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Reward-associated features capture attention in the absence of awareness: Evidence from object-substitution masking



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ABSTRACT

Reward-associated visual features have been shown to capture visual attention, evidenced in faster and more accurate behavioral performance, as well as in neural responses reflecting lateralized shifts of visual attention to those features. Specifically, the contralateral N2pc event-related-potential (ERP) component that reflects attentional shifting exhibits increased amplitude in response to task-relevant targets containing a reward-associated feature. In the present study, we examined the automaticity of such reward-association effects using objectsubstitution masking (OSM) in conjunction with MEG measures of visual attentional shifts. In OSM, a visualsearch array is presented, with the target item to be detected indicated by a surrounding mask (here, four surrounding squares). Delaying the offset of the target-surrounding four-dot mask relative to the offset of the rest of the target/distracter array disrupts the viewer's awareness of the target (masked condition), whereas simultaneous offsets do not (unmasked condition). Here we manipulated whether the color of the OSM target was or was not of a previously reward-associated color. By tracking reward-associated enhancements of behavior and the N2pc in response to masked targets containing a previously rewarded or unrewarded feature, the automaticity of attentional capture by reward could be probed. We found an enhanced N2pc response to targets containing a previously reward-associated color feature. Moreover, this enhancement of the N2pc by reward did not differ between masking conditions, nor did it differ as a function of the apparent visibility of the target within the masked condition. Overall, these results underscore the automaticity of attentional capture by rewardassociated features, and demonstrate the ability of feature-based reward associations to shape attentional capture and allocation outside of perceptual awareness.

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Introduction

In the real world, a multitude of sensory stimuli constantly compete for our attention, and it is therefore essential to select the most relevant ones for more extensive perceptual processing. Due to their behavioral relevance, sensory features associated with rewards tend to capture attention. Within the context of a visual search task, this capture has been observed in behavioral and electrophysiological measures, which show enhanced processing of a stimulus containing a previously rewarded feature. The specific pattern of behavioral results appears to depend upon the elements of the presented search array or scene in which such a feature is embedded, and can either be beneficial or detrimental

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to the task at hand. For example, when a reward-associated feature is embedded in a task-relevant stimulus, it tends to enhance task behavior, making viewers faster and more accurate in discerning relevant stimulus content (Störmer et al., 2014; Buschschulte et al., 2014; Della Libera and Chelazzi, 2006; Kiss et al., 2009). On the other hand, when a reward-associated feature is embedded in a task-irrelevant stimulus, decrements in behavior in a concurrent primary task are observed, reflecting an effect of distraction from that task (Hickey et al., 2010; Anderson et al., 2011a,b; Chelazzi et al., 2013; Hickey and van Zoest, 2013).

Regardless of its effect on task-relevant behavior, attentional capture by reward is reflected in neural measures of spatial attention allocation. In the context of a visual search task, and whether embedded in a distracter or task-relevant target, the capture of attention by a rewardassociated feature is accompanied by modulations of the N2pc, a negative-polarity event-related-potential (ERP) component that reflects the shift or capture of attention to a laterally presented target,



and that appears as an enhanced negative evoked potential over contralateral posterior parietal scalp peaking ~200 ms after target onset (Luck and Hillyard, 1994; Woodman and Luck, 1999). Studies using MEG have suggested that this index of spatial attentional shifts arises mainly from ventral extrastriate cortex (Hopf et al., 2000), and intracranial single unit recordings in nonhuman primates have localized an analogous effect to inferotemporal regions (Chelazzi et al., 1998). Modulations of the N2pc activity, such as higher amplitudes or earlier onset latencies, thereby provide a neural index of the enhanced spatial attentional capture by reward-associated features. Such patterns of results have been seen in a number of electrophysiological studies of reward in visual search (Hickey et al., 2010; Kiss et al., 2009; Qi et al., 2013; Donohue et al., 2016).

The automaticity with which reward-associated features can capture visual attention has been probed primarily in terms of stimuli that are visible but are task-irrelevant or ignored (e.g., Qi et al., 2013). Although these findings underscore the potency of reward-associations in driving attentional processes during visual search, the degree to which visual attention can be captured by a reward-associated stimulus or feature of which the viewer does not become aware would provide particularly telling information concerning the automaticity of these influences. One way to probe attentional capture in the absence of awareness is to create conditions in which a physically present target is rendered perceptually unseen by viewers, and to track the hallmark behavioral and neural indices of attentional capture as a function of reward across these conditions of awareness. This method, wherein an implicit or neural measure of a specific perceptual or cognitive process is tracked across varying levels of awareness reflected in an explicit behavioral measure of the same process, is known as the dissociation paradigm (Reingold and Merikle, 1988). Previous studies have employed this approach using a variety of methods and measures, which seem to support the idea that ecologically relevant features or objects can have an influence on visual attention even when presented outside of visual awareness. For example, the affective content of faces has been shown to lead to enhancements of visual processing, regardless of visibility (Jiang et al., 2009; Pegna et al., 2008; Pesciarelli et al., 2011; Smith, 2012). In addition, it has also been shown that ecologically relevant, but otherwise unseen, stimuli can capture attention, as reflected in their tendency to overcome inattentional blindness (Koivisto and Revonsuo, 2007) or facilitate subsequent target discrimination (Wetherill et al., 2014).

Of particular relevance in examining the deployment of visual attention to unseen visual targets is a study by Woodman and Luck (2003), which successfully dissociated the focusing of attention reflected in the N2pc from the construct of visual awareness. Specifically, these authors showed that the N2pc was present for targets that were masked by object substitution (described below), whether they were ultimately seen or unseen by the viewer, whereas those targets masked by a more traditional form of backward pattern masking did not elicit an N2pc when unseen. Whether or not the enhancement of the N2pc by reward-associated features would also be present under such circumstances would speak not only to the automaticity of reward processing, but also whether its ability to modulate attentional allocation can operate outside the purview of awareness. This issue is the main focus of the present study.

To create conditions of reduced visual awareness, masking by object substitution can serve as a particularly useful method. In objectsubstitution masking (OSM), an array of stimulus items (i.e., a single target item among an array of distracters) is briefly presented (~17–50 ms duration). The target item, which occurs in an unpredictable location in the array, is denoted as the target by a surrounding four-dot mask (Enns and Di Lollo, 2000; Giesbrecht and Di Lollo, 1998). On half of the trials, all elements of the briefly presented array (distracters, target, and mask) disappear simultaneously, which tends to leave the target visibility intact. On the other half of the trials, the four-dot mask remains on the screen for a short period of time (typically several hundred milliseconds) following the offset of the rest of the target/distracter array. In these instances, the visibility of the target is greatly reduced. The most favored account of the mechanism of OSM cites the convolution of a feedforward signal comprised of the offset-lagging mask with the reentrant signal containing the initial mask-plus-target information. This integration process is proposed to result in the representation of the mask (i.e., the only consistent element between the two signals) being substituted for the initial target-plus-mask as an input signal to later visual processing stages, and ultimately to perceptual awareness (Boehler et al., 2008; Di Lollo et al., 2000; Harris et al., 2013). Consequently, any process shown to occur despite the perceptually disruptive effects of OSM can be interpreted as occurring independently from this reentrant signaling mechanism.

Based on what is known about masking via object substitution, as well as previous findings regarding the capture of attention by rewarded visual features, the introduction of a feature-based reward association to masked targets can lead to one of several possible patterns of results. At the behavioral level, the rapid capture of attention by a reward-associated feature may make OSM less effective at reducing the visibility of such targets. An enhanced N2pc response in the case of reward-associated vs. reward-unassociated targets in the masked condition would likely accompany this behavioral result. Such an overall pattern of results would be consistent with previous findings pointing to the central role of attentional deployment in determining the efficacy of masking by object-substitution, wherein correctly discriminated masked targets were accompanied by an enhanced N2pc to the target location relative to those not consciously perceived (Harris et al., 2013; Prime et al., 2011).

On the other hand, it is possible that the behavioral changes associated with reward processing (e.g., increased accuracy) rely on the visual process that is disrupted by OSM. If so, no behavioral difference due to reward would be expected in the masked condition. The neural results would therefore be of central interest, with two main patterns of electrophysiological results being possible. One possibility would be that the N2pc enhancement in response to reward-associated features, like the corresponding behavioral effects, depends upon the process disrupted by OSM, thus resulting in no reward-related enhancement under conditions of reduced target visibility. Another intriguing possibility would be that an enhanced N2pc to reward-associated targets would still be elicited, even in the absence of awareness of that target and any behavioral effect of the reward association. This would indicate that reward-associated feature detection, and subsequent enhanced capture of visual attention, are part of a process that is independent from the low-level reentrant signaling that gives rise to awareness (Chelazzi et al., 2013; Woodman and Luck, 2003). That is, given the putative low-level reentrant mechanism by which OSM disrupts awareness, this would show that a feedforward signal from a stimulus containing a reward-associated feature is sufficient to capture attention automatically, even when that stimulus fails to reach awareness.

Methods

Subjects

Thirty-seven subjects participated in the experiment, of which two were ultimately excluded due to an insufficient number of trials following artifact rejection for eye movements and blinks. This yielded a total of 35 subjects in the grand average (all right-handed, 14 female) with a mean age of 26.4 ± 2.9 years. Participants were compensated for their time and performance, and informed consent was obtained for all subjects in accordance with protocol approved by the Institutional Review Board of the Otto-von-Guericke University in Magdeburg, Germany.

Stimuli and task

General

The stimuli and tasks were created using the Presentation software package (Neurobehavioral Systems, Inc., Albany, California) and were projected onto a screen 1 m in front of the subject. Prior to commencing the experiment, all subjects completed a flicker-fusion luminanceequating task in which the specific color values (as defined by relative red-green-blue (RGB) hue saturations) for the relevant colors (magenta and brown) were determined. Once the target color luminances were equated, and following a brief practice run of the object-substitutionmasking (OSM) task in greyscale, subjects completed two experimental tasks: a reward-association induction task, and an OSM task wherein targets could be of either a previously rewarded or unrewarded color (see below). Each session consisted of 3 runs of the rewardassociation induction task, followed by two OSM runs, then another single reward-association induction run to refresh the reward associations, followed by two more OSM runs, and so on, for a total of 5 reward association induction runs and 6 OSM runs. There were also separate runs in which the color of the mask itself could be associated with reward, but those results are not reported here.

Reward association induction/N2pc localizer task

For the reward association induction task (Fig. 1A), trials consisted of four circles of 1.7° diameter and subtending 6.3° relative to a central fixation cross, presented in the upper left, lower left, upper right, and lower right quadrants of the screen for a duration of 40 ms. In every trial, one of these circles was of either a magenta or brown hue (previously matched for luminance using the flicker-fusion task), whereas the remaining three circles were yellow, cyan, or gray, with one of each of these three other colors being presented on every trial, randomly assigned to the three remaining locations. Subjects were asked to indicate the location of the relevant color circle by pressing one of four buttons, each corresponding to a screen location, within 600 ms of target array onset. Subjects received feedback on every trial following their response, indicating whether their response was correct, incorrect, or correct but too slow. In addition, for one of the colors, arbitrarily assigned to each subject, feedback included a monetary value of +10cents for correct responses executed within the 600 ms time window, and +0 in the case of incorrect or slow behavior.

Color-target OSM task

For the OSM task (Fig. 1B), every trial consisted of an array of 15 greyscale ellipses (1.1° width and 1.7° length), each of randomly selected vertical or horizontal orientation, along with a single ellipse target of

either the previously rewarded or previously unrewarded target color (Fig. 1B). Participants were asked to report, via button press, the orientation of the target ellipse (horizontal or vertical), or to press a third button indicating 'no target present.' The target could appear in any one of the four locations previously assigned to the circles in the rewardassociation induction task. The target was surrounded by four small black squares that served as the mask, which onset simultaneously with the array. The target/distractor array remained on screen for a duration of 26 ms. For half of the trials, the four-dot mask offset with the entire array, while on the other half of trials, it remained on the screen for an additional 500 ms, inducing the substitution masking effect of reduced awareness of the target. In light of previous studies demonstrating that OSM is enhanced when targets and masks share shape or color features (Chen and Treisman, 2009; Gellatly et al., 2006), it should be noted that the masks and targets used in the OSM portion of the experiment always differed on both the color and orientation feature dimensions. Specifically, ellipse targets were always one of two orientations, whereas the target-marker masks were comprised of squares of an unchanging orientation, and only the target element ever contained relevant color features.

MEG acquisition

Magnetoencephalographic (MEG) activity was acquired using a BTI Magnes 3600 (4-D Neuroimaging, San Diego, CA) whole-head magnetometer with 248 SQUID sensors, and filtered online with a low-pass filter of DC-to-50 Hz (sample rate = 254 Hz per channel). For each participant, the head position was spatially registered using preauricular, nasion, inion, and centroid anatomical landmarks, as well as five localizer coils attached to the head (3Space Fastrak System, Polhemus, Colchester, VT, USA). Subject behavior and movement were monitored throughout the experiment via closed-circuit video, as well as via online monitoring of MEG data for artifacts.

Data analysis

Behavior

For each task, mean accuracy, detection, and response times (RTs) were measured. For the reward-association induction/N2pc-localizer task, these metrics were submitted to a within-subjects two-tailed

Phase	Trial structure	Targets	Task	Possible feedback
A. Reward association induction (N2pc localizer)	Example: Upper right target	•	Location discrimination (UL,UR,LL,LR)	Unrewarded targets "Correct" "Incorrect" "Too slow" Rewarded targets "Correct + 10" "Incorrect + 0" "Too slow + 0"
B. Color-target object subsitution masking	Upper right masked target	••	Target detection and orientation discrimination (3AFC: horizontal, vertical, no target present)	No feedback given

Fig. 1. A. *Reward association induction/N2pc localizer task design.* One relevant color target (either brown or magenta) was presented in an unpredictable location (upper left (UL), upper right (UR), lower left (LL), lower right (LR)) for each trial. Subjects indicated via button press the location of the relevant circle, and were given feedback on their performance. One color, chosen arbitrarily for each subject, was followed by monetary reward-associated feedback. B. *Color-target OSM task.* Subjects indicated the orientation of an ellipse occurring in one of four locations, indicated by a four-square surrounding mask. For half of the trials, this mask was delayed in offset by 500 ms relative to the target/distracter array, which was presented for 26 ms (masked trials). Targets could be of either the previously neutral or previously rewarded color. (AFC = alternative forced choice).

paired comparison across target color (reward-associated and rewardunassociated) conditions. In the case of the OSM task, these measures were submitted to a 2-by-2 repeated-measures ANOVA (with the factors of masking condition and reward-association of the target color).

MEG

For each participant, offline artifact rejection was performed via a peak-to-peak threshold criterion within the peristimulus time window of -100 ms to + 1000. Epochs with peak-to-peak amplitude values exceeding established thresholds were excluded from subsequent analysis. The sensitivity and selectivity of each threshold were evaluated on a subject-by-subject basis, and yielded a range of thresholds of 1.8 pT to 3.4 pT, with an average of 2.5 pT. Once these thresholds were set for each subject, they were applied blindly by an automatic computer algorithm for rejection of trials. On average, this led to the rejection of approximately 11.2% of trials across subjects (range of 3-16%). In the event that artifacts comprised 25% or more of a participant's data, the set was excluded from further analyses (as was the case for two subjects). Event-related magnetic field (ERMF) responses were extracted by time-locked averaging each participant's artifact-free data to the onset of stimuli for each condition. These averages were baseline corrected relative to a 100 ms pre-stimulus-array interval for statistical tests and plotting.

Repositioning and source modeling

The sensor array was repositioned for each subject using anatomical landmarks digitized during acquisition (preauricular points and nasion) to a reference sensor set based upon the average positions derived from 1500 previous sessions. To this end, a lead-field was calculated for every participant's data based on MNI anatomical data, resulting in a cortical surface (excluding the cerebellum) source space representation based on the Minimum Norm Least Squares algorithm (Fuchs et al., 1999). Sensor-space data were then reconstructed for each participant using the inverted lead-field obtained in the previous step. This creation of a standard space allowed data from multiple participants to be grandaveraged and the dipole sources underlying extracted MEG N2pc responses to be modeled and examined.

Source localization of the grand ERMF extracted N2pc was performed using Curry 7 (Compumedics Neuroscan, USA Ltd.) through the Minimum Norm Least Squares algorithm with a rotating dipole source. Source estimates were anatomically constrained by the 3D surface models (Fuchs et al., 1998) of the source compartment (cortical grey-to-white matter border) and the volume conductor compartment (cerebrospinal fluid space) of the MNI brain.

N2pc

The MEG N2pc marker of spatial attentional shifts was extracted, separately for each condition, by subtracting those ERMFs in response to targets occurring in the right visual field from those associated with targets occurring in the left visual field. This subtraction eliminates sensory-evoked similarities and leaves only the difference in responses as a function of the relative contralaterality of target responses, which is enhanced in the case of greater attentional allocation to targets. The N2pc, as extracted for the reward association induction/N2pc localizer task, provided the time window and sensors over which all subsequent statistical analyses of N2pc mean amplitude were performed. The relevant N2pc time window was identified by subjecting the mean amplitude difference between target-left and target-right ERMFs within the reward association induction/N2pc localizer task to a sliding-window t-test on consecutive time-samples between 100 and 500 ms poststimulus, with a window width of three time samples (11.8 ms). The first of five or more consecutively significant tests was identified as the onset of a significant effect (Guthrie and Buchwald, 1991; Schoenfeld et al., 2007; Schoenfeld et al., 2003a,b). These onset and offset values were then rounded to the nearest fifth millisecond (e.g., 127.8 ms would become 130). For statistical purposes, and to reduce the possible influence of alpha-band artifacts, a 100 ms-wide time window capturing the peak canonical N2pc effect, while excluding its edges (i.e., values of 0 fT), was used. MEG sensors of interest were selected by identifying, across all conditions in the reward association induction/N2pc localizer task, the time-point of maximal N2pc-related activity between 100 and 500 ms. The sensors lying within the maximal efflux and influx of this activity were averaged together after reversing the polarity of effluxassociated channels to achieve a uniformly negative polarity for plotting and statistics.

Mean amplitude N2pc responses were compared across relevant reward association, masking, and behavioral conditions within each task. Specifically, within the reward-association induction/N2pc localizer task, N2pc mean amplitudes were compared across conditions of reward-associated targets and reward-unassociated targets. For the OSM task, mean amplitude values for the N2pc were subjected first to a 2-by-2 repeated measures ANOVA with the factors of masking condition (simultaneous versus delayed offset of the four-square mask) and reward association (whether the target was of a previously rewarded or unrewarded color). Additionally, for the OSM task, this analysis was followed by a 2-by-2 repeated measures ANOVA with the factors of reward and target visibility within the masked condition (i.e., correct and incorrect responses to the masked target) to probe the presence of any extracted reward-associated N2pc enhancement across conditions of awareness.

Results

Behavior

Reward association induction task

For the location discrimination task of the reward-association induction phase of the study, targets of one color, when correctly located within the prescribed behavioral response time window (200–600 ms), were followed by a monetary reward. Accuracy was significantly higher for discs of a rewarded color than for discs of the unrewarded color (mean: 90%, and 83%, respectively; $t_{34} = 5.00$; p < .001; Fig. 2). Response times were also shorter for rewarded discs relative to unrewarded discs (429 ms and 453 ms, respectively; $t_{34} = 7.18$; p < .001). Overall, participants in the reward-association induction phase were both more accurate and faster in their responses to stimuli containing a reward-associated feature than to equally salient targets containing an unrewarded feature.

Color-target OSM task

In this OSM-based task, subjects were asked to discriminate the orientation of a color target ellipse surrounded by a black four-dot mask. Measures of mean accuracy showed significant main effects of masking $(F_{1.34} = 128.93, p < .001)$ and reward association $(F_{1.34} = 6.65, p = .01)$, with subjects being less accurate in discriminating the orientation of ellipses during masked trials, and also when the ellipses were of a previously unrewarded color relative to a previously rewarded color (see Table 1 for all values). The subjects' accuracy fell from 84% for unmasked trials to 68% in masked trials, and from 77% for targets of a previously rewarded color to 75% for those of a previously unrewarded color, with no interaction of masking and reward ($F_{1,34} = .006, p = .94$). Measures of overall target detection revealed a main effect of masking $(F_{1,34} = 19.1, p < .001)$, falling from 99% in the unmasked condition to 91% in the masked condition, no main effect of reward ($F_{1,34} = 1.7$, p = .21), and no interaction (F_{1,34} = .59, p = .45). Taken together, the lack of a significant interaction in both accuracy and detection shows that although the reward association, as induced in the initial task, transferred to measures of accuracy, it did not render targets containing a previously reward-associated feature any less susceptible to the effects of masking. No response time effects were observed.



Fig. 2. Summary of behavioral results. A. In the reward-association induction task, subjects were significantly more accurate and faster in reporting the location of a reward-associated color disc relative to an unrewarded color disc. In the OSM task (B), masking reduced accuracy. In addition, subjects were more accurate in identifying the orientation of the target ellipse when the target was of the previously rewarded color relative to the previously neutral color (collapsed across masking conditions, depicted below graph). No significant RT differences were observed for OSM task, although a trending main effect of masking was observed, with subjects slightly slower, on average, for masked trials. Error bars represent standard error of the mean.

MEG

N2pc extraction

Within each task, the MEG N2pc index of lateralized shifts of spatial attention was extracted by comparing mean amplitude values in response to left-sided targets to those associated with right-sided targets, collapsed across reward-association conditions as well as across behavioral performance. This yielded a canonical peak N2pc response during the poststimulus time window of 175-275 ms for the reward-association induction/ N2pc localizer task (evoked field responses to left visual field targets versus responses to right visual field targets; $t_{34} = 9.14$, p < .001), which thereby provided a spatio-temporal region of interest (ROI) to be used for the subsequent analyses. That is, this localizer N2pc provided the time window and sensor sites used for subsequent analyses for the OSM task (i.e., repeated-measures ANOVAs investigating masking-byreward effects, as well as target-visibility-by-reward effects within the masked condition). Collapsing across the factors of behavior and reward-association, a similar significant difference between responses to left and right visual field targets (N2pc) was extracted for OSM unmasked trials ($t_{34} = 8.17, p < .001$) and masked trials ($t_{34} = 7.80, p < .001$) p < .001). All subsequent analyses probing effects of reward association, masking, and target visibility thus consider as the dependent variable the mean amplitude of these extracted N2pc components in the localizer-established spatio-temporal ROIs (Fig. 4C and F).

N2pc modulation by reward-association

In the reward-association induction task, targets that were associated with a reward elicited a higher amplitude N2pc response during the 175–275 ms poststimulus time window than those associated with feedback in the absence of reward (-23.7 fT for rewarded versus -11.9 fT for unrewarded; t₃₄ = 3.2, p < .01; Fig. 3D). These results indicate that the reward association induction/N2pc localizer task was successful in establishing a color-feature reward association that reliably captured visual attention, as evidenced by an enhanced amplitude of the N2pc.

Within the color-target OSM task (Fig. 4), a main effect of reward (i.e., an amplitude enhancement; $F_{1,34} = 11.02$, p < .01) was observed, with no significant main effect of masking ($F_{1,34} = 1.6$, p = .22) or masking-by-reward interaction ($F_{1,34} = .01$, p = .92). Because it is reasonable to expect that this main effect of reward on the N2pc responses might have varied as a function of target visibility (reflected by behavioral performance) within the masked condition, an additional analysis was conducted within that condition. This analysis yielded a main effect of reward ($F_{1,34} = 8.3$, p < .01), no main effect of target visibility ($F_{1,34} = 1.8$, p = .19), and no interaction between the two factors ($F_{1,34} = .003$, p = .96). Thus, the reward association established in the induction/localizer phase of the experiment transferred to the OSM task, yielding larger amplitude N2pc responses to targets of the previously rewarded color relative to those targets of the previously neutral color. In addition,

Table 1

Summary of behavioral results. Accuracy and response time data (mean <u>+</u> standard error of the mean). Additional overall detection data are provided for the object-substitution masking task.

Reward-association induction	Accuracy (% correct; mean \pm SE)		Response time (<i>ms</i> ; <i>mean</i> \pm <i>SE</i>)
Unrewarded targets Rewarded targets Color-target object-substitution masking	83 ± 2.01 90 ± 1.00 Accuracy (% correct: mean + SF)	Detection (%: $mean + SF$)	454 ± 6.10 430 ± 5.34 Response time (ms: mean + SE)
Unmasked	Accuracy (so concer, mean ± 52)		Response time (ins, mean ± 52)
Previously unrewarded color target	83 ± 1.50	$98 \pm .54$	545 ± 10.94
Previously rewarded color target	84 ± 1.52	$99 \pm .43$	543 ± 11.26
Masked			
Previously unrewarded color target	67 ± 1.89	91 ± 1.9	549 ± 10.76
Previously rewarded color target	69 ± 2.20	92 ± 2.3	547 ± 10.72



Fig. 3. Reward association induction/N2pc localizer task. A. Cortical source estimations for the N2pc difference wave extracted for the reward-association induction/localizer task. Current source density modeling localized the peak N2pc difference (250 ms) to bilateral ventral–occipital–temporal regions. B. Topographical field distribution for the N2pc peak difference, with selected and rectified channels (foci of influx and inverted polarity foci of efflux averaged together) indicated by ellipses. C. N2pc (target-left minus target-right) as extracted for unrewarded (black trace) and rewarded targets (green trace). D. A reward-associated enhancement of this N2pc difference wave was observed during the 175–275 ms poststimulus time window for targets associated with monetary feedback (green bar) relative to those associated with neutral feedback (gray bar). Error bars represent standard error of the mean.

this reward-associated enhancement of the N2pc and did not vary as a function of masking condition or target visibility.

Discussion

The present study investigated the capture of attention by a rewardassociated visual feature (color) in the absence of awareness induced by object-substitution masking, wherein the reward-associated feature was embedded in masked targets. Results indicate that a new, arbitrary reward association at the level of the color feature can still capture attention, even when it does not reach a viewer's awareness. That reward captures visual attention as reflected in behavioral and neural measures has been shown in multiple studies (e.g., Della Libera and Chelazzi, 2006; Hickey et al., 2010; Kiss et al., 2009). The present study shows further that when this reward-association was not only orthogonal to the task at hand, but was even masked from perceptual awareness by object-substitution, the neural index of enhanced attentional capture by the reward-associated feature was still preserved.

Reward-associated features implicitly capture attention during OSM

Previous studies have implicated a low-level reentrant mechanism of disruption in OSM, which provides a mechanistic framework for interpreting the present results (Boehler et al., 2008; Di Lollo et al., 2000; Harris et al., 2013). Specifically, OSM has been proposed to disrupt visual awareness by way of a mismatch in V1 between the feedback reentrant signal for the target stimulus that has already offset and the feedforward signal of the mask that is left on the screen during the delayed mask offset period on masked trials (Di Lollo et al., 2000). This mechanism of low-level reentrant signal integration has been further investigated and supported by some recent studies utilizing measures of neural activity. One study employing EEG measures of the cascade of

visual processes occurring during an OSM task showed that the difference in ERP activity between seen and unseen targets within the masked condition appears after the initial sweep of feedforward activity, with the visual-evoked P1 responses that reflect early extrastriate activity being unaffected (latency 80–120 ms), but with later activity over the occipital pole between 130 and 170 ms poststimulus being reduced in the case of unseen (i.e., effectively masked) targets (Harris et al., 2013). An earlier MEG study, seeking to identify the anatomical locus of disruption, modeled sources of activity differences during the time period immediately following initial feedforward signaling in V1, which also supported the idea that differential low-level recurrent activity is responsible for the behavioral effects of OSM (Boehler et al., 2008). Finally, an earlier study employing hemodynamic measures localized effective masking to a network of brain regions including striate cortex as well as later object-processing-related regions (Weidner et al., 2006).

In light of this converging evidence for a low-level reentrant mechanism of disruption in OSM, the present results show that a feedforward signal corresponding to an initial target/distracter array that contains a reward-associated feature is sufficient to enhance the capture of attention even in the absence of awareness. Thus, the detection of a rewardassociated feature by the visual system, much like the more general shifting of attention it enhances, is subserved by processes parallel to, and mostly independent from, the disrupted reentrant process underlying the OSM perceptual effect (Woodman and Luck, 2003).

OSM and attentional deployment reflected in the N2pc

Although the main effects of rewardassociation of the targets within the OSM task were of primary interest, the dynamics of the N2pc as a reflection of attentional deployment in the context of OSM should also be noted. Here, the mean amplitude of the N2pc was not affected by the masking by object substitution. In addition, within the masked



Fig. 4. Color-target OSM. A. Cortical source estimations for the N2pc difference wave extracted for the unmasked condition of the color-target OSM task. Current source density modeling localized the N2pc difference at its peak (250 ms) to bilateral ventral–occipital–temporal regions. B. Topographical field distribution for the N2pc peak difference, with the selected peak channels indicated by black ovals. C. N2pc extracted for unmasked targets of a previously unrewarded (black trace) and rewarded (green trace) color. D. Cortical source estimations for the N2pc difference wave extracted for the masked condition of the color-target OSM task. Current source density modeling localized the peak N2pc difference (250 ms) to bilateral ventral–occipital–temporal regions, as well as to early visual cortical regions. E. Topographical field distribution for the N2pc peak difference, with the selected peak channels indicated by black ovals. F. N2pc responses as extracted for correctly identified masked targets of a previously unrewarded (black trace) and rewarded (green trace) color. D. Sahed traces on the lower plot depict N2pc responses to targets of a previously unrewarded (green) color that were not correctly identified. G. A significant main effect of reward was observed during the relevant N2pc time window (175–275 ms poststimulus), with previously reward associated color targets eliciting a higher mean amplitude N2pc than those of a previously incurrent vas observed during the relevant N2pc time window (175–275 ms poststimulus), which did not differ as a function of visibility. Error bars represent standard error of the mean.

condition, the amplitude of the N2pc did not vary as a function of perceptual visibility as reflected by behavioral performance (i.e., comparing the N2pc associated with hits to that associated with missed targets). This consistently evoked N2pc is in line with previous studies that showed an intact N2pc response across behavior within the masked condition in OSM (Prime et al., 2011; Woodman and Luck, 2003). On the other hand, this is in contrast with our recent study showing that the N2pc is reduced in amplitude within the masked condition for targets that are effectively masked (i.e., unseen) (Harris et al., 2013). This difference is likely explained by the fact that in the studies showing a consistent N2pc response across behavior, the array duration was sufficient (83 ms in both cases) for the subject to consistently shift attention to the target location, whereas the array duration in our previous study was much briefer (17 ms). As for the present study, which also uses a relatively short array duration (26 ms), the target location was additionally cued in a salient way, containing a previously relevant color among greyscale distractors. This salient pop-out cue may have contributed to the N2pc not being reduced as a function of masking or visibility.

What makes the difference between a modulated and intact N2pc response within the masked condition during OSM remains of interest and merits further investigation. It is likely that, in addition to the core mechanism of low-level reentrant signaling, fluctuations in the efficacy of attentional deployment across a briefly presented, more uniformly salient display also play a role in the observed effects of OSM on the N2pc, as seen previously (Harris et al., 2013), and consistent with proposed mechanisms that center on visual attention as a determinant of masking efficacy (Poder, 2013; Smith and Ratcliff, 2009). That said, even in the case of equivalently effective attentional deployment within the masked condition for hits and misses, disrupted reentrant signaling can still give rise to reduced visual awareness in OSM, as it has in the present experiment. That the effect of reward indexed by the N2pc is present in a manner independent of perceptual visibility during OSM further dissociates the mechanism of visual awareness disruption from attentional capture.

Conclusion

The present study examined the perseverance of implicit attentional capture by reward-associated features across conditions of awareness as disrupted by object-substitution masking. The current findings demonstrate that a new, arbitrary reward-associated feature, when later embedded in visual targets in a separate, unrewarded OSM task, continues to capture attention even when that target does not reach perceptual awareness. Overall, the present findings underscore the ability of feature-based reward-associations to shape attentional capture and allocation outside of perceptual awareness.

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