Predictive Distractor Context Facilitates Attentional Selection of High, but not Intermediate and Low, Salience Targets

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Abstract: It is well established that we can focally attend to a specific region in visual space without shifting our eyes, so as to extract action-relevant sensory information from covertly attended locations. The underlying mechanisms that determine how fast we engage our attentional spotlight in visual-search scenarios, however, remain controversial. One dominant view advocated by perceptual decision-making models holds that the times taken for focal-attentional selection are mediated by an internal template that biases perceptual coding and selection decisions exclusively through target-defining feature coding. This notion directly predicts that search times remain unaffected whether or not participants can anticipate the upcoming distractor context. Here we tested this hypothesis by employing an illusory-figure localization task that required participants to search for an invariant target amongst a variable distractor context, which gradually changed-either randomly or predictably—as a function of distractor-target similarity. We observed a graded decrease in internal focal-attentional selection times-correlated with external behavioral latencies-for distractor contexts of higher relative to lower similarity to the target. Critically, for low but not intermediate and high distractortarget similarity, these context-driven effects were cortically and behaviorally amplified when participants could reliably predict the type of distractors. This interactive pattern demonstrates that search guidance signals can integrate information about distractor, in addition to target, identities to optimize distractor-target competition for focal-attentional selection. *Hum Brain Mapp* 36:935–944, 2015. © 2014 Wiley Periodicals, Inc.

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INTRODUCTION

It is well established that we are able to focally attend to a specific region in visual space even without shifting our eyes, so as to extract action-relevant information from the covertly attended location. This ability—first demonstrated experimentally by Hermann von Helmholtz one and a half centuries ago—has been metaphorically likened to a moveable "spotlight" of attention. The behavioral literature on visual selective attention has provided ample evidence that participants can shift focal attention to the location of

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Figure I.

Examples of search arrays used in the present illusory-figure search tasks. This design allowed us to gradually manipulate the similarity between target and distractor stimuli—defined in terms of the number (one vs. two vs. three) of local elements a Kanizsa-square shared with the simultaneously presented distractor items.

an action-relevant object more rapidly as the physical dissimilarity of the target to the distractor objects increases [Duncan and Humphreys, 1989; Navalpakkam and Itti, 2007]. However, the precise mechanisms that dynamically control *how fast* we engage our attentional spotlight in visual-search scenarios are, as yet, less well understood.

One dominant view advocated by contemporary perceptual decision-making models [Olivers et al., 2011; Woodman et al., 2007] holds that focal-attentional selection is mediated by an internal attentional set, or search template, that exclusively specifies target-defining features. Accordingly, when participants are required to search for a given object (e.g., a green apple), these models assume that selection is guided solely by global biasing of feature analyzers specialized for coding target-matching properties (e.g., color: green; form: circular). The underlying idea is that location-specific analyzer units accumulate sensory evidence towards an attention shift-initiating criterion [Smith and Ratcliff, 2004] faster the more precisely a given object matches the prespecified target template. This is not to say that these models envisage focal-attentional selection to be unaffected by distractor information. If distractors are defined by similar as compared to dissimilar features as the target, for instance, location-specific analyzers would likewise accumulate sensory evidence in favor of distractors-thereby putatively delaying focal-attentional target selection (for implicit space- and dimension-based crosstrial biasing of distractor information, see also [Chun and Jiang, 1998] and [Töllner et al., 2012a], respectively). In fact, previous studies examining primate single-cell [Treue and Martínez Trujillo, 1999] and human hemodynamic [Egner and Hirsch, 2005] brain activity support this view, showing that the output of target-coding analyzer units is amplified when participants attended to the respectively coded information. However, as these studies contrasted brain activity between situations in which participants did, versus did not, attend to one of two types of overlapping surface information (e.g., red vs. green [Treue and Martínez Trujillo, 1999], or houses vs. faces [Egner and Hirsch, 2005]), their explanatory value with regard to search-guiding mechanisms remains limited.

The current study was designed to explore the role of the physical stimulus context in the *timing* of attentionalspotlight shifts, and whether internal search-guiding signals can integrate information about distractor (context)as well as target-identity for facilitating focal-attentional target selection. To permit deeper insight into the neural mechanisms underlying the initiation of context-based attentional-spotlight shifts, we coupled millisecond-bymillisecond scalp-recorded voltage fluctuations to mental chronometry data during an illusory-figure search task. Participants were instructed to localize (left vs. right display hemifield) an invariant Kanizsa square [Conci et al., 2006, 2011; Davis and Driver, 1994], composed of four inward-facing pacman elements, presented among seven nontarget configurations, composed either randomly or predictably of one, two, or three inward-facing (together with three, two, or one outward-facing) pacman elements (see Fig. 1). In order to directly assess whether the speed of attentional-spotlight shifts (i.e., focal-attentional selection) can be biased by (i) distractor predictability, (ii) distractortarget similarity, or (iii) a mixture of both, our analyses focused on a particular waveform of the event-related potential which is elicited most prominently over parietooccipital areas contralateral to the location of an attended stimulus: the posterior contralateral negativity (PCN),¹ which is generated in the ventral occipito-temporal cortex [Hopf et al., 2002] and is generally accepted to reflect focal-attentional selection of task-relevant objects in visual space [Eimer, 1996; Töllner et al., 2012a; Woodman and Luck, 1999]. Of note, the speed with which focal attention is deployed in feature singleton search is independent of

¹Traditionally, this potential has been referred to as "N2-posteriorcontralateral" (N2pc). However, recent evidence [Shedden and Nordgaard, 2001; Wiegand et al., 2013] clearly showed that this wave is triggered independently—in terms of timing and activation—of the nonlateralized N2. Thus, to avoid any misleading associations or interpretations regarding the timing aspect, we follow the suggestion of Jaskowski et al. [Jaskowski et al., 2002], and others, to use the temporally more neutral label PCN (instead of N2pc).



Figure 2.

Behavioral and neural processing times. A: Reaction times separately for nonpredictive (light grey lines) and predictive distractor surrounds (dark grey lines), as a function of distractor-target similarity. B: PCN times separately for nonpredictive (light grey lines) and predictive distractor surrounds (dark grey lines), as a function of distractor-target similarity.

the respectively engaged task set, i.e., independent of whether participants are required to detect, localize, or identify the target object [Töllner et al., 2012b].

Following the dominant notion put forward by models of visual-selective attention [Duncan and Humphreys, 1989; Olivers et al., 2011; Woodman and Luck, 2007] that focalattentional selection is mediated exclusively by target featurespecifying templates, we should observe gradually decreasing PCN (and, thus, manual reaction) times for distractors of low relative to intermediate and high similarity to the target, with no further modulation by the predictability of the distractor context. By contrast, if search-guiding signals can additionally integrate information about distractor settings, we should observe PCN (and, thus, reaction) times that are speeded further when participants can reliably anticipate the upcoming distractor identities. For instance, stimulus surround predictability may act on the sensory representations of the distractors by lowering their impact on the preattentive competition for selection [Desimone, 1998]. Such an expectancy-driven downregulation would automatically translate into a selection advantage for the target, in that sufficient sensory evidence for initiating focal-attentional spotlight shifts to the target (as reflected by the PCN timing) would be accumulated sooner. Theoretically, such top-down controlled distractor predictability effects could determine neural and/or behavioral response times either additively to or interactively with stimulus-driven similarity effects.

MATERIALS AND METHODS

Participants

Twelve participants (four female) took part in this study. Their ages ranged from 20 to 30 (median 25) years. All had normal or corrected-to-normal vision; none reported a history of neurological disorder(s). Participants provided written informed consent and were either paid or received course credit. 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, Task, and Study Design

The search displays (see Fig. 1) consisted of one Kanizsa square,² composed of four inward-facing pacman inducers, among seven nontarget configurations, composed of either one, two, or three inward-facing (together with three, two, or one outward facing) pacman elements. On each trial, target and nontarget configurations (radius: 1.2° of visual angle) were presented in grey (1.83 cd/m^2) and arranged around the circumference of an imagery circle (of radius 3.0°) around a central white fixation cross; the screen

²We deliberately used Kanizsa squares because they allow for a clean, graded manipulation of distractor-target similarity, defined in terms of the number of local pacman elements (1 vs. 2 vs. 3) target and distractors could share. Arguably, using "simpler" stimulus settings might actually make it more difficult to examine distractor-target similarity in a non-confounded manner. For instance, symmetry-associated factors play a role in orientation search, where, e.g., horizontal targets presented amongst vertical distractors yield slower RTs than targets of only 67° tilt, even though the former are physically more dissimilar to the distractors. In color search, similarly, there would be varying contributions of the chromatic cone-opponent channels and the luminance channels to mid- and high-level processing of different colors [Jennings and Martinovic, 2014], providing a source of confounds.

background was black (0.02 cd/m²). Configurations were spaced equidistantly, with the target presented randomly at one of the six lateral positions. Participants were instructed to maintain central eye fixation throughout the experimental trials, and to make a 2-alternative forcedchoice response, as fast and accurately as possible, indicating the target side (left vs. right positioning relative to the vertex of the search array) by pressing the spatially congruent mouse button with their left or right thumb, respectively.

Two distinct distractor predictability conditions (nonpredictive vs. predictive) were performed consecutively in a dimly lit, sound-attenuated, and electrically shielded experimental chamber (IAC), with the order of the two conditions counterbalanced across participants. Search displays were presented on a 17" computer screen, mounted at a viewing distance of approximately 75 cm. Each condition consisted of 12 blocks of 72 trials each, resulting in a total of 1,728 trials. In the nonpredictive condition, distractor-target similarity varied randomly on a trial-bytrial basis throughout all 12 blocks. By contrast, the predictive condition was divided into three sessions consisting of four blocks each, with each session presenting one of three different distractor-target similarity conditions (see above); participants were informed of the respective level of distractor-target similarity at the start of each session. The order of the three sessions within the predictive condition was counterbalanced across participants. 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 200 ms. Trials were terminated by the participant's response or after a maximum time limit of 1000 ms. In case of a response error, or if no response was given within the maximum time window allowed, the word "FEHLER" (German word for "ERROR") was centrally presented for 1 s. The subsequent intertrial interval displayed a white central fixation cross for a randomly chosen duration of either 0.95, 1, or 1.05 s. Prior to the start of each of the two conditions, at least one block of practice was administered in order for participants to become familiarized with the stimulus material. After each block, participants received summary performance statistics (mean error rate and reaction time) as feedback information.

EEG Recording and Data Analysis

The electroencephalogram (EEG) was continuously sampled at 1 kHz using Ag/AgCl active electrodes (acti-CAP system; Brain Products Munich) from 64 scalp sites, which were in accord with the international 10-10 System. To monitor for blinks and 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 (BrainProducts, Munich) with a 0.1–250 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 nonstereotypical noise; subsequently, the data were band-pass filtered using a 0.5-30 Hz Butterworth IIR filter (24 dB/Oct). Next, an infomax-independent component analysis was run to identify components representing blinks and horizontal eye movements, and to remove these artifacts before backprojection of the residual components. For the PCN analyses, the continuous EEG was then epoched into 500-ms segments relative to a 200-ms prestimulus interval, used for baseline correction. Only trials with correct responses and without artifacts-defined as any signal exceeding $\pm 60 \mu$ V, bursts of electromyographic activity (as defined by voltage steps/sampling point larger than 50 μ V) and activity lower than 0.5 µV within intervals of 500 ms (indicating dead channels)-were accepted for further analysis on an individual-channel basis before averaging the eventrelated potential (ERP) waves. To extract the PCN from overlapping target selection-unspecific components, ERPs from parieto-occipital electrodes (PO7/8) ipsilateral to the target's location were subtracted from contralateral ERPs. The latencies of the PCN were defined individually as the maximum negatively directed deflection in the time range 150-350 ms post-stimulus. PCN amplitudes were computed averaging five sample points before and after the maximum deflection.

Differences in behavioral (reaction times, error rates) as well as neural measures (PCN latencies/amplitudes) were assessed by conducting separate two-way repeated-measures analysis of variance (ANOVA) with the factors distractor-target similarity (low, intermediate, high) and distractor predictability (predictable, nonpredictable). Significant main effects and/or interactions were further verified by means of post hoc comparisons (Tukey's honest significant difference test).

RESULTS

Behavioral Data

As depicted in Figure 2, we found behavioral performance to vary markedly as a function of stimulus context: participants exhibited faster reaction times (RTs) [F(2,22) = 139.20, P < 0.001] and produced fewer errors [F(2,22) = 83.70, P < 0.001] for targets of higher dissimilarity to the objects in their surround. Importantly, these stimulus-driven effects interacted with distractor predictability [RTs: F(2,22) = 31.16, P < 0.001; Errors: F(2,22) = 4.17, P < 0.029]: reactions were initiated faster and were less error-prone for targets least similar to distractors (RTs: 366 ± 29.4 ms vs. 409 ± 40.3 ms, P < 0.001; Errors: 2.0% vs. 4.0%, P < 0.012) but not (or less markedly so) for targets of intermediate (RTs: 409 ± 36.5 ms vs. 433 ± 43.5 ms,



Figure 3.

Target-synchronized grand-average ERP waveforms of the present study. **A**: ERPs elicited contra- and ipsilateral to the target location at electrodes PO7/8. **B**: Correlation between an individual's decrease in reaction and PCN times when responding to targets of low, relative to high, similarity to the distractors. **C**:

P < 0.021; Errors: 4.6% vs. 4.8%, P > 0.625) and high similarity (RTs: 489 ± 51.4 ms vs. 469 ± 48.1 ms, P > 0188; Errors: 14.0% vs. 12.9%, P > 0.287), with predictive relative to nonpredictive distractor surrounds.

Electrophysiological Data

The corresponding event-related potential waves are plotted in Figure 3A–C. As can be seen, the rise of the PCN started earlier [F(2,22) = 18.34, P < 0.001] and was boosted [F(2,22) = 33.11, P < 0.001] for targets that differed physically more (as compared to differing less) from the distractors. Of note, this similarity-based decrease in PCN timing correlated with the speed-up of RTs (r = 0.579; P < 0.02; Fig. 3B). Mirroring the RT pattern, these PCN context effects depended further on distractor predictability [interaction latencies: F(2,22) = 7.29, P < 0.004; interaction amplitudes: F(2,22) = 3.52, P < 0.047]: in particular, the

PCN (contralateral-minus-ipsilateral difference) waves and scalp distribution maps as a function of distractor-target similarity, separately for nonpredictive (left panel) and predictive distractors (right panel). For illustration purposes, the grand-average waves were low-pass filtered at 12 Hz (24 dB/Oct).

significantly fastest and strongest PCN waves were elicited by targets of low similarity relative to the distractors (266 ms; -2.29μ V), parametrically followed by targets of intermediate (276 ms; -1.68μ V) and high similarity (285 ms; -1.08μ V). Critically, PCN responses elicited by targets of low similarity rose even earlier (258 vs. 274 ms) and were amplified further (-2.52μ V vs. -2.07μ V) when participants could anticipate the upcoming stimulus context. Subsequent post hoc comparisons confirmed that the effects of distractor predictability on the PCN were evident for targets of low (latencies: P < 0.003; amplitudes: P < 0.037), but not for targets of intermediate (latencies: P < 0.277; amplitudes: P < 0.482), similarity with the distractors.

To further control for the possibility that these amplitude differences are attributable to variability differences across conditions, we ran additional analyses on the PCN width—which, according to this interpretation, should have been increased for conditions of higher relative to lower variability. To extract the PCN width for each condition, we subtracted PCN onsets from PCN offsets (both determined using the jackknife-based scoring method [Ulrich and Miller, 2001]) and submitted these difference values to a repeated-measures ANOVA with the factors distractor predictability and distractor-target similarity. The effects of both factors, as well as their interaction, were far from significance (all F_c values < 0.359), effectively ruling out the possibility that the current PCN amplitude results were due to variability differences.

Next, we controlled for the possibility that the above PCN results may have been confounded by simultaneously activated motor processes. As is inherent in localization task designs, the side of the target (e.g., left position) was invariably linked to the side of the motor effector (in the present example: left thumb), so that response production processes-as indexed by the Lateralized Readiness Potential (LRP)-are not automatically cancelled out by the averaging process. Thus, we plotted the time course of both PCN and LRP waves simultaneously at electrodes PO7/8 and C3/4, respectively, together with the corresponding topographical scalp distribution maps for the three 20-ms time windows before and after the PCN maximum. As can be seen from the scalp distribution maps in Figure 4, the rise and the maximum (which was taken for statistical analyses) of the PCN were triggered independently of the LRP, which emerged-on average-42 milliseconds after the PCN.3 Of note, for the time windows following the PCN maximum, the topographical maps suggest that location-specific target information was directly transferred from visual areas to the corresponding effector-specific motor areas, in line with the notion that search-guiding "master map" activity is sufficient to indicate the target's location [Töllner et al., 2013].

DISCUSSION

By examining brain electrical activity, the current study was designed to test a core assumption of contemporary visual-selective attention models [Duncan and Humphreys, 1989; Olivers et al., 2011; Woodman and Luck, 2007], namely, that attentional sets, or templates, mediate focal-attentional selection *exclusively* towards targetdefining feature coding. In line with this influential notion, we observed a graded decrease in internal focal-attentional selection times—correlated with external behavioral latencies—with increasing physical difference of an invariant target relative to its variable distractor surround. Challenging this influential notion, however, these context-based effects were behaviorally and cortically amplified for targets of low, but not (or less markedly so) of intermediate and high, similarity when participants could reliably predict the type of distractors. To our knowledge, these findings provide the first demonstration that the times taken to internally select and overtly respond to an invariant target are determined by both the predictability of the distractor context and the physical difference between distractor and target items in an interactive manner.

Predicting Distractor Contexts in Multilevel Visual Hierarchies

While this interactive pattern is hard to reconcile with pure "target template" accounts, these findings can be readily accommodated by salience summation models [Itti and Koch, 2001; Müller et al., 2010; Töllner et al., 2010; Wolfe, 1994] that envisage preselective feature contrast computations to be penetrable by internal, top-down controlled, system settings. According to this type of model, focal-attentional selection is accomplished at the level of an overall-saliency map, which is dynamically driven by the input from dimensionally organized analyzer units (e.g., for color, shape) that continuously compute the presence of feature-contrast for all locations in parallel. Once a master map unit is activated above threshold, focalattention is deployed to the location represented by this unit in a competitive, winner-take-all fashion [Lee et al., 1999]. Within this architecture, a Kanizsa square produces stronger feature contrast signals within the shape module-based on boundary contour computation and surface filling-in processes [Conci et al., 2009; Grossberg and Mingolla, 1985; Mattingley et al., 1997]-if the physical similarity to its surrounding non-square configurations is decreased. As stronger shape-specific feature contrast signals translate directly into enhanced saliency signals when integrated at the master map level,⁴ the threshold for triggering attentional spotlight shifts is reached earlier [Smith and Ratcliff, 2004], shortening overall search times. Crucially, master map activations are sufficient to indicate the presence and/or location (as required by the current taskset) of a feature contrast signal, but they are agnostic as to the exact value (e.g., the form: square) that gives rise to this difference. Precise knowledge about the target's identity, by contrast, would require the engagement of additional, post-selective processes to extract-via recurrent feedback connections-the respective feature information [Ahissar and Hochstein, 2004; Lamme and Roelfsema, 2000; Töllner et al., 2012b].

While the stimulus-driven similarity effects discussed so far can also be accounted for by templates that accumulate evidence in favor of a particular target feature (e.g.,

³As illustrated in Figure 4, the descending part of the PCN was temporally overlapping with the LRP maximum. As these waves represent the average of more than a thousand trials of temporal variance, however, one can conclude that the time windows following the PCN maximum represent trials with rather slow response times for the PCN but (different) trials of intermediate speed for the LRP.

⁴Note that this notion of salience summation generalizes across dimensions (see, e.g., [Töllner et al., 2011]).

Target-synchronized grand-average event-related lateralizations (ERLs). LRP (upper panel) and PCN waves (lower panel) obtained by subtracting activity ipsilateral to the side of the motor effector and, thus, target location from contralateral activity at electrodes C3/4 and PO7/8, respectively. The intermediate panel shows the corresponding 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 three 20-ms time intervals before and after the PCN maximum.

square), this notion cannot explain the expectancy-driven context effects, which indicate that search guidance signals must integrate distractor-related information at some stage before target selection. One possibility of how distractor information may be exploited to further optimize attentional guidance is by configuring an additional template that specifies the exact distractor (feature) identities [Humphreys and Müller, 1993]. Similar to target templates, such distractor templates may reside in the prefrontal cortex [Miller et al., 1996; Tomita et al., 1999], modulating-via feedback connections to lower visual areas-the activity of neurons that code distractor-related features. Instead of enhancing neuronal activity in visual cortex, distractor templates may rather operate via reducing the output of distractor-coding analyzer units, thereby lowering the distractor's impact on the preattentive competition for 1998]. selection [Desimone, This downregulation would implicitly affect the strength of suppressive lateral

iso-feature interactions [Beck and Kastner, 2005; Li, 1999] in favor of the target, so that sufficient sensory evidence necessary to reach for selecting the target focally—as reflected by the PCN timing (see below)—may be accumulated faster.

In this regard, a recent study by Beck and Kastner [Beck and Kastner, 2005] provides insight into how stimulus similarity modulates competitive interactions in extrastriate areas. The study contrasted hemodynamic brain responses to pop-out displays, in which a task-irrelevant item differed redundantly in (both) color and orientation from three neighboring items, with heterogeneous displays, in which all four items differed from each other in these feature dimensions. This contrast revealed that the presentation of a pop-out item eliminated suppressive sensory interactions in extrastriate areas that typically emerge from multiple, simultaneously presented stimuli. In the light of the current results, Beck and Kastner's pattern of differential activations between pop-out and heterogeneous displays may actually reflect a continuum, rather than (as they concluded) a present/absent dichotomy, of sensory suppression mechanisms. In other words, suppressive sensory interactions may be invoked gradually with increasing similarity among neighboring items but may be reduced when distractor identity is known in advance.

Moreover, the finding that the benefit deriving from predictable distractor context decreased with increasing distractor-target similarity further points to a multiplicative modulation of these interactions [Ayaz and Chance, 2009], with the same top-down factor generating beneficial effects that scale with physical distractor-target contrast. This interactive pattern suggests that distractor templates facilitate search performance only if distractor and target items are sufficiently distinct from one another (as with the current distractors of low similarity to the target). If distractors share 50% or more of the local feature information with the target (such as the current distractors of intermediate and high similarity), by contrast, distractor templates will fail to successfully suppress distractor information in lower visual areas. There may be also some additive cost for operating this context-based top-down control mechanism, explaining why the observed predictability effect turned, at least numerically, negative (i.e., into a cost) for the lowest feature contrast.

Finally, it is worth noting that the present findings are generally consistent with another class of (conceptual) models explaining expectancy effects in visual cortex, known as "predictive coding" [Rao and Ballard, 1999]. This framework assumes likewise a multilevel hierarchy of visual areas that communicate reciprocally via feedforward and feedback connections, where feedback signals carry "predictions" from higher to lower level visual areas, whereas the feedforward signals project the deviations i.e., residual errors—between the predictions and the actual visual inputs [Summerfield and Egner, 2009]. The general assumption underlying this framework is that the brain constantly attempts to avoid the coding of redundant components of the visual inputs through minimizing the prediction error. Applied to the present dataset, it would thus appear that the brain can make use of statistical regularities (in this case: constant distractor identities) only in the high-salience (i.e., low-similar) target condition. In other words, the reliability of the prediction error in search scenarios with predictive distractor surrounds would depend largely on the physical distinctiveness of the target relative to the distractors. While this framework could conceivably provide an account of the present data, it does not specify the neural machinery by which error minimization may actually be achieved in the current search scenario. Arguably, more work is required to marry the notion "predictive coding" with mechanistic accounts of attentional selection in visual search, such as that sketched above.

The PCN as a Neural Measure of Visual Salience

The finding that PCN waves were gradually increasing with decreasing distractor-target similarity has important implications with regard to the nature of the processes that underlie this component. While the general view holds that the PCN can be linked to the orienting of focal attention to task-relevant objects in visual space, there is an ongoing debate as to the exact mechanisms that give rise to this potential-whether they reflect target selection [Eimer, 1996; Luck and Hillyard, 1994], distractor suppression [Hopf et al., 2002], or a mechanism integrating both [Hickey et al., 2009; Töllner et al., 2011]. Töllner and colleagues [Töllner et al., 2011], for instance, have recently proposed that the PCN wave may reflect the target's saliency signal as envisaged by salience summation models (see above). This proposal was motivated by the observation that the PCN was gradually shifted in time and reduced in amplitude for targets of lower, relative to higher, feature similarity with the distractors. Of note, this saliency-based activation pattern is complementary to the current results by demonstrating an identical response profile in terms of the timing and amplitude of the PCN when, contrary to the current design, the target was variable within an invariant distractor context. Thus, only when combining the results of both the previous [Töllner et al., 2011] and the current study can one conclude unequivocally that the activations represented by the PCN indicate the physical difference (i.e., salience) of a given location relative to its surrounding locations, rather than a particular feature value that singles out the target from its surround. Or, put in terms of the saliency map hypothesis [Koch and Ullman, 1985], salience-based PCN activations are "featureless" representations because they are agnostic as to the exact feature (e.g., green) that gave rise to this signal.

This is not to say, however, that the ventral occipitotemporal cortex (i.e., the neural generator of the PCN, [Hopf et al., 2002]) is the one-and-only processing level that codes the conspicuity of objects in the human brain. Instead, our findings add to the mounting evidence that visual saliency is represented at numerous levels across the visual pathways, including the pulvinar [Robinson and Petersen, 1992], striate cortex [Zhaoping, 2002], extrastriate cortex [Beck and Kastner, 2005], lateral intraparietal area [Gottlieb et al., 1998], and the frontal eye fields [Sato et al., 2003]. In particular, in line with Treue [Treue, 2003] who argued in favor of a distributed saliency map, our findings suggest at least three functionally distinct purposes for which feature-contrast and/or saliency signals may be represented at different levels in the brain: First, the initial processing levels-striate and extrastriate visual areasencode the presence of feature contrast separately for distinct feature dimensions (e.g., color, shape), thus providing the basis for subsequent covert and overt attention shifting. Next, these pre-attentively computed feature contrast signals are combined into one overall-saliency map at the subsequent stage-the ventral occipito-temporal cortexbased on which covert attention shifts can be accomplished. Third, the activation landscape on this salience representation may then be transmitted to a third processing level-the frontal eye fields-whenever focal attention is to be shifted *overtly* to the target's location.

Distractor Templates: Rejecting Single Items Versus Suppressing Homogenous Contexts

The present idea that search guidance signals are integrating information about distractor settings bears, at first sight, a close resemblance to the notion put forward by Woodman and colleagues [Arita et al., 2012; Woodman and Luck, 2007], namely, that people can configure a "template-for-rejection." For example, Woodman and Luck [Woodman and Luck, 2007] reported decreased RTs when one of the distractor items matched, versus did not match, an object concurrently maintained in working memory (WM). This RT benefit has been taken to suggest that the contents of WM can be flexibly used to either facilitate or inhibit processing of matching items, so that participants may have avoided attending to items matching distractors. However, the Woodman and Luck study differs critically from the present one with respect to the stimulus material, the experimental design and, thus, the interpretation of the results: First, Woodman and Luck [Woodman and Luck, 2007] implemented a WM paradigm requiring participants to actively maintain a particular item in WM for subsequent recall, with the critical condition being that this single item could either match or not match one distractor item during the intermediate search task. In the current study, by contrast, participants were asked to search for a pre-defined invariant target, without being required to first explicitly memorize, then maintain, and finally recall any potential distractor items in addition to the search task. Second, each individual item presented in the search arrays of Woodman and Luck [Woodman and Luck, 2007] had the same physical salience (i.e., all six items were of different colors), making searches inefficient

and serial. By contrast, there was only one item in the current study—the target—that differed from the remaining homogenous distractor items, yielding efficient and spatially parallel search. Third, the task set (i.e., stimulusresponse mapping rule) used by Woodman and Luck required precise target identification, whereas the current task demanded simple target localization.

Finally, it is worth noting that the conclusions drawn by Woodman and colleagues [Arita et al., 2012; Woodman and Luck, 2007] were based on behavioral measures only. Thus, arguably, the manipulation they employed [Woodman and Luck, 2007] would have affected, in the first instance, the elicitation of the CDA, but not the PCN, wave. As demonstrated by Luria and Vogel [Luria and Vogel, 2011], the amplitudes of this signal become stronger as search difficulty increases, indicating increased demands for postselective target-matching operations in visual WM when search is serial [Woodman and Luck, 2007]. Accordingly, the timing effects reported by Woodman and Luck may originate from postselective, rather than preattentive, processing (time) demands to successfully match and/or reject potential target items in visual WM. The timing effects observed in the current study, by contrast, stem from a functionally distinct processing stage, namely, preattentive coding and the associated times required for triggering attentional spotlight shifts to the target's location. In sum, even though rejecting single items versus suppressing homogenous contexts lead both to behavioral RT benefits, the underlying mechanisms may differ substantially. While the former may expedite the times for matching candidate target items and/or rejecting distractor items against the target template in visual WM, the latter does speed up the times for directly selecting the target candidate item in visual space.

CONCLUSION

In conclusion, besides identifying a neural correlate of stimulus context in the human brain, the current findings provide electrophysiological evidence against the strong stance that the times taken for focal-attentional selection are mediated by templates that bias perceptual coding and selection decisions exclusively through target-defining feature coding. Instead, our results demonstrate that search guidance signals can integrate information about distractor, in addition to target, identities to optimize distractortarget competition for selection. Whether these distractor predictability effects level off, or even increase, when people are provided with two (or more) rather than just one distractor-related information in advance remains an open issue to be addressed in systematic future studies. Another challenge for the future is to explore whether target and distractor information is maintained by one-and-the-same or distinct search templates. This corresponds to the currently debated questions of how many items can be maintained simultaneously by a single attentional template and whether such target/distractor templates are represented

by the same or different sets of neurons which bias perceptual selection processes. In any case, the present findings disclose a more elevated role of distractor information in attentional selection than previously thought, with widespread implications for all major types of psychological and neurocognitive paradigms (e.g., attentional blink [Raymond et al., 1992], change detection task [Vogel et al., 2005], dual task [Töllner et al., 2012c], TVA's whole report task [Wiegand et al., 2014]) that measure human motor actions in response to spatially filtered sensory signals.

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