

Selective manipulation of target identification demands in visual search: The role of stimulus contrast in CDA activations

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In classic visual pop-out search, response times are slowed remarkably when participants are required to precisely identify (e.g., vertical vs. horizontal orientation) as compared to simply localize (e.g., left vs. right position) a feature singleton target. This cost associated with stimulus identification has been recently proposed (Töllner, Rangelov, & Müller, 2012) to derive from the engagement of postselective recurrent processes that via feedback connections extract the information required for motor-response selection. Here, we examined whether the contralateral delay activity (CDA), an asymmetric neural marker generally assumed to reflect active maintenance of stimulus information in visual short-term memory (vSTM), may further index the degree of postselective processing requirements in visual search. Employing a compound-search task, we selectively manipulated the ease/difficulty of identifying the response-critical target orientation attribute (horizontal vs. vertical)—irrespective of the target-defining color feature (red vs. green)—by introducing different levels of stimulus-background contrast. As expected, we found a monotonic reaction time increase to be associated with gradually increasing CDA magnitudes as the stimulus contrast decreased. Thus, our findings provide direct evidence that CDA activations provide a useful tool to estimate the amount of postselective recurrent processing recruited to extract detailed object information from vSTM.

Introduction

In classic visual pop-out search, reaction times (RTs) are slowed down markedly when participants are required to identify (e.g., color vs. shape) as compared to simply localize (e.g., left vs. right position) a feature singleton target among distracter items, with RTs being generally longer the more precisely the target needs to be identified (e.g., Sagi & Julesz, 1985a; Müller, Krummenacher, & Heller, 2004). For instance, identifying the precise target-defining feature (e.g., blue vs. green) takes longer than identifying the visual dimension (e.g., color vs. shape) that defines the target. Recently, Töllner, Rangelov, and Müller (2012) proposed that the RT cost associated with stimulus identification demands originates from the additional recruitment of postselective perceptual processes necessary to extract, via recurrent feedback connections (see also Lamme & Roelfsema, 2000, for a detailed review of feedforward and feedback processing in vision), identity information mandatory for subsequent motor-response decisions. In contrast, such recurrent identification processes may be reduced or even absent for simple localization and detection responses, which presumably can be realized on the basis of feed-forward visual processing.¹

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Support for this notion (Töllner, Rangelov, & Müller, 2012) stems primarily from the differential activation patterns of the posterior contralateral negativity (PCN)² and the lateralized readiness potential (LRP), two asymmetric waveforms of the event-related potential (ERP) generally accepted to reflect space-specific allocation of focal attention (e.g., Luck & Hillyard, 1994; Eimer, 1996; Woodman & Luck, 1999) and effector-specific production of motor responses (e.g., Coles, 1989; Eimer, 1998), respectively. In particular, in a comparison of several task set conditions (i.e., localization vs. detection vs. discrimination vs. compound) that required different stimulus-response mappings to be performed on physically identical pop-out search stimuli, Töllner, Rangelov, and Müller (2012) found no influence of task type whatsoever on the elicitation of the PCN. Such task set-insensitive PCN responses can be taken as evidence that any task-relevant target is selected automatically with the same speed whether or not the task set engaged requires deeper stimulus analysis to reveal the target's featural identity. By contrast, the stimulus-locked LRP was substantially delayed when the task set demanded precise identification, as compared to simple localization, of the target. Hence, the RT cost attributable to the identification task demands must originate at some stage subsequent to focal-attentional selection but prior to motor-response production. From the combined analysis of PCN and LRP responses, however, it remained unclear to what degree postselective perceptual versus response selection processes contributed to this RT cost.

Contralateral delay activity as an index of in-depth analysis of visual input

However, there is another electroencephalographic brain response that promises to be informative about the involvement of postselective perceptual processing in the behavioral stimulus identification effect in a more fine-grained fashion, namely, the contralateral delay activity (CDA). This neural marker is a negative potential most prominent over parietal, occipital, and temporal electrodes contralateral to the side of an attended visual location or hemifield (e.g., Vogel & Machizawa, 2004; Gazzaley & Nobre, 2011; Reinhart et al., 2012; Wiegand et al., in press). In studies that require the active encoding and maintenance of information in visual short-term memory (vSTM), this potential shows a sustained activation during the retention interval (which is why one pool of researchers prefer the term Sustained Posterior Contralateral Negativity; see Jolicoeur, Brisson, & Robitaille, 2008, for a detailed review). Combining ERP recordings from macaque and humans, together with intracranial local

field potentials from macaque, Reinhart et al. (2012) recently revealed a distributed neural network to generate the CDA. In particular, they found especially prefrontal areas (FEF, SEF) to exhibit close relationships, in terms of timing and activation levels, to memory-based behavioral performance, indicative of a contribution of these areas to the sustained surface CDA measurable at posterior electrode sites. Vogel and Machizawa (2004; see also Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; Ikkai, McCollough, & Vogel, 2010), in one of the most influential studies of CDA involvement in working memory tasks, revealed CDA activation to increase systematically with the number of objects maintained in vSTM, with the amplitude reaching an asymptotic level when an individual reached her/his vSTM storage capacity limit. This pattern demonstrates a direct relationship between neural CDA activity and the capacity of visual working memory.

Of importance for the present study, the CDA has also been reported in a growing body of studies that required participants to initially search for the task-relevant target among distracter objects (e.g., Mazza, Turatto, Umiltà, & Eimer, 2007; Emrich, Al-Aidroos, Pratt, & Ferber, 2009; Carlisle, Arita, Pardo, & Woodman, 2011; Luria & Vogel, 2011; Woodman & Arita, 2011; Wiegand, Finke, Müller, & Töllner, 2013; Anderson, Vogel, & Awh, 2013). For instance, Mazza et al. consistently observed CDA activations immediately following PCN responses in visual search, but only when the task set required finer, in-depth analysis of the selected item. In particular, by comparing the sensory-driven event-related EEG lateralizations elicited in localization and discrimination tasks, Mazza et al. found the CDA to be triggered selectively for the latter task only; whereas, the PCN was virtually indistinguishable between the two types of tasks. To further verify that the CDA elicited in such visual attention tasks is comparable to that observed in visual memory tasks but functionally different from the PCN, Jolicoeur et al. (2008) examined PCN and CDA responses as a function of memory load in a visual choice response task. Participants were required to encode (i.e., identify) and respond to either one or two out of four possible colored digits presented bilaterally in the visual displays. Mirroring the pattern of Vogel and Machizawa (2004), the authors found that the number of items to be processed had a significant impact on the activation and duration of the CDA but not the PCN component. This electro-cortical dissociation was taken as evidence for two functionally distinct cognitive functions underlying the PCN and CDA. Together with recent PCN reports (e.g., Brisson & Jolicoeur, 2007; Töllner, Zehetleitner, Gramann, & Müller, 2010, 2011; Conci, Töllner, Leszczynski, & Müller, 2011; McDonald, Green, Jannati, & Di Lollo, in press), these

results provide additional support for the view that the PCN reflects the engagement of visuo-spatial attention on laterally presented target objects. By contrast, the CDA is specifically related to the location-specific encoding and/or in-depth analysis of visual input in vSTM, thus reflecting similar cognitive operations to those involved in classical working memory tasks.

Logic of the present study

The present study was designed to investigate a direct implication of the functional distinction between the PCN and CDA responses as drawn by Jolicoeur and colleagues (2008, see also Mazza et al., 2007), namely, that the CDA indexes postselective in-depth analysis of information at already attended stimulus locations. On this assumption, CDA activations should increase gradually as more, relative to less, recurrent processing needs to be engaged in order to extract the object identity information required for subsequent response selection. To systematically examine this prediction, we combined mental chronometry data with event-related EEG lateralizations in two visual search tasks that differed in the depth of signal processing required for determining the correct response. The first compound-search task required participants to initially search for a pop-out target (defined variably across trials by the color red or green) before they could decide upon the appropriate motor response (defined by the target's vertical or horizontal orientation). Note that this compound task logic (e.g., Kingstone, 1992; Pollmann, Weidner, Müller, Maertens, & von Cramon, 2006; Töllner, Gramann, Müller, Kiss, & Eimer, 2008) elegantly dissociates target-defining features, which determine PCN responses, from response-critical features, which presumably influence CDA activations. Accordingly, this design permitted us to selectively manipulate the ease/difficulty with which participants could extract the response-critical target orientation, namely, by introducing three different stimulus-background contrast levels created by Gaussian “blurring” of orientation information (see Figure 1); henceforth, this variable will be referred to as stimulus-background orientation contrast. Exactly the same physical stimulus material was additionally employed in a second control task requiring participants to make simple localization (left vs. right position), rather than precise identification (see above), responses.

In both experiments, we analyzed RT performance together with both PCN and CDA responses to dissociate preattentive from postselective perceptual processes as a function of task set and stimulus-background orientation contrast. First, we expected to find slower behavioral response latencies for identification relative to localization responses, replicating

previous findings (e.g., Sagi & Julesz, 1985b; Mazza et al., 2007; Töllner, Rangelov, & Müller, 2012). Second, because we used the identical physical stimulus material for both the localization and identification tasks, we expected the PCN timing, indexing focal-attentional selection of the target, to be unaffected by the respectively engaged task set and stimulus-background orientation contrast—as the latter should affect only the salience of the response-defining feature. By contrast, assuming the recruitment of an additional recurrent process in which participants are required to extract target identity information, we expected a CDA wave to be manifest when the task demanded target identification; whereas, the CDA was expected to be reduced, or entirely absent, when the task required simple target localization. Third, for the identification task, we expected a gradual increase in the CDA response with decreasing stimulus-background orientation contrast, indicative of increasing post-selective processing demands for extracting the target's exact orientation feature value (vertical vs. horizontal).

Methods

Participants

Fifteen volunteers (five female) took part in this study for either monetary payment or course credit. Two participants had to be excluded from the analyses due to excessive horizontal eye movement artifacts. The ages of the remaining 13 participants ranged from 20 to 30 (median 25) years. All had normal or corrected-to-normal vision, and none reported a history of neurological disorders. Participants gave their written informed consent prior to performing the experiment. The experimental procedure was approved by the ethics committee of the Department of Psychology, University of Munich, in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Stimuli and study design

Except for the colors and contrast modulations used for the present stimuli (see below), the search displays were identical to those of Töllner et al. (2008), Töllner et al. (2010), and Töllner, Rangelov, and Müller (2012). That is, search displays consisted of eight colored shape stimuli presented on a gray background and arranged in a circular formation (radius: 4.6° of visual angle) around a central white fixation point (see Figure 1). In each trial, one of the six lateral locations contained a feature singleton target, equally likely defined by the

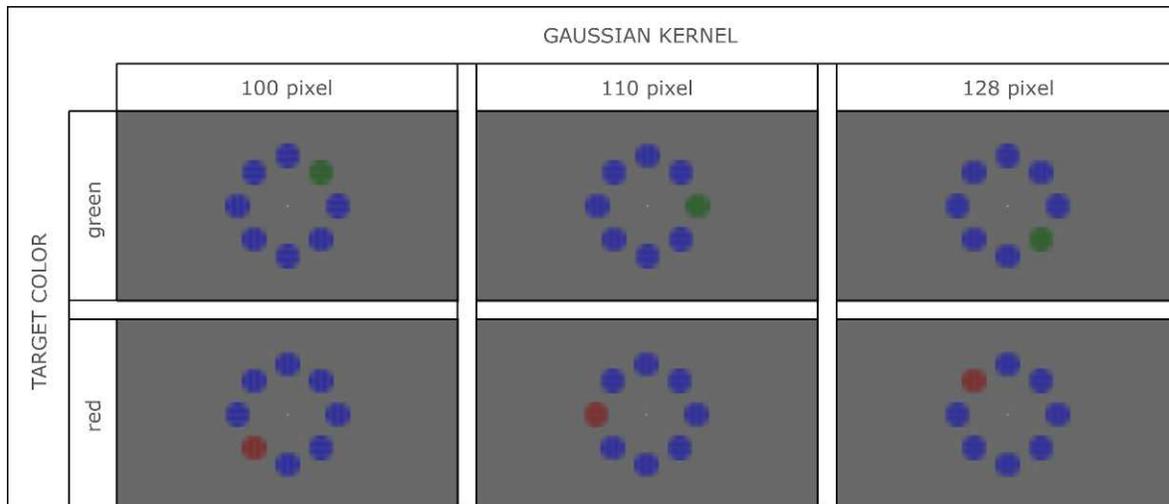


Figure 1. Examples of search displays used in the present study. The color (red vs. green), orientation (vertical vs. horizontal), stimulus-background contrast (high, intermediate, low) as well as position (at one of the six lateral locations) of the target varied randomly on a trial-by-trial basis. Participants were required to give a speeded forced-choice response indicating either the featural identity (vertical vs. horizontal orientation; Experiment 1) or location (left vs. right position; Experiment 2) of the color-defined feature singleton.

color red (i.e., a single red circle/disk; CIE .622, .344, 6) or green (i.e., a green circle/disk; CIE .293, .589, 6), together with seven homogenous distracter items (i.e., blue circles/disks; CIE .144, .066, 6). Each stimulus outline contained a grating composed of three gray bars ($0.4^\circ \times 2.4^\circ$) separated by two gaps ($0.3^\circ \times 2.4^\circ$), which were randomly oriented either vertically or horizontally. Three different levels of stimulus-background orientation contrast (high, intermediate, low) were realized by applying Gaussian (blurring) filters with radii of 100, 110, and 128 pixels, respectively, to the stimuli. These transformations particularly affected the conspicuousness of the bar's contours without, however, modulating the salience of the respective colors. Within a given trial, both target and distracter items were presented with identical contrast levels. Participants were instructed to maintain central eye fixation throughout the experimental trials and to make a two-alternative forced-choice response as quickly and accurately as possible. Participants were required to identify the target's orientation (vertical vs. horizontal) in one experiment and to localize the target's positioning relative to the midline of the search display (left vs. right) in the other (control) experiment by pressing the respectively assigned mouse buttons with their left or right thumb.

The two experiments (identification/localization task) were controlled by an IBM-PC compatible computer using Matlab routines and Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) and were performed consecutively in random order in a dimly lit, sound-attenuated, and electrically shielded experimental booth (IAC). Search displays were

presented on a 17-in. CRT screen (85-Hz refresh rate), mounted at a viewing distance of approximately 75 cm. Each experiment consisted of nine blocks of 72 trials each, resulting in a total of 1,296 trials. In both experiments, target-defining features and stimulus-background orientation contrast varied randomly on a trial-by-trial basis throughout all blocks. A trial started with the presentation of a white central fixation cross for 500 ms, which was immediately followed by the search array shown for 100 ms. Trials were terminated by the participant's response or after a maximum time limit of 1000 ms. Response times were measured relative to the onset of the search displays. In case of a response error or if no response was given within the maximum time allowed, a red minus sign (i.e., “–”) was centrally presented for 1000 ms, signaling erroneous behavior. The subsequent intertrial interval displayed a white central fixation cross for a randomly chosen duration of either 950, 1000, or 1050 ms. Prior to the start of each individual experiment, at least one block of practice was administered in order for participants to become familiarized with the stimulus material and the required stimulus-response mapping. After each block, participants received summary performance statistics (mean error rate and RT) as feedback information.

EEG recording and data analysis

The electroencephalogram was continuously sampled at 1 KHz using Ag/AgCl active electrodes (actiCAP system, Brain Products, Munich) from 64 scalp

sites, which were in accord with the international 10-10 System. To monitor for blinks and horizontal eye movements, the electrooculogram was recorded by means of electrodes placed at the outer canthi of the eyes and, respectively, the superior and inferior orbits. All electrophysiological signals were amplified using BrainAmp amplifiers (Brain Products, Munich) with a 0.1 to 250-Hz bandpass filter. During data acquisition, all electrodes were referenced to FCz and re-referenced off-line to averaged mastoids. All electrode impedances were kept below 5 k Ω .

Prior to segmenting the EEGs, the raw data was visually inspected in order to manually remove non-stereotypical noise and then high-pass filtered using a Butterworth infinite impulse response filter at 0.5 Hz (24 dB/Oct). Next, an infomax independent component analysis was run to identify components representing blinks and/or horizontal eye movements and to remove these artifacts before back-projection of the residual components. For the PCN and CDA analyses, the continuous EEG was then epoched into 500-ms segments relative to a 200-ms prestimulus interval, which was used for baseline correction. To further control for remaining activity possibly related to horizontal eye movement shifts in the individual segments, we discarded all trials in which the signal exceeded $\pm 20 \mu\text{V}$ in the channels F9/F10. Only trials with correct responses and without artifacts—defined as any signal exceeding $\pm 60 \mu\text{V}$, bursts of electromyographic activity (as defined by voltage steps/sampling point larger than $50 \mu\text{V}$), and activity lower than $0.5 \mu\text{V}$ within intervals of 500 ms (indicating “dead” channels)—were accepted for further analysis on an individual-channel basis before averaging the ERP waves. To extract the PCN and CDA waves from overlapping target location-unspecific components, ERPs from parieto-occipital electrodes (PO7/PO8) ipsilateral to the target’s location were subtracted from contralateral ERPs. The latencies of the PCN and CDA were defined individually as the maximum negatively directed deflection in the time period 150–300 ms and, respectively, 300–500 ms poststimulus. PCN and CDA amplitudes were computed averaging five sample points before and after the respective maximum deflection.

Differences in behavioral (reaction times, error rates) as well as neural measures (PCN latencies/amplitudes; CDA latencies/amplitudes) were assessed by conducting separate within-subject two-way repeated-measures analyses of variance (ANOVAs) with the factors “task set” (identification, localization) and “stimulus-background contrast” (high, intermediate, low). Significant main effects and/or interactions were further substantiated by means of post-hoc comparisons (Tukey HSD).

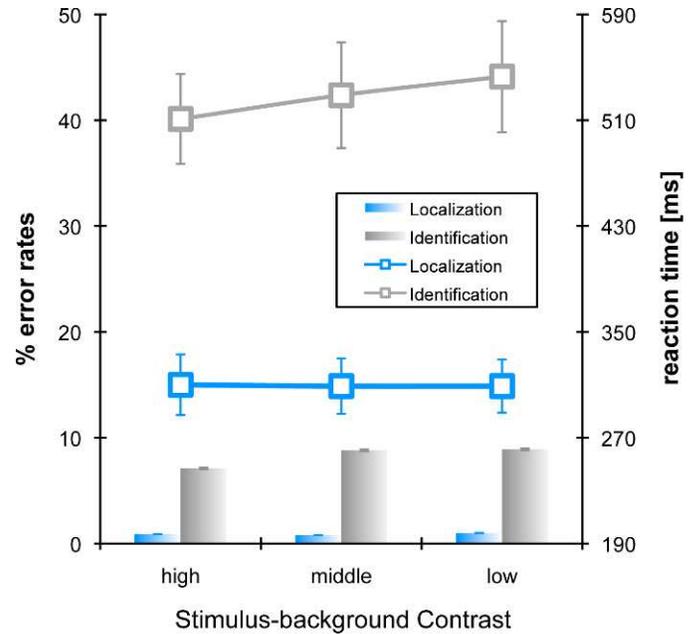


Figure 2. Behavioral results. Reaction times (lines) and error rates (bars) as a function of task set (identification, localization) and stimulus-background contrast (high, intermediate, low).

Results

Behavior

As can be seen in Figure 2, participants’ RTs were determined interactively by task set and stimulus-background contrast: interaction, $F(2, 24) = 32.42$, $p < 0.001$. RTs were markedly slower when the participants’ task required featural identification (Experiment 1, gray lines) as compared to simple localization (Experiment 2, blue lines) of the singleton target: main effect of task set, $F(1, 12) = 958.14$, $p < 0.001$. Furthermore, RTs were monotonically increasing with decreasing stimulus-background orientation contrast for target identification (511 ms < 529 ms < 543 ms) but not for localization (310 ms = 309 ms = 309 ms) responses. Subsequent post-hoc comparisons confirmed that all three contrast levels differed significantly from each other in the compound task (all p values < 0.05). An overall similar pattern was obtained for the error rates: interaction, $F(2, 24) = 3.83$, $p < 0.036$. Participants made significantly more errors in the identification (gray bars) as compared to the localization (blue bars) tasks: main effect of task set, $F(1, 12) = 270.94$, $p < 0.001$, with a contrast-based modulation for the former (identification, 7.1% < 8.8% = 8.9%) but not the latter (localization, 0.9% = 0.8% = 1.0%) task.

Posterior contralateral negativity

Figure 3a presents grand-average target-synchronized contralateral versus ipsilateral ERP waveforms separately for the identification (Experiment 1, right panel) and localization tasks (Experiment 2, left panel). For both tasks, a solid PCN was triggered, evident as a more negatively (i.e., less positively) directed deflection in the P2 time range approximately 180–240 ms following stimulus onset. In line with previous reports (e.g., Hopf et al., 2006; Töllner, Zehetleitner, Krummenacher, & Müller, 2011), PCN scalp distributions (see Figure 3b) confirmed that the difference waves were elicited most prominently over lateral parieto-occipital scalp sites.³ The corresponding (contralateral minus ipsilateral) difference waves are plotted as a function of stimulus-background contrast and task set in Figure 3c. As can be clearly seen, none of these factors did modulate the rise of the PCN, evidenced statistically by the absence of significant effects on PCN amplitudes and latencies (all p values > 0.14).

Contralateral delay activity

Following the PCN response,⁴ a CDA wave was discernable; that is, a second more negative-going (i.e., less positive) potential with a maximum between 360 and 420 ms poststimulus over lateral parieto-occipital scalp sites (see Figure 3b) for the identification but not the localization task. In line with our hypotheses, this CDA waveform was strongly dependent on stimulus-background orientation contrast with gradually stronger activations observable for low-contrast, relative to high-contrast, targets. To statistically corroborate that the CDA was elicited reliably for the identification and absent for the localization task, we initially conducted a repeated-measure ANOVA with the single factor period (baseline vs. CDA activation) separately for each experiment. Baseline activation values were calculated—identical to CDA activations (see above)—by averaging five sample points before and after the maximum negative-going deflection within the 200-ms prestimulus period. This analysis confirmed our initial observations of CDA presence for the identification task, $F(1, 12) = 9.74$, $p < 0.009$, and CDA absence for the localization task, $F(1, 12) = 0.04$, $p > 0.95$. Next, we examined the impact of stimulus-background orientation contrast on CDA amplitudes and latencies in the compound task by performing a repeated-measures ANOVA with the single factor stimulus-background contrast (high, intermediate, low). Consistent with our observations, this analysis revealed statistically, $F(2, 24) = 13.24$, $p < 0.001$, the strongest amplitudes for low-contrast targets ($-1.71 \mu\text{V}$) and monotonically decreasing deflections for targets of intermediate (-1.33

μV) and high stimulus-background contrast ($-1.09 \mu\text{V}$); no effect was obtained for the CDA latencies, $F(2, 24) = 0.44$, $p > 0.64$.

Discussion

By focusing on two sensory-driven event-related EEG lateralizations, the current study was designed to provide deeper insight into the neural mechanisms responsible for the RT costs associated with precise featural identification as compared to simple localization of a feature singleton target in visual search. Our results show that manipulating the ease/difficulty of extracting the response-critical feature—irrespective of the target-defining feature—resulted in selective modulations of CDA but not PCN responses. This clear-cut electro-cortical dissociation reveals identical time demands for focal-attentional target selection (as indexed by the PCN timing) whatever the specific task set (localization, identification) and the stimulus-background orientation contrast. By contrast, both factors were found to interactively determine the amount of perceptual processing (as indexed by the CDA amplitude) subsequent to focal-attentional target selection.

The PCN as a neuro-chronometric measure of feedforward-driven attentional selection

The fact that the PCN was immune to task set differences replicates previous findings (e.g., Mazza et al., 2007; Töllner, Rangelov, & Müller, 2012), providing further support for the notion that the PCN signal reflects the saliency signal generated by the target at the level of the attention-guiding overall-saliency map (e.g., Töllner, Zehetleitner, Gramann, & Müller, 2011). On this view, the deployment of focal attention is determined by the attentional landscape of a retinotopically organized saliency map, which continuously integrates or sums feature contrast signals computed by a set of preattentive, dimensionally organized feature analyzer units (e.g., for color, orientation, motion). Once a location-specific overall-saliency map unit is activated above threshold, focal attention will be deployed to the location represented by this unit, based on a competitive winner-take-all process. According to this notion, the PCN should be triggered in identical fashion as long as the target's saliency signal (i.e., its total feature contrast relative to the surrounding items but not what we refer to here as its contrast to the background) is held constant—as was the case in the present study. By contrast, the PCN should be triggered differentially when target saliency is manipulated, with *gradually* increasing activations as target

Localization Task

Identification Task

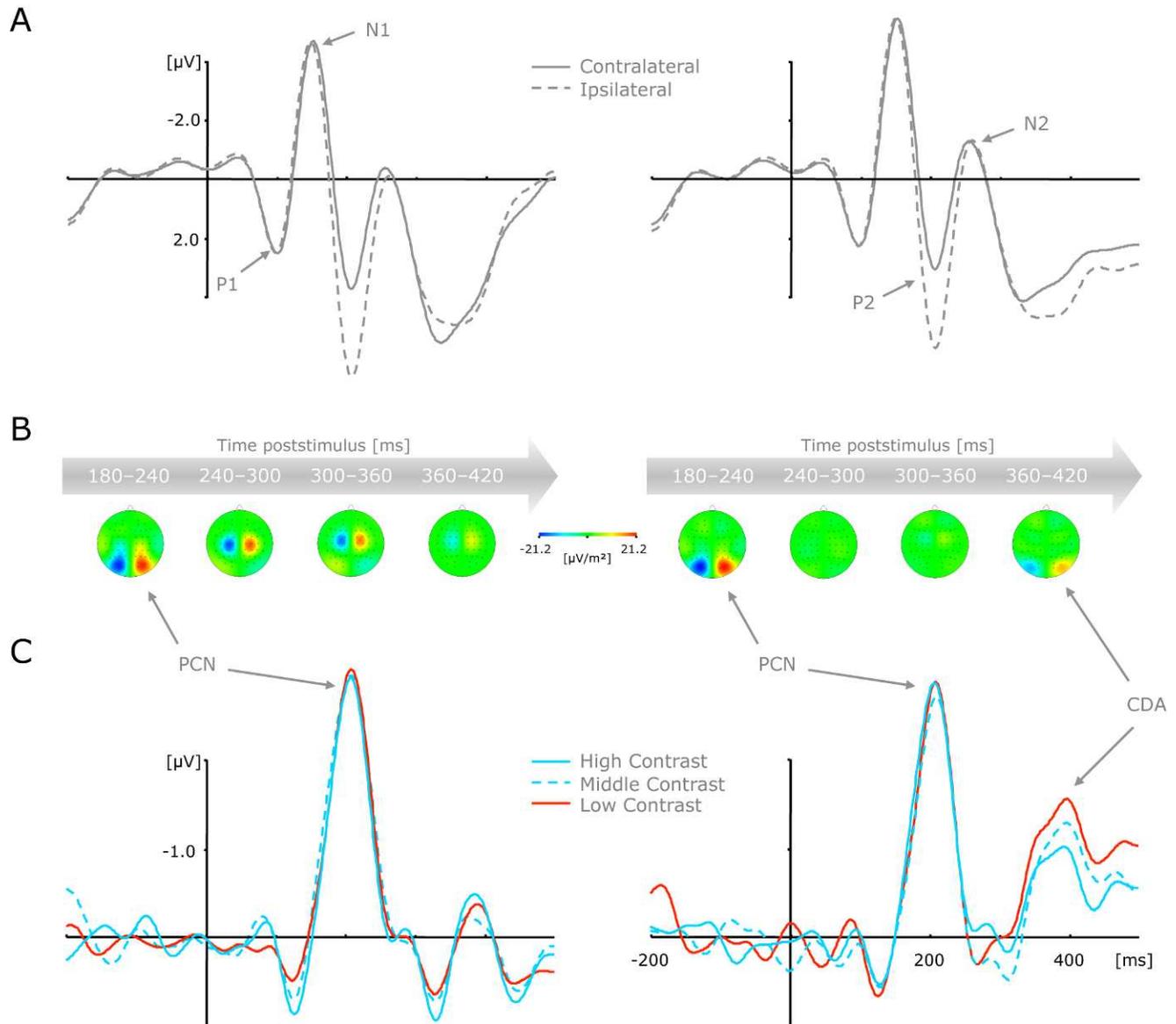


Figure 3. Electrophysiological results. (A) Grand-average target-synchronized contralateral versus ipsilateral ERP waves in the 500-ms interval following stimulus onset, relative to a 200-ms prestimulus baseline, at electrodes PO7/PO8. (B) Topographical scalp distribution maps computed by mirroring the contralateral-minus-ipsilateral difference waves (to obtain symmetrical voltage values for both hemispheres based on spherical spline interpolation) for the successive time intervals of 180–240 ms, 240–300 ms, 300–360 ms, and 360–420 ms poststimulus. (C) The corresponding PCN difference waves obtained by subtracting ipsilateral from contralateral activity as a function of stimulus-background contrast (high, middle, low), separately for the localization (left panel; Experiment 2) and identification tasks (right panel, Experiment 1).

feature contrast increases. Exactly this pattern was established by Töllner, Zehetleitner, Gramann, and Müller (2011).

Although attention-guiding saliency representations are derived largely in bottom-up fashion, they can also be biased by internal system settings relating to intertrial history (e.g., Töllner et al., 2008) or target

expectancy (e.g., Töllner, Strobach, Schubert, & Müller, 2012): The PCN signal has been found to be amplified for predictable (vs. nonpredictable) targets as well as for cross-trial repetitions (vs. changes) of the target-defining dimension. According to salience summation models (e.g., Müller et al., 1995, 2010), these boosted activations originate from a “top-down”

modulation of weights assigned to dimension-specific feature contrast signals in the *preattentive* computation of the search-guiding overall-saliency map. Note, however, that such internal biases are established prior to the onset of the target in a trial; that is, they do not represent feedback during actual target processing. On the other hand, visual stimuli can activate the visual cortex within 50–60 ms after their onset (Foxe & Simpson, 2002) so that there would be sufficient time for multiple iterations of feedback signals before the emergence of the PCN. Thus, even though such feedback operations may operate prior to target selection, it is unlikely that they actually represent the PCN itself. Rather, they may play an important role in the formation of the PCN, for instance, by suppressing the target's surround via “sharpening” the target's feature-contrast representation in lower-level, retinotopic visual areas (V1, V2/V3, etc.). Applied to the functional architecture envisaged in the saliency map hypothesis (Koch & Ullman, 1985), processing is conceived as essentially *feedforward-driven*, involving the bottom-up directed transmission of the target signal from lower-level *feature-specific* maps—*up* the visual hierarchy—to the “*featureless*” overall-saliency map. Accordingly, the target's representation on this map, as putatively indexed by the PCN, is sufficient to signal its presence or location (and thus allow focal-attentional selection) but is “agnostic” as to the exact features that gave rise to this representation. Once selected by focal attention, *feedback-driven* (attentional) processing comes into play, involving top-down directed recurrent processes from the saliency map—*down* the visual hierarchy—to lower-level feature maps for returning the target's identity-defining features.

The CDA as a neuro-chronometric measure of feedback-driven stimulus identification

The present CDA findings add to the mounting evidence (e.g., Mazza et al., 2007; Jolicoeur et al., 2008; Luria & Vogel, 2011; Wiegand et al., 2013) that the processes that give rise to the CDA in visual search are directly linked to the postselective in-depth analysis of object identity information at already attended locations. In particular, we found gradually increasing CDA magnitudes with decreasing stimulus-background orientation contrast for identification, but no CDA elicitation whatsoever for localization task, demands. This pattern of effects is exactly as predicted from the notion recently proposed by Töllner, Rangelov, and Müller (2012), according to which simple localization responses are accomplishable solely based on feedforward visual processing. By contrast, when object identity information is required for subsequent motor-response decisions, recurrent processes are additionally

required to extract the response-critical information from vSTM representations. Following Lamme and Roelfsema (2000; see also Gramann, Töllner, & Müller, 2010; Müller et al., 2010), it is suggested that this extraction process may be realized by the recruitment of recurrent processes that feed back from the attention-guiding saliency map to hierarchically lower stages (i.e., presumably dimensionally organized feature maps) in order to return the response-critical feature value (e.g., that the target is oriented “horizontally”).

The gradual amplification of CDA responses with decreasing stimulus-background orientation contrast is closely in line with the idea that a sensory signal must reach a response-triggering threshold in order to become transferred to subsequent, in the present case, motor-related stages of processing (e.g., Green & Swets, 1966; Hanes & Schall, 1996). Applied to the current data set, this view suggests that increased CDA activations with low-contrast, relative to high-contrast, targets may reflect a higher amount of recurrent processing necessary for accumulating sufficient sensory evidence to reveal the response-defining (vertical vs. horizontal) orientation feature from the background. Accordingly, the timing of the CDA can be taken to indicate the temporal locus for identifying the response-critical stimulus attribute from vSTM representations in visual search tasks.

Similarities and differences to other CDA determinants

The fact that the CDA occurred in a time window some 360–500 ms poststimulus, even though the search display disappeared after 100 ms, strongly indicates that this postselective extraction process operates on visuo-spatial representations maintained in vSTM. Arguably, these representations are essentially the same as the representations involved in working memory tasks (e.g., Klaver et al., 1999; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). The only difference, however, is that the latter are kept activated and sustained during the retention interval in working memory tasks; whereas, the representations in the current visual search task are no longer maintained or left to decay (see Figure 3) once a decision concerning the object identity could be reached.

Furthermore, the present data pattern appears, at first sight, to be closely related to a recent finding reported by Luria and Vogel (2011), namely, that the CDA varies as a function of the visual search demands. Luria and Vogel varied the difficulty of the search task to be performed by manipulating the homogeneity of the distracter items: distracters were either all identical (i.e., “easy” condition), all different (i.e., “difficult”

condition), or partially identical/different (i.e., “intermediate” condition) within the task-relevant visual hemifield (for further methodological details, see Luria & Vogel, 2011). Using this procedure, Luria and Vogel found CDA responses to be enhanced as the search difficulty increased, which they interpreted in terms of a stronger reliance on working memory representations with difficult relative to easy searches. However, there is one fundamental difference between Luria and Vogel’s and the present study: The difficulty manipulation employed by Luria and Vogel did substantially affect the salience of the target relative to the items in its surround, thereby changing the nature of the task from an efficient, spatially parallel pop-out search (“easy” condition) to an inefficient, serial search (“difficult” condition). It should be noted that this manipulation does, in the first instance, influence the elicitation of the preceding PCN wave (which is indicative of visuo-spatial selection) as is evident in Luria and Vogel’s experiments 2 and 3. Thus, as suggested by these authors, the enhanced CDA triggered with serial relative to pop-out searches may be attributable to the increased demands of matching candidate target items (i.e., distracters from the search array) against the target template. Because there are likely several candidate targets in serial search as compared to just one in pop-out search, there would be iterative matching operations in this condition, for which candidate items would need to be buffered in vSTM (owing to the brief display duration).

At marked variance with Luria and Vogel’s (2011) design, the difficulty manipulation used in the present study did not change the target’s salience relative to its surround at all, thus ensuring the pop-out nature of the search task for all stimulus-background contrast conditions. In agreement with this, the present PCN responses were wholly unaffected by the difficulty manipulation—in marked contrast to the CDA wave, which increased gradually as a function of stimulus-background contrast. Given that there was always only a single, highly salient “pop-out” item in our search displays, it is unlikely that this CDA amplification was due to increased demands for temporary storage of candidate targets (i.e., distracters from the search array) and more frequent template matching operations for low-contrast, relative to high-contrast, pop-out searches.

Finally, our study design appears also linked to another recent working memory study (Ikkai et al., 2010), which, likewise, manipulated the contrast of the items to be stored in vSTM. In more detail, the arrays employed by Ikkai et al. were either of high or low contrast and consisted of either two or four differently colored items, with the task-relevant visual hemifield being pre-cued by an arrow (pointing to the left or right) on a trial-by-trial basis. Importantly, the colors

of all items within the pre-cued hemifield had to be precisely identified and memorized in this working memory task, as participants were asked to respond whether the memory and test arrays were identical or not. Using this design, however, Ikkai et al. observed exactly the opposite pattern: Reduction of the stimulus contrast had no influence on the CDA (despite significant behavioral effects) while yielding significantly attenuated PCN amplitudes. Based on this pattern, the authors reasoned that the CDA might be immune to any sensory factors, being driven exclusively by the number of objects represented in vSTM.

In the light of these and other results (Vogel et al., 2005), an alternative explanation for the enhanced CDA amplitudes with lower stimulus-background contrast observed in the present study may be that this pattern simply results from poor filtering of nearby distracters when the target contrast is low.⁵ Despite these, at first glance, close similarities between Ikkai et al. (2010) and our study, it seems rather improbable that this alternative explanation can account for the current data set. Note that in the study of Ikkai et al., there were always multiple task-relevant items defined by the same color features that subsequently also determined the required response, namely, to indicate whether or not the test array was the same as the memory array. In the current study, by contrast, there was always only one task-relevant pop-out item defined by a feature (i.e., red vs. green color) entirely unrelated to that determining the subsequent response (i.e., vertical vs. horizontal orientation). Accordingly, because our contrast manipulation affected selectively the response-critical target attribute but not the feature that singled out the target from its distracter surround (with displays disappearing after 100 ms), it would appear rather unlikely that the current CDA results may be driven by differential, contrast-dependent filtering of nearby distracters. The view that the current contrast manipulation did not affect the filtering of distracters is further supported by the fact that the PCN (which indexes spatial filtering) was insensitive to stimulus-background contrast. Ikkai et al., by contrast, found decreased PCN activations for reduced stimulus contrast (see above), in line with the notion that the PCN reflects the target’s saliency signal (see, e.g., Töllner, Zehetleitner, Gramann, & Müller, 2011).

In sum, the current study revealed stimulus-background contrast as a critical determinant of the CDA in visual search scenarios that require participants to search for and identify a single, highly salient “pop-out” target defined by a feature that differs from the response-critical target attribute (i.e., compound search). Based on the current data set, however, it remains an open issue whether or not this factor of stimulus contrast is additive to or interacts with an individual’s memory storage capacity in

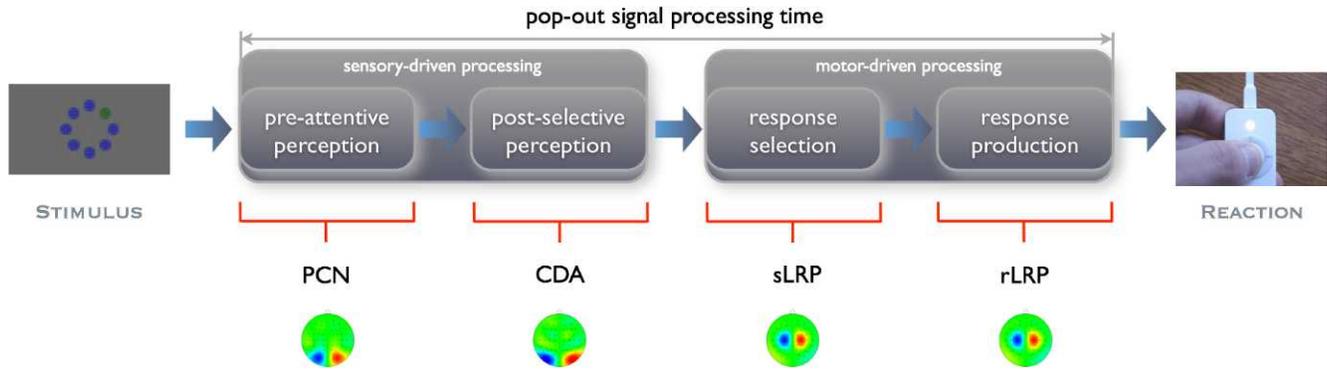


Figure 4. Schematic of the suggested approach for temporally disentangling four functionally distinct sensory- and motor-related substages of the human information-processing stream: (1) the PCN latency indexes the time required for focal-attentional target selection in visual space; (2) the CDA (minus PCN) timing indexes the time required for extracting detailed stimulus identity information from vSTM; (3) the stimulus-locked LRP (minus CDA) timing indexes the time required for selecting the appropriate motor response; (4) finally, the response-locked LRP timing reflects the time required by motor-response production processes.

determining the CDA response. Future studies may systematically address this question in order to establish whether the revealed pattern generalizes across paradigms from visual search to working memory tasks and vice versa.

Quartering RTs via event-related lateralizations of the EEG

The characteristics of the CDA as revealed by the current study have fundamental implications with regard to the *precision* of dissociating RT effects on the basis of event-related EEG lateralizations in visual search. When analyzed together with the PCN, the stimulus-locked LRP, and the response-locked LRP, the temporal processing demands of the following four functionally distinct substages of the human information-processing stream can be electro-cortically dissociated: (a) preattentive perception, (b) postselective perception, (c) motor-response selection, and (d) motor-response production (see Figure 4).

In particular, preattentive perceptual processes encode the whole stimulus array initially in parallel and determine when and where the attentional spotlight will be engaged. Accordingly, the temporal information of the PCN, which reflects the point in time when the target becomes focally selected in visual space (e.g., Luck & Hillyard, 1994; Eimer, 1996; Töllner, Zehetleitner, Gramann, & Müller, 2011; Töllner, Müller, & Zehetleitner, 2012), can be used to estimate the times demanded by feedforward visual processing⁶ to determine the presence and location of the target. Post-selective perceptual processes extract then, via recurrent feedback connections, the response-critical stimulus information at the respectively attended location. As elaborated above, the temporal processing

demands of this postselective extraction process are derivable from the CDA timing, which indicates the point in time at which the target's identity is revealed from vSTM representations. Next, response selection processes (indexed by the stimulus-locked LRP) determine the appropriate motor response required by the respectively extracted stimulus attribute, as defined by a previously established task set (i.e., stimulus-response mapping rule). Finally, response production processes (indexed by the response-locked LRP) generate and execute the motor response thus selected. It should be noted, however, that this approach of quartering reaction times is only feasible when the shape of the CDA (contralateral minus ipsilateral difference) wave is elicited monophasic rather than being sustained in nature so as to allow the extraction and usage of its temporal information. Accordingly, an adequate signal-to-noise ratio (see, for instance, Luck, 2005, for a detailed overview of the “standard” rules) in combination with precise target identification demands (see above) seem to be an inevitable prerequisite for this approach being employable.

Conclusions

In conclusion, the present findings advance our understanding of the processes underlying the CDA wave in studies of visual search. Here, we could directly demonstrate that this neural marker does not simply, or only, reflect the amount of information to be stored and maintained in vSTM (e.g., Vogel & Machizawa, 2004; Jolicoeur et al., 2008; Wiegand et al., in press), but also the degree of postselective perceptual processing recruited for extracting detailed object identity information from vSTM representations. However,

whether this factor of stimulus contrast is additive to or interacts with memory storage capacity in the elicitation of the CDA remains an open question to be addressed in future studies. Nonetheless, our data clearly demonstrate that systematic analysis of the CDA together with multiple event-related EEG lateralizations—such as the PCN, stimulus-locked LRP, and response-locked LRP—can help to improve the precision of electro-cortically dissociating RT effects in visual search tasks.

Keywords: attention, stimulus contrast, recurrent processing, electroencephalography

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Footnotes

¹This view is substantiated by the behavioral finding that participants can report the target's identity only at chance level when they are asked on the very last trial of a visual-search “detection” task, that is, just after they had correctly responded “target present” to a variably defined color or orientation target (Müller et al., 2004).

²This component has been also referred to as “N2-posterior-contralateral” (N2pc). However, based on recent evidence (e.g., Shedden & Nordgaard, 2001; Töllner, Müller, & Zehetleitner, 2012) that underscores the independence of this component in terms of both timing and activation from the nonlateralized N2, we prefer the term PCN instead of N2pc to avoid any misleading associations or interpretations.

³For the localization but not the identification task, there was also a strong lateralized activity over the motor areas—the LRP—evident within the two time windows directly after the PCN. This potential can be seen for localization responses because the side of the target (e.g., left position) was invariably linked to the required—spatially congruent—motor effector (in the

example: the left thumb) and, thus, not cancelled out by the averaging process. Notably, the manifestation of the LRP immediately following the PCN provides further support for the notion that master map activity (as indexed by the PCN) is sufficient to indicate the target's location, with the location information being transferred directly to motor response-related stages (see Töllner, Rangelov, & Müller, 2012).

⁴Prior to the PCN response, the data suggest an additional posterior contralateral positivity (Ppc; as recently observed by Jannati, Gaspar, & McDonald, in press) in the localization task, which appears to be most pronounced for high-contrast targets and gradually decreasing for intermediate- and low-contrast targets. However, this observation could not be substantiated statistically as indicated by the absence of a significant effect, $F(2, 24) = 1.47$, $p > 0.25$, of stimulus-background contrast on Ppc amplitudes. (We thank John McDonald for suggesting this analysis.)

⁵We thank Edward Vogel for suggesting this alternative explanation.

⁶This is not to say that “feedforward processing” in the present sense equals the very first sweep of visual processing through the brain. Concerning this issue, there is also a debate as to the exact mechanisms that drive the PCN: While the currently dominant view holds that the PCN reflects re-entrant processes (e.g., McDonald et al., in press), others have recently argued in favor of a feedforward-driven process (e.g., Töllner, Rangelov, & Müller, 2012).

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