inhibition applied onto the location the distracting information is bound to. Besides this

original hypothesis, a number of alternative explanations have been proposed (Milliken, Tipper, Houghton, & Lupianez, 2000; Neill, Valdes, Terry, & Gorfein, 1992; Park & Kanwisher, 1994). In turn, it has been argued that the NLP effect probably reflects multiple processes with the aftereffect of distractor inhibition being one aspect among others (May et al., 1995; Tipper, 2001). While our experiment was not specifically designed to distinguish between the alternative theoretical accounts, we are getting back to this debate in the discussion of our results. Throughout this paper, though, we are adopting a pro-distractor-inhibition attitude.

Besides characterizing the general brain-electrical signature of NLP, a major aim of the present study was to investigate differences between inhibitory mechanisms engaged during more 'automatic' selection compared to more 'controlled' selection. Phenomena of attentional learning and automatization have been the topic of several theoretical accounts of selective attention (Kruschke, 2003; Lubow & Kaplan, 1997; Mackintosh, 1975; Shiffrin & Schneider, 1977). For instance, the 'attentional trace' theory (Alho, Lavikainen, Reinikainen, Sams, & Näätänen, 1990; Näätänen, 1990) considers that the aspect of selective attention which is indicated by Nd-like ERP waves (referring to a negative-going difference-ERP component which is obtained by subtracting ERPs to attended features from ERPs to unattended features) seems to depend on the amount of 'afferent feedback' a given to-be-attended feature had been experiencing (Alho et al., 1990; Hansen & Hillyard, 1988; Näätänen, 1990; Wijers, Mulder, Gunter, & Smid, 1996). This means, that if the same relevant target feature has repeatedly and consistently matched incoming sensory information, this feature gets quickly associated with a learned attentional response and can thus be selected more easily.

The critical question addressed by the present study is whether an analogous notion holds for unattended stimulus features and the locations they are bound to (i.e. the acquisition of a learned response away from the distracting information).

To address this issue experimentally, we compared event-related potentials for DT and Control trials under 'sustained attention' and 'transient attention' (cf. Eimer, 1997). Under sustained attention neither the identity of the relevant target stimulus nor the identity of the irrelevant distractor stimulus changed throughout an experimental block. This condition was supposed to implicate a strong automatic attentional response towards target locations and away from distractor locations as well. Under transient attention the identities of target and distractor were randomly exchanged from trial to trial implicating weak automatic attentional responses.

Eimer (1997) compared ERP effects of sustained and transient attention to non-spatial stimulus features in a procedure where target and distractor stimuli were presented successively (not simultaneously as in the NP paradigm). This study revealed an enhanced selection negativity (the difference between successively presented target and distractor stimuli) in the sustained attention condition. However, since target and distractor where not presented simultaneously potential inhibitory mechanisms are supposed to be different from those employed in the NLP paradigm.

The ERP literature dealing with correlates of visual search suggests that the search-related N2pc component (posterior and <u>c</u>ontra-lateral to the visual half-field side of target presentation) might be a component of particular interest (Eimer, 1996; Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004; Hopf et al., 2000; Luck, Fan, & Hillyard, 1993). The N2pc emerges specifically when a target is selected among distractors, and even so when only a single distractor is placed in

the opposite visual half-field (Eimer, 1996). Luck et al. (1997) showed that the magnitude of the N2pc amplitude is enhanced by factors that increase the severity of distractor interference. A possible interpretation of this finding is that the N2pc evolves through a biased competition process between target and distractor features, involving the enhancement of target locations and the suppression of distractor locations (Chelazzi, Duncan, Miller, & Desimone, 1998; Desimone, 1998; Luck et al., 1997).

To our knowledge only one ERP study explicitly based on the negative priming paradigm has been published yet (Mayr, Niedeggen, Buchner, & Pietrowsky, 2003). In contrast to the present study, Mayr et al. realized a negative <u>identity</u> priming procedure and presented auditory stimuli. Thus, it appears to be difficult to derive hypotheses about ERP effects in the present study. Indeed, we observed a completely different set of ERP components affected by the location priming manipulation.

Methods

Subjects

Twenty-eight paid volunteers (aged 19-34 years, 13 females) participated in this study after written informed consent was obtained. All subjects were right-handed and had normal or corrected-to-normal vision.

Apparatus, Stimuli, and Procedure

In each trial subjects were presented with one distractor letter and one target letter at two out of four possible locations (see Figure 1). The four locations were marked by underlines separated by a 4° visual angle being visible continuously across trials. A centrally presented letter cue

indicated the relevant target letter which could be 'X' or 'O'. The distractor letter was always the letter which was not the target.

--- Figure 1 here ---

In order to realize the two attentional context conditions we introduced two experimental blocks with block sequence balanced across subjects. In the sustained attention block the target was the letter 'O' and the distractor was the letter 'X' fixed for all trials. In the transient attention block the letters 'X' and 'O' were randomly exchanged between target and distractor from trial to trial. In both blocks the centrally presented pre-cue preceded the target-distractor pair by 500 ms. All three letters were displayed until the response was made or timeout after 1500 ms. The interval between the response and the next cue was 250 ms.

Stimulus presentation was controlled by a standard PC and displayed on a standard CRT monitor. Subjects responded by pressing the 'S', 'D', 'J', and 'K' keys of a standard PC-keyboard with their left and right hand index and middle fingers in a spatially compatible way to the four display positions.

We employed a continuous priming procedure with each probe trial also serving as the prime for the next trial. In 'DT' trials (prime <u>D</u>istractor location becomes probe <u>T</u>arget location) the target was presented at the previous distractor location and the distractor was presented at one of the two previously empty locations. In control trials both the target and the distractor were presented at previously empty locations. As Christie & Klein (2001) have pointed out, this design is not optimal in the sense that it potentially introduces response strategies (e. g., considering that probe targets never appear at the prime target position) which might interact with the priming manipulation. However, Christie & Klein also showed that this bias does not seem to be critically altering negative priming effects. Furthermore, as is argued in the discussion section the particular brain-electrical correlates of NLP we observed in the present study are unlikely to be influenced by the involvement of confounding response strategies.

For each block and each subject a quasi-random sequence of conditions was computed off-line with the following constraints: equal number of DT and control trials, equal number of transitions between the conditions, equal number of the twelve possible different arrangements of target and distractor locations for both conditions. In the transient attention block all possible transitions between DT, control, target switching and target repetition were additionally balanced.

In the sustained attention block 144 DT and 144 control trials were implemented. Each of these conditions contained 96 trials in which target and distractor appeared at different visual half-field sides. In the transient attention block we had 192 DT and 192 control trials and each condition contained 96 switch and 96 repeat trials. Each of these four conditions contained 64 trials with target and distractor presented at different visual half-field sides. The basic analyses of the behavioral data and the EEG data were based on the full stimulus sets. As explained later, certain analyses of event-related lateralizations were performed with the reduced bi-lateral stimulus sets.

Furthermore, we considered only the cue repetition trials from the transient attention block. Thus, the prime-probe pairs that entered the analysis were physically identical for both blocks.

EEG recording and data analysis

The EEG was recorded from 29 Ag/AgCl electrodes positioned according to the international 10-20 standard and referenced to Cz. The electrode positions included Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, FC3, FCz, FC4, T3, T4, C3, Cz, C4, CP3, CPz, CP4, P3, Pz, P4, T5, T6, O1, Oz, O2, and bilateral mastoids. Electrode impedance was kept below 5kOhm. Bipolar horizontal EOG was recorded from electrodes located at the outer canthi of both eyes. Bipolar vertical EOG was recorded from above and below the left eye. The amplifier (SYNAMP, model 5083, Neuroscan) bandpass was 0.05-30 Hz, and a notch-filter was set to 50 Hz. EEG and EOG were sampled at 200 Hz and stored on disk.

Off-line pre-processing was performed with the Brain Vision Analyzer software (version 1.05, Copyright ©Brain Products GmbH 1998-2004). Visualization and parametrization were performed with the in-house software EkpScan (version 1.06.05, Copyright ©EEG-Lab University of Trier 1998-2005). The EEG was re-referenced to algebraically linked mastoids, artifacts due to eye movements were corrected via the Gratton et al. (1983) algorithm. Epochs with non-physiological artifacts (absolute amplitudes exceeding +/-200 μ V, difference between successive time points > 100 μ V) were removed (less than 2% of all epochs). The EEG was epoched for 1700 ms intervals, starting 200 ms before cue presentation. The averaged time courses for each condition were baseline-corrected relative to the mean signal intensity during the 200 ms time interval preceding the target-distractor pair.

Event-related lateralizations (ERL) were computed with the Brain Vision Analyzer software equivalent to Coles et al. (1995) based on the following algorithm:

ERL = [Average(right electrode - left electrode)_{target left}

+ Average(left electrode - right electrode)_{target right}]/2

According to this equation, a positive ERL deflection reflects activity that is stronger contralateral to the target position whereas a negative ERL deflection reflects activity that is weaker contra-lateral to the target position.

Results

Behavioral results

Reaction times

We computed a two-way ANOVA with the factors attentional context (sustained vs. transient) and priming (DT vs. control). The significant main effect priming ($\underline{F}(1,27)=60.16$, $\underline{p}(\underline{F})<0.001$, $\underline{eta^2}=0.70$) indicated slower response times for DT (511.05 ms; s.e.=12.99) than for control (494.48 ms; s.e.=12.86). This effect did not significantly differ between the attentional context conditions (interaction priming by attentional context: $\underline{F}(1,27)=1.81$, n.s., $\underline{eta^2}=0.06$). The significant main effect of attentional context ($\underline{F}(1,27)=53.70$, $\underline{p}(\underline{F})<0.001$, $\underline{eta^2}=0.67$) indicated faster response times for sustained attention (460.44 ms; s.e.=13.50) than for transient attention (545.10 ms; s.e.=14.71).

Percent errors

A two-way ANOVA with the factors attentional context and priming revealed no significant main effect priming ($\underline{F}(1,27)=3.70$, n.s., $\underline{\text{eta}}^2=0.12$) and no significant interaction priming by attentional context ($\underline{F}(1,27)=0.33$, n.s., $\underline{\text{eta}}^2=0.01$). The significant main effect of attentional

context ($\underline{F}(1,27)=44.88$, $\underline{p}(\underline{F})<0.001$, $\underline{eta}^2=0.62$) indicated fewer errors for sustained attention (1.9%; s.e.=0.19) than for transient attention (6.3%; s.e.=0.62).

EEG results

The analysis of EEG data included regular ERPs and event-related lateralizations (ERLs). For both analyses a comparison of DT and Control trials under the two different attentional context conditions was performed for three visually identified ERP/ERL components (the non-lateralized posterior N2, the lateralized posterior N1, and the N2pc).

The analysis of ERLs included an additional step where only stimuli with bilateral targetdistractor pairs were included. This was done to eliminate the putative overlay with ERL components which are merely caused by the uni-laterality of stimulus presentation and not by target-specific selection processes.

> --- Figure 2 here ---Figure 3 here ---

Event-related potentials

Figures 2 and 3 depict ERPs for DT and Control under sustained attention and under transient attention. For both context conditions the posterior N2 was enhanced for DT compared to Control. We submitted N2 average amplitudes (interval 250-290 ms) for three sets of pooled posterior electrode positions ([O1, Oz, O2], [T5, T6], [P3, Pz, P4]) to a three-way ANOVA with the independent variables electrode set, attentional context and priming. Only one effect of interest reached significance, namely the main effect priming ($\underline{F}(1,27)=27.45$; $\underline{p}<0.001$; $\underline{eta}^2=0.50$). All interactions involving priming and/or attentional context failed significance

(priming by attentional context: $\underline{F}(1,27)=0.001$; n.s.; $\underline{\text{eta}^2}<0.001$; priming by electrode set: $\underline{F}(1.79_{\text{Greenhouse-Geisser}},48.40_{\text{Greenhouse-Geisser}})=1.72$; n.s.; $\underline{\text{eta}^2}=0.06$; priming by attentional context by electrode set: $\underline{F}(1.83_{\text{Greenhouse-Geisser}},49.36_{\text{Greenhouse-Geisser}})=1.85$; n.s.; $\underline{\text{eta}^2}=0.06$).

> --- Figure 4 here ------ Figure 5 here ---

Event-related lateralizations

Figure 4 shows ERLs for the DT and the control condition under sustained attention (left panels) and under transient attention (right panel). For both attentional contexts, DT compared to the control condition is associated with a reduced positive ERL amplitude in the N1 time range indicating a weaker signal deflection contra-lateral to the target position in DT trials. Furthermore, particularly pronounced in the sustained attention condition, DT compared to Control is associated with an enhanced N2pc amplitude indicating a stronger signal deflection contra-lateral to the target position in DT trials.

For each ERL component average amplitudes (N1_{sustained} = 180-205 ms; N1_{transient} = 190-215 ms; N2pc_{sustained} = 230-290; N2pc_{transient} = 255-315) were entered into a two way ANOVA including the independent variables priming, and attentional context. Considering the different scalp distributions, the analysis of the N1 lateralization included the four pooled electrode pairs O1_2, T5_6, P3_4, and CP3_4 and the analysis of the N2pc included the two pooled electrode pairs O1_2 and T5_6.

For the N1 lateralization, only the main effect priming was significant (priming: $\underline{F}(1,27)=15.06$; p=0.001; <u>eta²</u>=0.36; priming by attentional context: $\underline{F}(1,27)=0.01$; n.s.; <u>eta²</u><0.001). For the

N2pc, both the main effect priming and the interaction priming by attentional context were significant (priming: $\underline{F}(1,27)=8.18$; $\underline{p}=0.008$; $\underline{eta}^2=0.23$; priming by attentional context: $\underline{F}(1,27)=6.83$; p<0.014; $\underline{eta}^2<0.20$).

The above analyses were based on both uni-lateral and bi-lateral target-distractor pairs. To eliminate the potential overlay of general lateralization effects caused by the uni-lateral stimuli, we computed ERLs selectively for bi-lateral target-distractor pairs. Exemplarily depicted for the T5_6 electrode pair, Figure 5 shows ERLs based on all stimuli and ERLs based on bi-lateral stimuli only. As expected, the exclusion of unilateral target-distractor pairs completely eliminates the general contra-lateral N1 amplification and reveals that the negative priming effect is consistent with a contra-lateral N1 reduction specifically for the DT condition. Furthermore, the N2pc is clearly established as a discrete ERL component.

Two ANOVAs parallel to those performed for the full stimulus set using the same averageamplitude windows revealed the same pattern of results for the selected set of bi-lateral stimuli. For the N1 lateralization, only the main effect priming was significant (priming: $\underline{F}(1,27)=9.14$; p=0.005; $\underline{eta}^2=0.25$; priming by attentional context: $\underline{F}(1,27)=0.52$; n.s.; $\underline{eta}^2<0.019$). For the N2pc, both the main effect priming and the interaction priming by attentional context were significant (priming: $\underline{F}(1,27)=7.38$; p=0.011; $\underline{eta}^2=0.22$; priming by attentional context: $\underline{F}(1,27)=7.81$; p<0.009; $\underline{eta}^2<0.22$).

Discussion

The aim of the present study was to compare brain-electrical correlates of negative location priming (NLP) under two different attentional context conditions (sustained attention vs. transient attention). Besides characterizing the general signature of NLP, the central hypothesis was that inhibitory mechanisms of attentional selection would depend on the engagement of either more automatic (sustained attention) or more controlled (transient attention) mechanisms. Furthermore, though the experiment was not explicitly designed for that purpose, our results turned out to be useful to argue for and against the various explanations suggested for the behavioral NLP effect.

The comparison of the ERPs/LRPs for DT trials and control trials revealed two different patterns. First, parallel for both context conditions we found a diminished amplitude in the N1 time range for DT trials contra-lateral to the target position and an enhanced posterior N2 amplitude for DT trials. Second, specific for selection under sustained attention the N2pc amplitude was enhanced for DT compared to Control.

Before turning to more detailed considerations regarding the theoretical significance of the observed brain-electrical NLP effects, one first general conclusion seems appropriate considering the particular ERP/LRP components affected by the DT vs. Control manipulation. All three components had onset latencies of below 250 ms after probe onset and were maximal over posterior electrode sites. These general characteristics are in line with the common view that these components can be related to (relatively) early attentional processes. Therefore, it seems unlikely that the modulations observed for these components are caused by confounding response-strategies induced by the unbalanced design we employed (Christie & Klein, 2001).

Furthermore, this seems inconsistent with the post-perceptual episodic retrieval account of NLP (Neill et al., 1992) which suggests that the probe target location serves as a retrieval cue for 'do not respond' information from the prime episode if that location was occupied by the previous distractor. It is important to note, though, that this does not generally exclude such mechanisms to be contributing to the behavioral NLP effect. First, we did not specifically use manipulations to force related effects to reveal themselves. Second, ERP effects not necessarily need to parallel behavioral effects. And third, episodic retrieval might just not play a role in the specific version of the negative priming paradigm we implemented. In fact, the first published ERP study on this topic implemented a identity priming procedure with auditory stimuli which demonstrated effects that are consistent with the episodic retrieval account (Mayr et al., 2003).

N1: The NLP lateralization effect indicates inhibition of return

Common to both context conditions, we observed an amplitude reduction of the posterior N1 contra-lateral to the target position for the DT condition compared to the control condition. A similar effect has been reported for <u>neutral</u> probe stimuli (containing neither target features nor distractor features) presented at previous distractor locations (Luck et al., 1993). This observation is in line with the notion that the posterior N1 component reflects an orienting response towards the spatial location of <u>any</u> sensory event (Heinze, Luck, Mangun, & Hillyard, 1990; Luck, Heinze, Mangun, & Hillyard, 1990). Accordingly, the N1 lateralization effect in the present study can be assumed to occur at a level where task-related distinctions between target and distractor features are not yet considered. This is also supported by the fact that the N1 component was not lateralized in the control condition (when only bilateral stimuli were analyzed) suggesting that in this case attention is equally oriented to both the target location and the distractor location.

However, assuming that the N1 is reflecting processing on a pre-selection level, the NLP lateralization effect is unlikely to stem from distractor-specific inhibition applied during target selection in the prime trial. Rather, this effect appears to be consistent with an 'inhibition-of-return' (IOR) explanation of NLP (Christie & Klein, 2001; Milliken et al., 2000; Pratt & Abrams, 1999). According to this account, <u>both</u> target and distractor locations are reflexively and non-specifically inhibited. This is fundamentally different from the distractor inhibition account which assumes that specifically the distractor location is inhibited during directed target selection (i. e., at a stage where target and distractor features do matter). In line with our result, a study explicitly investigating the IOR phenomenon found the N1 to be reduced when a current target appeared at a previously occupied location (Prime & Ward, 2004).

The inhibition-of-return explanation is also supported by the observation that the attentional context manipulation did not affect the N1 lateralization effect. Since this process does not consider the distinction between features of targets and distractors, it should not matter whether or not feature-related attentional learning processes are taking place.

N2pc: The NLP effect indicates a learning-based distractor-repelling attentional response In contrast to the modulation of the non-lateralized N2 discussed later, the NLP effect associated with the N2pc was affected by the attentional context manipulation, being observed specifically under sustained attention but not under transient attention.

Different from the N1-related lateralization effect, the N2pc component was also present in the control condition (considering bilateral stimuli only). Thus, the N2pc is supposed to indicate a process that generally considers the task-related distinction between target and distractor features, which is a well established notion in the literature (Eimer, 1996; Hopf et al., 2004; Hopf

et al., 2000; Luck et al., 1993). Results obtained by Hopf et al. (2004) using a visual search procedure suggest that the N2pc is generated by two neuronal sources, one early component localized in parietal cortex and another slightly later component localized in lateral occipital cortex. However, visual search comprises serial search processes (associated with the early parietal source) which are probably not employed in the single-distractor context present in the NLP paradigm. Thus, it seems likely that the N2pc observed in the present study is generated in the lateral occipito-temporal cortex (see also Luck et al., 1997).

These general characteristics ascribed to the N2pc suggest that the amplitude enhancement we observed for DT trials is likely to reflect the after-effects of inhibition specifically applied to the previous distractor position during target selection in the previous trial.

Furthermore, the finding that the N2pc NLP effect is specific for sustained attention fits to the central assumption made in the introduction. We hypothesized that under these circumstances target selection involves a strong automatic attentional response not only towards the target feature but also away from the distractor feature – and importantly, that this learned attentional response is co-registered with location. In other words, if target and distractor are constant across an experimental block, each spatial position acquires the potential to attract attention if a target feature is 'recognized', and to repel attention if a distractor feature is 'recognized'. Accordingly, the residual inhibition, which is left after such a distractor-repelling attentional response, is causing the subsequent selection of a target at that location to be more effortful.

All other theoretical accounts of the NLP effect seem unlikely given the activation pattern we observed for the N2pc. First, the general functional-anatomical characteristics of the N2pc

component are inconsistent with a role in 'episodic memory retrieval' (Neill et al., 1992). Second, both the 'inhibition of return' account (Milliken et al., 2000; Pratt & Abrams, 1999) and the 'feature mismatch' account (Park & Kanwisher, 1994) would predict similar NLP effects in the both attentional context conditions.

Non-lateralized N2: The NLP effect indicates a negatively biased focus of controlled attention The N2 at posterior electrodes exhibited a non-lateralized amplitude enhancement for DT trials compared to control trials common to both context conditions. This stands in contrast to the N2pc which occurred approximately in the same time window but was enhanced in DT trials exclusively under sustained attention. One might argue that the N2 NLP effect is not generic but just an average of the lateralized NLP effect as it is visible in the N2pc. However, the fact that these two components can be dissociated with the attentional context manipulation strongly suggests that the process indicated by the N2 effect is not identical with that indicated by the N2pc effect.

The N2 (N2b) has been suggested to reflect the control of target selection and/or further extraction of information carried by a stimulus with the relevant target feature (Mangun & Hillyard, 1995; Wijers et al., 1996). According to recent neuroimaging studies, the posterior parietal cortex is one essential brain area involved in attentional control (Yantis et al., 2002; Yantis & Serences, 2003). One way of defining what 'control' means in this context is that a parietal representation of the to-be-selected target feature is engaged which can then be matched to incoming sensory information. To the degree that the spatially registered sensory information is matching the to-be-attended target feature, the specific bindings between the parietal 'control representation' and occipito-temporal sensory representations are strengthened. Likewise, to the

degree that these two representations are not matching, the bindings are weakened. Both mechanisms imply a shift of attention to the target location and away from the distractor location, which is supposed to be reflected by the emergence of the N2pc component.

According to this interpretation, the N2 amplitude enhancement in DT trials reflects a more effortful matching process because the bindings between control representation and previous distractor location are still weakened. In other words, shifting the attentional focus to a previous distractor location is more difficult.

Conclusions

Two main conclusions can be drawn from our results. First, brain-electrical correlates of NLP are multi-facetted. On the one hand, the NLP modulation of the N1 seems to be consistent with an inhibition-of-return explanation. On the other hand, the NLP modulations of the posterior N2 and the N2pc seem to be consistent with the biased competition model of selection as a special version of the distractor-inhibition account of NLP.

Second, the N2 and N2pc effects can be interpreted to reflect modulations of two different aspects of the same biased competition selection process. On the one hand, the N2pc NLP effect is supposed to be a) based on a level where competition between target and distractor features is being resolved, and b) caused by a low-level learned attentional response. On the other hand the N2 modulation is supposed to be a) based on a level where the to-be-attended target feature and the sensory input are matched to each other, and b) caused be a higher-level attentional shifting impairment towards a previously non-matching distractor location.

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Figure 1

A. Examples for the DT condition and the control condition. The small letter in the middleposition ('o') indicates the to-be-selected target letter. The experimental conditions are defined by prime-probe pairs. In the DT condition, the probe-target appears at a prime-distractor position. In the control condition, the probe-target appears at a previously neutral position. B. The timing of the sequence of prime trials and probe trials.

Figure 2

ERPs for the DT condition (solid) and the control condition (dashed) under sustained attention. The amplitude of the posterior N2 is enhanced for DT relative to Control.

Figure 3

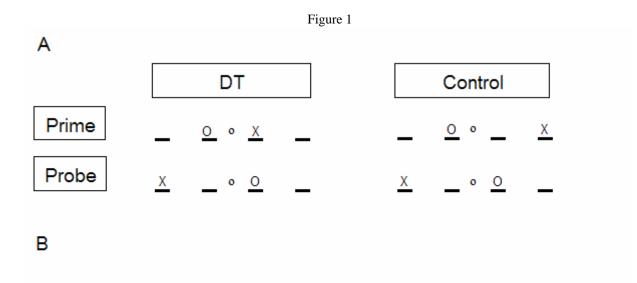
ERPs for the DT condition (solid) and the control condition (dashed) under transient attention. As for sustained attention (Figure 2), the amplitude of the posterior N2 is enhanced for DT relative to Control.

Figure 4

Event-related lateralizations (ERLs) for the DT condition (solid) and the control condition (dashed) under sustained attention (left panel) and transient attention (right panel). Positive deflections indicate stronger signal intensity contra-lateral to the target position. The ERLs are based on both bi-lateral and uni-lateral target-distractor pairs. Differences between DT and Control are present for the lateralized N1, the N2pc. While the N1 lateralization is weaker for DT than Control in both context conditions, the N2pc is enhanced for DT as compared to Control under sustained attention only.

Figure 5

Event-related lateralizations (ERLs) at the T5_6 electrode pair for the DT condition (solid) and the control condition (dashed) under sustained attention (left panel) and transient attention (right panel). The upper panel shows ERLs based on all stimuli (same as in Figure 4) and the lower panel shows ERLs selectively based on bi-lateral target-distractor pairs. Positive deflections indicate stronger signal intensity contra-lateral to the target position. For illustration purposes, the graphs also include information about the statistical significance of the DT-Control comparisons at T5_6.



500 ms	max. 1000 ms	250 ms	500 ms	
cue onset	prime onset	response/ prime & cue offset	cue onset	probe onset (prime for next trial)



SUSTAINED ATTENTION

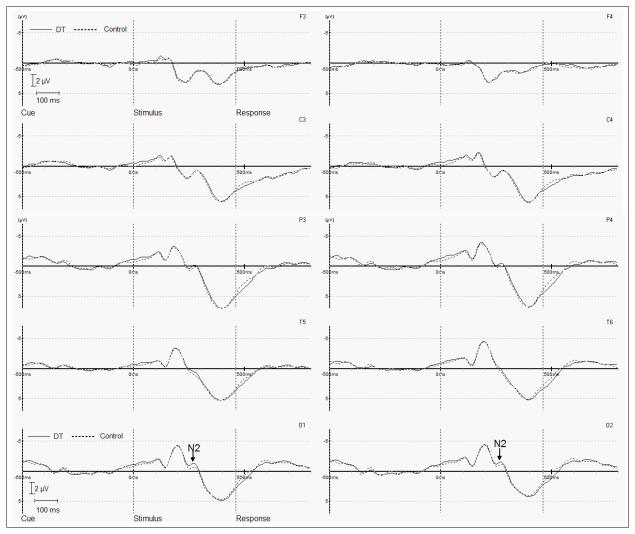


Figure 3

TRANSIENT ATTENTION

