

Neural structures involved in visual search guidance by reward-enhanced contextual cueing of the target location



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ABSTRACT

Spatial contextual cueing reflects an incidental form of learning that occurs when spatial distractor configurations are repeated in visual search displays. Recently, it was reported that the efficiency of contextual cueing can be modulated by reward. We replicated this behavioral finding and investigated its neural basis with fMRI. Reward value was associated with repeated displays in a learning session. The effect of reward value on context-guided visual search was assessed in a subsequent fMRI session without reward. Structures known to support explicit reward valuation, such as ventral frontomedial cortex and posterior cingulate cortex, were modulated by incidental reward learning. Contextual cueing, leading to more efficient search, went along with decreased activation in the visual search network. Retrosplenial cortex played a special role in that it showed both a main effect of reward and a reward \times configuration interaction and may thereby be a central structure for the reward modulation of context-guided visual search.

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1. Introduction

A growing body of evidence shows that learned reward associations can lead to attentional capture by the rewarded item. This has been observed for covert shifts of attention (Anderson et al., 2011) as well as overt eye movements (Camara et al., 2013; Hickey and van Zoest, 2012; Theeuwes and Belopolsky, 2012). Reward can be associated with a feature, but also with a target location, guiding visual search to the rewarded location (Hickey et al., 2014), even when it has become irrelevant due to a target location change (Camara et al., 2013).

However, all these studies have in common that the reward-associated item competes with a salient target for attention, slightly slowing down an otherwise efficient visual search. This was different in a recent study on reward-modulated contextual cueing using an inefficient visual search task (Tseng and Lleras, 2013). Contextual cueing is observed when the same spatial target-distractor configuration is repeatedly shown during an experimental session, leading to reduced search times. This contextual cueing effect occurs incidentally, i.e. in the absence of an intention to learn, and mostly implicitly, without awareness of learning (Chun and Jiang, 1998). This distinguishes the contextual cueing paradigm from explicit memory-guided search, which has

been shown to be enhanced at rewarded target locations (Doallo et al., 2013). Visual search in contextual cueing paradigms is typically inefficient, requiring several eye movements before the target is found. Instead of an immediate capture of attention, as in the experiments discussed above, contextual cueing entails a less direct form of search guidance, leading to reduced search times due to more straightforward scan paths (Brockmole and Henderson, 2006; Manginelli and Pollmann, 2009; Peterson and Kramer, 2001; Tseng and Li, 2004). Nevertheless, a recent study showed that contextual cueing could be modulated by assigning different reward values to individual repeated displays (Tseng and Lleras, 2013). After participants had finished searching a display, a reward cue indicated a high or low reduction of the remaining workload in the task. Tseng and Lleras observed a strong contextual cueing effect for displays with high value, whereas contextual cueing for low-value displays developed much more slowly. An explicit recognition test at the end of the experiment yielded no evidence for explicit, intentional learning of repeated displays. Moreover, by presenting the value assignment only after visual search had ended, it was ensured that participants could not voluntarily prepare to attend with greater effort to high value displays (compare Murayama and Kitagami (2014), for a similar post-cueing procedure).

Reward modulation of contextual cueing would require an association of the reward value with the complex target-distractor configuration or a subset thereof (contextual cueing is observed when only part of the display is repeated, e.g. Geyer et al., 2010; Jiang and Leung,

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2005; Jiang and Wagner, 2004). This would be considerably more complex than the simple association of reward with a specific color or location used in the attentional capture studies mentioned above.

However, there may be an alternative explanation for reward modulation in the contextual cueing paradigm. In repeated displays, not only the distractor configuration is repeated, but also the target is repeatedly presented at the same location, offering the opportunity for target location probability cueing. Probability cueing of the target location (Miller, 1988) was recently investigated in the context of visual search (Jiang et al., 2013). Other than transient inter-trial priming (Kristjánsson and Campana, 2010), probability cueing is a long-term memory phenomenon that can be observed several days after learning (Jiang et al., 2013). In the contextual cueing paradigm, target locations are typically repeated equally often in novel displays and in repeated displays in order to remove probability cueing of the target location as a confound of contextual cueing (e.g. Chun and Jiang, 1998). However, Schlagbauer et al. (2014) pointed out that it was unclear if Tseng and Lleras (2013) had associated reward value consistently with target locations in novel displays in the same way as in repeated displays. In their own experiments, they found evidence for a reward modulation of probability cueing rather than of contextual cueing. Thus, it is currently an open question how these two types of cueing contribute to the reward modulation of visual search in repeated displays.

The present study aimed at investigating the neural architecture underlying reward modulation of contextual cueing in visual search. Specifically, our aim was to investigate the processing of previously learned reward associations with spatial contexts. Therefore, we carried out a training session during which the participants incidentally learned to associate specific target–distractor configurations with differential reward value. In a subsequent fMRI session, they searched the same displays, but in the absence of reward. During training, high and low reward values were associated with specific target locations for novel and repeated displays alike. For the repeated displays, reward value was thus associated both with a specific target location and the associated distractor configuration whereas for novel displays it was only associated with the repeated target location. In this way, reward modulation of contextual cueing could be assessed by the interaction of configuration (repeated, novel) and value (high, low). In addition, reward modulation of target probability cueing could be assessed by the contrast of novel high versus low reward displays.

Contextual cueing was expected to lead to faster search times for repeated displays during the fMRI session. This, in turn, was expected to lead to less activation in the brain areas supporting visual search (Pollmann and von Cramon, 2000), particularly the dorsal attention network supporting overt and covert attention shifts (Corbetta et al., 2008; Wager et al., 2004), in line with a previous study on contextual cueing (Manginelli et al., 2013a).

When a search display became associated with high reward during training, we expected it to elicit increased activation in brain areas known to represent reward value, particularly the ventral frontomedial cortex (Critchley and Rolls, 1996; Elliott et al., 2008; Gläscher et al., 2012; Liu et al., 2011; Tremblay and Schultz, 1999) but also the posterior cingulate cortex (Liu et al., 2011).

If the association of reward value with a particular search display facilitates incidental learning of this display, search times will be shortened for repeated presentations of the same display – the contextual cueing for repeated displays will be enhanced, leading to an interaction of configuration \times reward. This interaction was expected to reduce activation in the search network further for repeated high-reward displays.

Contextual cueing depends on medial temporal structures (Geyer et al., 2012; Kasper et al., 2015; Manns and Squire, 2001; Preston and Gabrieli, 2008). More generally, the posterior parahippocampal gyrus has been shown to be particularly important for context memory (for a recent review, see Ranganath and Richey, 2012). The posterior parahippocampal gyrus is connected with the retrosplenial cortex/posterior cingulate and angular gyrus, areas that support spatial memory,

scene perception and navigation (Baumann et al., 2010; Bohbot et al., 2000; Ekstrom et al., 2011; Janzen and van Turennout, 2004; Schinazi and Epstein, 2010; Sommer et al., 2005; Uncapher et al., 2006). Perhaps most closely related to the current task, Summerfield et al. (2006) have shown right retrosplenial cortex, left parahippocampal gyrus and right angular gyrus to be preferentially involved in memory retrieval for scenes. If contextual cueing is modulated by reward, this may lead to differential activation for repeated high versus low reward configurations in these areas.

2. Methods

2.1. Participants

Nineteen right-handed volunteers without any history of neurological impairment took part in the experiment (7 males; mean age: 24.6 ± 4.7 years, range: 20–38 years). All had normal or corrected-to-normal vision and were naive as to the purpose of the present research. All the participants provided written informed consent for taking part in this study. The study was subdivided into two experimental phases, a training session in a psychophysical lab and an fMRI session conducted a few days later (1–6 days, mean: 2.28 days). The participants received a reimbursement for their participation. This reimbursement was variable for the training session, dependent on the number of errors. Because only few errors were made, the variability of the earned reward was low (mean: €19.38, range: €18–21). For the fMRI session it was fixed (€15). The experiments were approved by the Ethics Committee of the University of Magdeburg. Three participants were excluded from the analysis due to technical problems during the fMRI data acquisition.

2.2. Training session

2.2.1. Stimuli

All experiments were carried out with version 3 of the Psychophysics Toolbox (Brainard, 1997) running in Matlab (MathWorks, Sherborn, MA) on an MS-Windows computer. In the training session, the participants viewed stimuli on a 24-inch screen monitor (resolution: 1920×1200 pixels; refresh rate: 60 Hz). The viewing distance of 60 cm was ensured by using a chin rest.

The experimental design was a variant of a contextual cueing paradigm (Chun and Jiang, 1998; Exp. 1). The display consisted of an array of twelve black items that were presented on a gray background (Fig. 1). These items were a T-shaped target that was rotated 90° clockwise or counterclockwise (balanced across trials) and eleven L-shaped distractors rotated by 0° , 90° , 180° , or 270° . The line junction of the L-shapes had an offset of 4 pixels to make them more similar to the T-shape, in this way increasing the task difficulty (Jiang and Chun, 2001). The size of the items was $1.25^\circ \times 1.25^\circ$. The positions of the items were chosen on four imaginary concentric circles with radii of 2.03° , 4.74° , 7.43° , and 10.15° . These circles comprised 4, 12, 20, and 28 equidistant possible item locations, respectively. Twenty-four target locations were chosen on the two outer circles. Target and distractor positions were balanced across all displays to ensure that each visual quadrant contained six target locations and that each display contained three items in each quadrant.

2.2.2. Procedure

Trials started with the presentation of a fixation cross for 1 s followed by a search display (Fig. 1). Participants were instructed to report the orientation of the target as fast and accurately as possible by pressing the left or right arrow key on a standard keyboard. The search display was presented until a manual response occurred. Correct responses were followed, after a blank interval of 0.2 s, by the picture of a coin (size: $9.1^\circ \times 9.1^\circ$) that informed the participant about the received reward. If participants reported an incorrect orientation of the target item a low-pitch tone (300 Hz, 0.5 s) was provided as feedback before

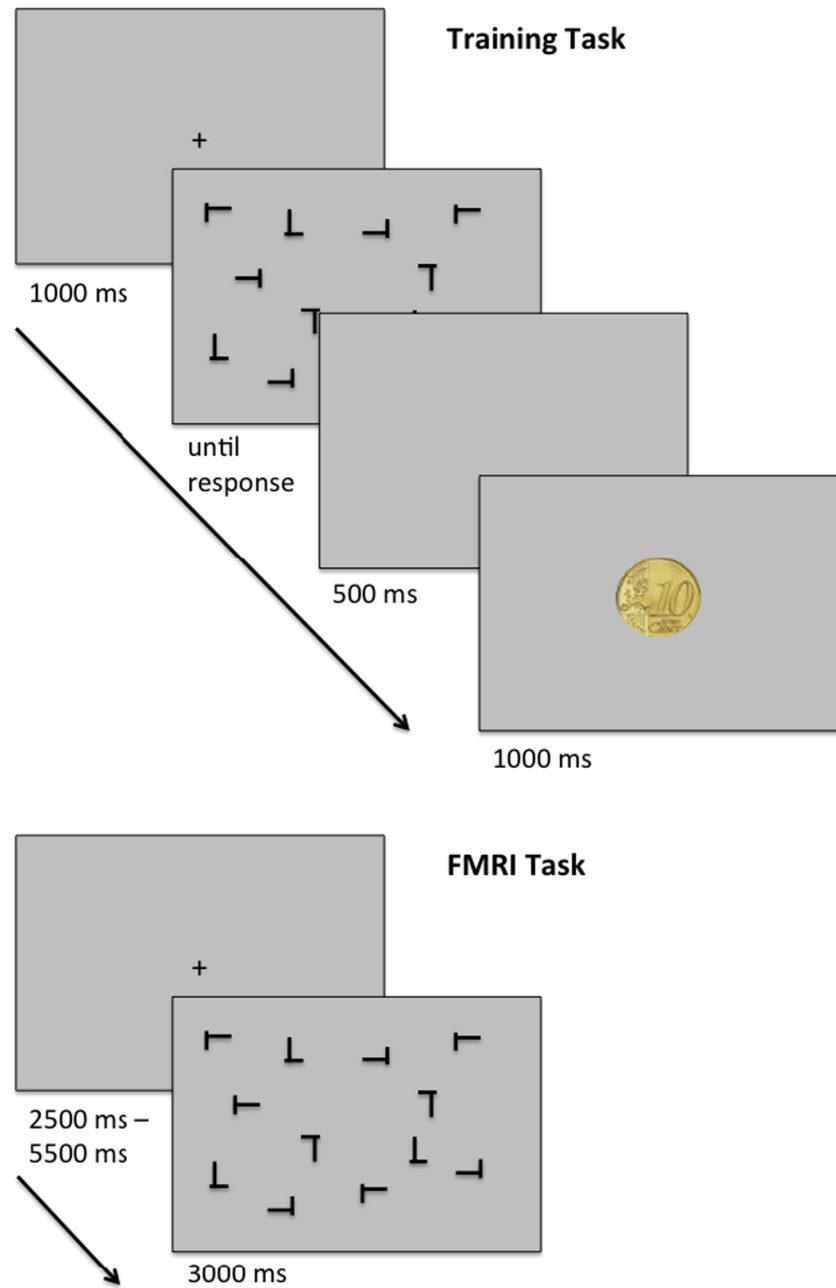


Fig. 1. Trial schema for the training (top) and fMRI (bottom) sessions.

offset of the search display. Trials with incorrect responses, as well as trials with response times longer than 2.5 s were not rewarded and instead of a coin a red circle was shown. Trials were separated by a constant inter-stimulus interval of 1.5 s showing a blank screen.

A session consisted of 16 blocks of 24 trials, with each of the 24 target locations presented once in random order. In half of the trials, the position and orientation of the distractors were kept constant along with the target location. Only the orientation of the target varied – the T was tilted to the left or to the right equally often within blocks – in order to prevent cueing of response-related processes. In the novel display condition, the distractor configuration was randomly arranged for each presentation of the target at the given location and was not repeated in the course of the experiment.

Each half of the 24 target locations was combined with a high or, respectively, a low reward value (In one participant, four target positions were associated with high as well as low reward values in different trials

in the training session. The subject was kept in the analysis because these trials may introduce noise to the data, but the majority of this subject's trials still convey meaningful information). This assignment was applied to repeated and novel displays alike, which is important to avoid confounding of reward modulation of contextual cueing and target location probability cueing (Schlagbauer et al., 2014). This led to four task conditions: highly rewarded repeated configurations (HR), highly rewarded novel configurations (HN), lowly rewarded repeated configurations (LR), and lowly rewarded novel configurations (LN). The reward value for the trials was established in the training session by showing the image of either a 10 Euro Cent coin or a 1 Euro Cent coin after correct responses. In addition, the accumulated reward was indicated after each block of trials. Subjects were instructed that on every trial the indicated reward was earned if the response was correct and did not exceed a response time window of 2.5 s. Apart from that, the reward was not dependent on performance.

2.3. fMRI session

In the fMRI session the same task as in the preceding training session was used, with the following exceptions. Stimuli had a size of $0.83^\circ \times 0.83^\circ$ and were presented on imaginary circles of 1.99° , 4.60° , 7.30° , and 9.93° diameter. Trials did not contain a reward post-cue. Participants received a fixed compensation for their participation. Thus, the reward modulation identified in this session reflects the past reward experience during the training session that persisted over a period of a few days.

Stimuli were presented via a D-ILA projector to a back-projection screen placed in the bore of the scanner behind the participant's head. Subjects viewed the screen through a mirror mounted on top of the head coil. Two-alternative button press responses were recorded by a custom-built response box.

The search displays were presented for 3 s irrespective of the response times. Subsequent trials were separated by inter-stimulus intervals (mean: 4 s; range: 2.5–5.5 s, exponential distribution) during which a fixation cross was shown. Participants had to report the target orientation by pressing buttons of the response box with their right hand. If no response was recorded while the search display was shown, it was registered as a miss.

2.3.1. fMRI acquisition

Magnetic resonance images were acquired with a 3 T Siemens Trio Scanner equipped with an eight-channel head coil. Functional whole brain data were acquired using a T2* weighted echo-planar imaging sequence (TR: 2000 ms; TE: 30 ms; flip angle: 80° ; phase encode direction A→P; interleaved slice order). For each participant, four runs with 340 volumes were obtained within a scanning session. Each volume consisted of 34 transverse slices (field of view: 192 mm, matrix: 64×64 pixels, 3 mm isometric voxels, inter-slice gap: 0.3 mm). For each participant, a three-dimensional high-resolution T1-weighted image of the whole brain was also acquired in the same session with an MPRAGE sequence (TR: 2500 ms, TE: 4.77 ms, TI: 1100 ms, 192 transverse slices, matrix: 256×256 , 1 mm isometric voxels).

2.3.2. fMRI-analysis

2.3.2.1. Pre-processing. The DICOM data were converted to the NiftI image format with the mcvter tool (<http://lcni.uoregon.edu/~jolinda/MRIConvert>). Data pre-processing and statistical analyses were performed with tools of the FSL package, version 5.0.2 (Smith et al., 2004; Jenkinson et al., 2012; www.fmrib.ox.ac.uk/fsl). The fMRI data were corrected for head motion by aligning all image volumes with the middle volume of each run with FSL's MCFLIRT tool (Jenkinson and Smith, 2001; Jenkinson et al., 2002). After extraction of the brain from surrounding tissue with the BET tool (Smith, 2002), the functional data were spatially smoothed with a Gaussian kernel at a full-width-at-half-maximum of 5 mm. A temporal high-pass filter was applied to the time series with a cutoff period of 120 s to remove low-frequency confounds.

For each participant, FLIRT (Jenkinson and Smith, 2001) was used to align the functional images to the individual structural high-resolution image with a boundary-based registration (Greve and Fischl, 2009; BBR) using a 12 degrees-of-freedom (DOF) affine transformation. The high-resolution image of each participant was co-registered to the MNI152 standard template (2 mm isometric voxel resolution) by applying a 12 DOF affine transformation with FLIRT that was further refined by a subsequent nonlinear transformation with the FNIRT tool.

2.3.2.2. GLM analysis. The GLM analysis was carried out with the FEAT tool version 6.00. A generalized linear modeling (GLM) analysis was applied to each run separately using FILM with local autocorrelation correction (Woolrich et al., 2001).

The presentation of the displays for the four task conditions, HR, LR, HN and LN, were modeled as boxcar function with a fixed duration for the presentation time of 3 s for correct trials only. Error trials were modeled as regressor of no interest. The regressors were convolved with a double-gamma function. The temporal derivative of these regressors was included in the GLM analysis to account for small timing differences (Friston et al., 1998). Motion correction parameters were included in the model to reduce nuisance effects.

The four regressors were used for a 2×2 ANOVA with the factors of configuration (repeated and novel), reward value (high and low), and the interaction terms of both factors. The statistical maps obtained for each run were combined on a group level with a mixed effects analysis that modeled the data from one session of a single subject as fixed effect and the data across participants as mixed effects. The statistical z-maps were thresholded at $z > 2.3$ and corrected for multiple comparisons on a cluster level at $p < 0.01$. Statistical maps were shown for selected slices following the dual-coding approach suggested by Allen et al. (2012) that represents the parameter estimates of the model fit as color and the associated z-value as color transparency. Clusters of voxels that passed thresholding were shown in solid color and were outlined with a contour line. Brain structures corresponding to these clusters of significant voxels were identified with the Harvard–Oxford cortical atlas (Desikan et al., 2006) provided by the FSL package.

Displays were visible for a fixed duration of 3 s in order not to confound the experimental variables with changing display presentation times. However, because search times were shorter than display presentation, post-response events may have occurred that were not captured by our standard HRF model. In order to investigate this question, we ran an additional analysis using finite impulse response modeling (FIR). In this analysis, 6 time bins of 2 s width were used to model the response, with onsets beginning 2 s before the response (to capture response preparatory effects) until 8 s postresponse. These bins were not convolved with a model of the vascular response. Again, only correct trials were used and motion correction parameters were included in the analysis. Statistical analyses were identical to those described above.

2.4. Explicit recognition test

After the fMRI session, a display recognition test was performed outside the scanner. This task included all twelve repeated distractor configurations and twelve novel configurations that were not previously shown. In the repeated displays the target was replaced by an additional distractor. Likewise, the novel displays contained only L-shapes. The 12 repeated displays were repeated four times whereas twelve novel displays were randomly generated four times. The participants had to indicate, with a mouse pointer on a computer screen, where they remembered the target to have been located within each display during the actual search task. The X and Y coordinates for the position of the mouse pointer were recorded for further analyses. No feedback about the correctness of the chosen location was given. Following the explicit recognition task the participants completed a questionnaire about their subjective perception of the experiment.

3. Results

3.1. Behavioral data

3.1.1. Training session

3.1.1.1. Search times. Trials with incorrect responses as well as trials with search times shorter than 200 ms or three standard deviations above the participant's average search time were excluded from the search

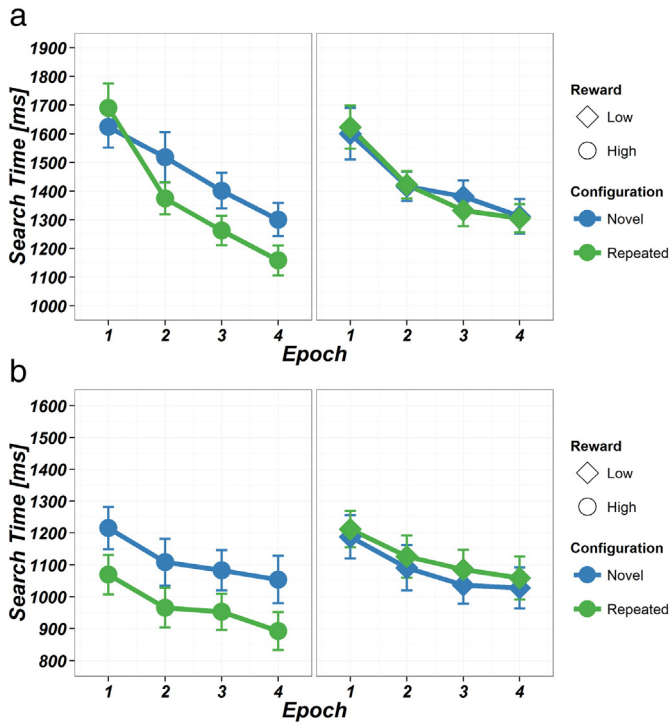


Fig. 2. Mean search times in the training (a) and fMRI (b) sessions. Bars indicate standard errors of the mean.

time analyses. Data were aggregated into epochs consisting of four blocks each. A repeated-measures ANOVA with configuration (novel, repeated), reward (high, low) and epoch (epochs 1–4) as factors was performed. It yielded a significant main effect of epoch [$F(3,45) = 38.313, p < 0.001$], indicating faster search times as the experiment progressed (Fig. 2a). The significant main effect of configuration [$F(1,15) = 6.19, p < 0.05$] reflected shorter search times for repeated (mean = 1393.099, SD = 200.90) compared to novel configurations (mean = 1441.263, SD = 239.72). The reward main effect was not significant [$F(1,15) = 0.202, p = 0.659$]. The significant

configuration \times epoch interaction [$F(3,45) = 6.734, p < 0.001$] replicated the typical contextual cueing pattern with increasingly shorter search times for repeated than novel configurations. The significant reward by epoch interaction [$F(3,45) = 4.499, p < 0.01$] was due to decreasing search times over the course of the session particularly for highly rewarded configurations. The three-way interaction narrowly missed statistical significance [$F(3,45) = 2.356, p = 0.084$].

3.1.1.2. Accuracy. Overall, participants' performance was highly accurate (median proportion of errors = 0.038, interquartile range (IQR) = 0.037).

Participants' accuracy was analyzed by means of a repeated measures analysis of deviance on a logistic regression model of the error frequency, with configuration (novel, repeated), reward (high, low) and epoch (epochs 1–4) as factors. The main effect of configuration [$\chi^2(1) = 4.87, p < 0.05$] was significant, indicating higher accuracy for repeated displays. Likewise, the main effect of epoch [$\chi^2(3) = 72.55, p < 0.001$] was significant, reflecting overall task improvement, i.e. fewer errors over the course of the task. In contrast, the main effect of reward [$\chi^2(1) = 1.89, p = 0.169$] was not significant. Only one of the interactions was significant (Configuration \times epoch: [$\chi^2(3) = 8.81, p < 0.05$] reflecting a higher increase in accuracy over time for repeated displays). Thus, there was no indication of a speed-accuracy trade-off.

3.1.2. fMRI session

3.1.2.1. Search times. The same ANOVA as for the training session was carried out on search times obtained during the fMRI session (Fig. 2b) with the same exclusion criteria. A significant main effect of epoch [$F(3,45) = 26.885, p < 0.001$] reflected decreased search times as the session progressed. The main effects of configuration [$F(1,15) = 9.897, p < 0.01$] and reward [$F(1,15) = 30.682, p < 0.001$] were also significant. Among the interactions, only configuration \times reward was significant [$F(1,15) = 31.374, p < 0.001$ all other $F(3,45) < 0.62, p > 0.60$]. Together, these effects were due to faster search times in HR compared to all other conditions.

Paired sample t-tests (Holm-adjusted) yielded significant differences between HR and HN [$t(15) = 7.819, p < 0.001$]. In contrast, no significant difference was observed between LR and LN [$t(15) = -1.282, p = .17$]. The three-way interaction was not significant [$F(3,45) =$

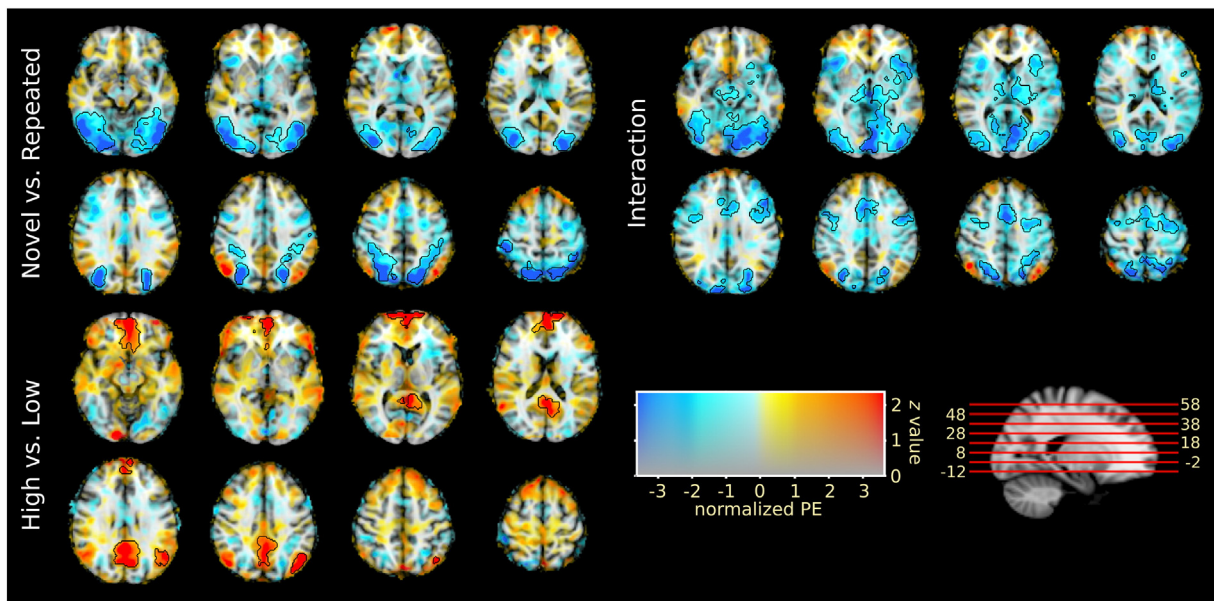


Fig. 3. fMRI activation maps for the main effects of configuration (repeated versus novel displays), reward (high versus low) and their interaction ((HR-HN)-(LR-LN)). The statistical map represents the parameter estimates of the model fit as color and the associated z-value as color transparency. Clusters of voxels that passed thresholding are shown in solid color and are outlined with a contour line. Left hemisphere is on the right.

0.082, $p = 0.97$]. This was expected since most of the context learning occurred already in the training session and no reward was given in the scanner session, leaving no opportunity for additional reward learning.

3.1.2.2. Accuracy. Overall, participants' performance was again highly accurate (median proportion of errors = 0.022, IQR = 0.021).

Participants' accuracy was again analyzed by means of a repeated measures analysis of deviance on a logistic regression model of the error frequency, with configuration (novel, repeated), reward (high, low) and epoch (epochs 1–4) as factors. The main effect of configuration [$\chi^2(1) = 16.90$, $p < 0.001$] was again significant, indicating higher accuracy for repeated displays. This effect was qualified by a significant

configuration \times reward interaction [$\chi^2(1) = 7.14$, $p < 0.01$] due to the particularly high accuracy in the repeated high-reward displays. All other main effects and interactions were not significant. Again, there was no indication for a speed-accuracy trade-off.

3.1.2.3. Recognition test. Wilcoxon signed rank tests between novel and repeated display configurations that revealed no significant differences in the recognition of target location, either for the lowly rewarded configurations ($V = 39$, $p = 0.1439$) or for the highly rewarded configurations ($V = 82$, $p = 0.4954$). Thus, no evidence was found for explicit recognition of repeated target–distractor configurations for any of the reward assignments.

Table 1
Table of activations.

Cluster size [voxel]	z Score	p Value	Maximum voxel & center of gravity [X; Y; Z]			Harvard-Oxford cortical structural atlas ^a	Juelich histological atlas	Talairach label
<i>Novel display vs. repeated display (N–R)</i>								
7461	5.58	<0.001	34	–82	6	22% lateral occipital cortex, superior division	29% WM optic radiation R	Right cerebrum. Temporal lobe. Subgyral. White matter
			35	–68.3	16.1			
7036	5.12	<0.001	–28	–82	22		53% WM optic radiation L	Left cerebrum. Occipital lobe. Middle occipital gyrus. White matter
			–32	–70.3	13.8			
<i>High reward vs. low reward (H–L)</i>								
3220	4.15	<0.001	0	48	–12	68% paracingulate gyrus, 10% cingulate gyrus, anterior division	\	Left cerebrum. Limbic lobe. Anterior cingulate
			–0.05	48.9	–1.34			
2833	4.14	<0.001	–6	–46	8	52% precuneus cortex, 43% cingulate gyrus, posterior division	\	Left cerebrum. Limbic lobe. Posterior cingulate. Gray matter. Brodmann area 23
			–3.05	–54.2	25.5			
781	3.82	0.0078	–48	–66	42	63% lateral occipital cortex, superior division	63% GM inferior parietal lobule PGp L, 39% GM inferior parietal lobule Pga L	Left cerebrum. Temporal lobe. Middle temporal gyrus. White matter
			–45.7	–66.2	34.2			
607	3.7	0.0304	44	–60	36	48% lateral occipital cortex, superior division, 17% angular gyrus	64% GM inferior parietal lobule PGp R, 40% GM inferior parietal lobule Pga R	Right cerebrum. Temporal lobe. Middle temporal gyrus. White matter
			49.9	–59	29			
<i>Interaction: reward \times configuration (LR–LN)–(HR–HN)</i>								
11,208	5.05	<0.001	–8	–86	–8	27% intracalcarine cortex, 24% lingual gyrus, 18% precuneus cortex	64% GM visual cortex V1 BA17 L, 20% WM optic radiation L, 10% GM visual cortex V2 BA18 L	Left cerebrum. Occipital lobe. Lingual gyrus. White matter
			–16.6	–61.5	4.79			
4565	4.59	<0.001	–24	–4	48	35% juxtapositional lobule cortex (formerly supplementary motor cortex), 33% cingulate gyrus, anterior division	10% GM premotor cortex BA6 L	Left cerebrum. Limbic lobe. Cingulate gyrus. White matter
			–8.1	5.34	42.9			
2248	4.47	<0.001	40	–76	–8	34% lateral occipital cortex, inferior division	\	Right cerebrum. Occipital lobe. Inferior occipital gyrus. White matter
			39.8	–73.8	–0.42			
1141	4.51	<0.001	–32	22	4	63% insular cortex	\	Left cerebrum. Sub-lobar. Insula. White matter
			–36.7	14.7	0.188			
723	3.83	<0.001	24	–66	54	57% lateral occipital cortex, superior division	10% GM superior parietal lobule 7P R, 10% GM superior parietal lobule 7A R	Right cerebrum. Parietal lobe. Precuneus. White matter
			24.7	–66.5	47.3			
583	4.21	0.0315	38	14	4	43% frontal operculum cortex, 23% insular cortex	\	Right cerebrum. Sub-lobar. Insula. White matter
			38.8	19.5	2.43			

^a Only structures with probabilities $\geq 10\%$ are reported.

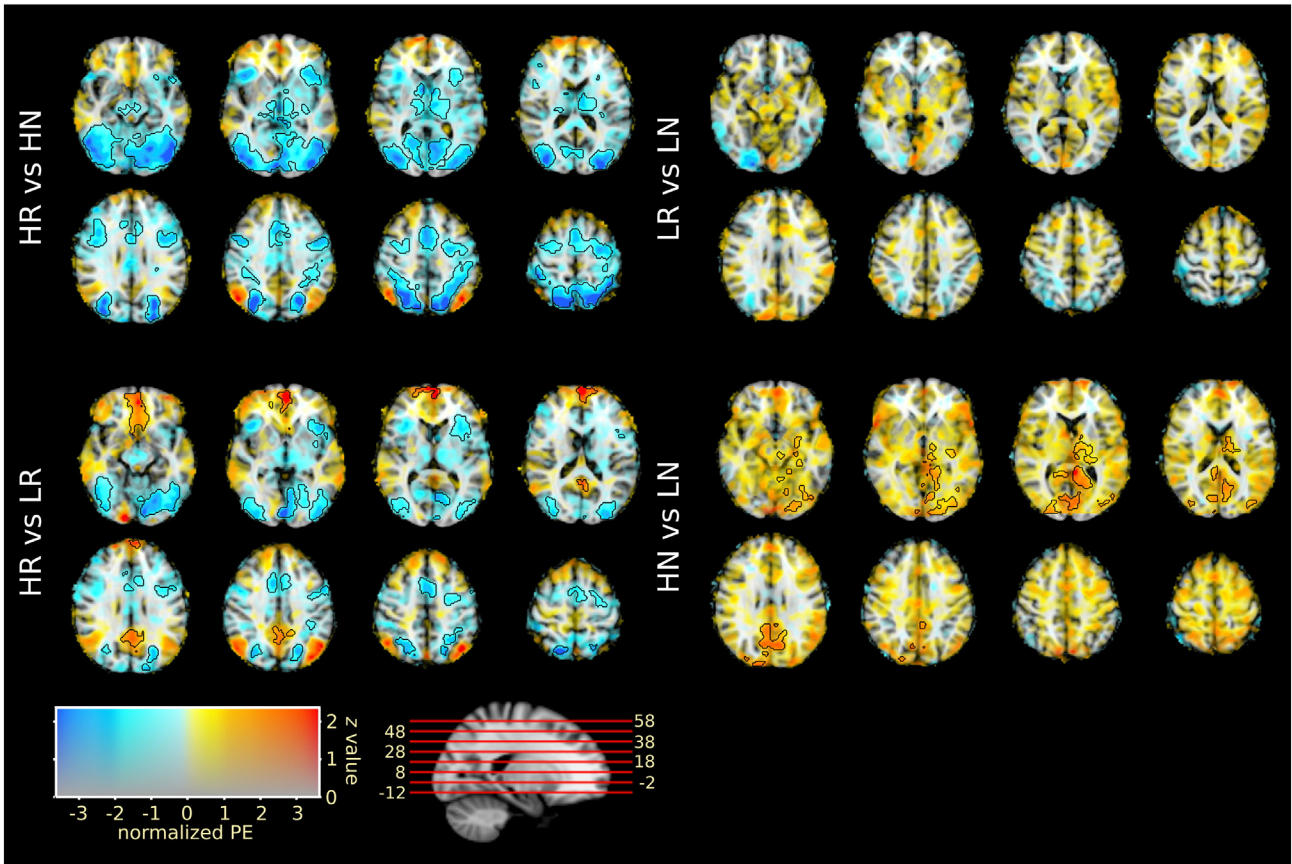


Fig. 4. FMRI activation maps for selected contrasts. Upper row: repeated versus novel displays associated with high reward (left: HR–HN) respectively low reward (right: LR–LN). Lower row: high reward versus low reward association for repeated displays (left: HR–LR) respectively novel displays (HN–LN). See Fig. 3 for legend. Left hemisphere is on the right.

3.2. Functional imaging data

The contrast of novel versus repeated display configurations yielded significantly increased activation in the lateral occipital cortex and along the intraparietal sulcus (Fig. 3; Table 1). The reverse contrast did not yield significant activation.

The contrast of high versus low reward – but please note that any effects cannot be due to reward itself, since reward was never delivered during the fMRI session – yielded increased activation in a cluster including the ventral frontomedial cortex extending into the paracingulate gyrus and the frontal pole. Further activation clusters were observed bilaterally in the lateral occipital cortex, reaching into

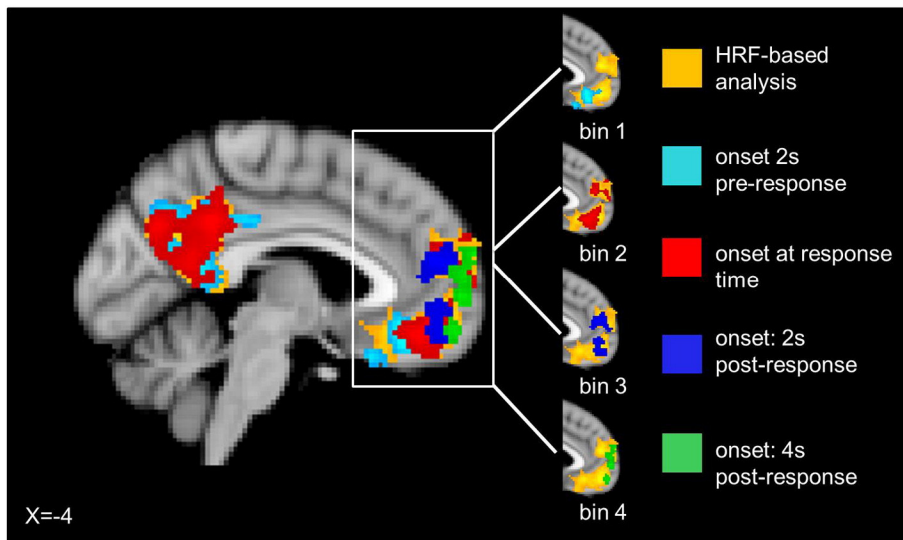


Fig. 5. FMRI activation maps for the FIR-analysis. The main effect of reward is shown as an overlay of subsequent activations. Colors indicate the onset time of the time bins that led to significant activations (see Section 2.3.2 for details). Left hemisphere is on the right.

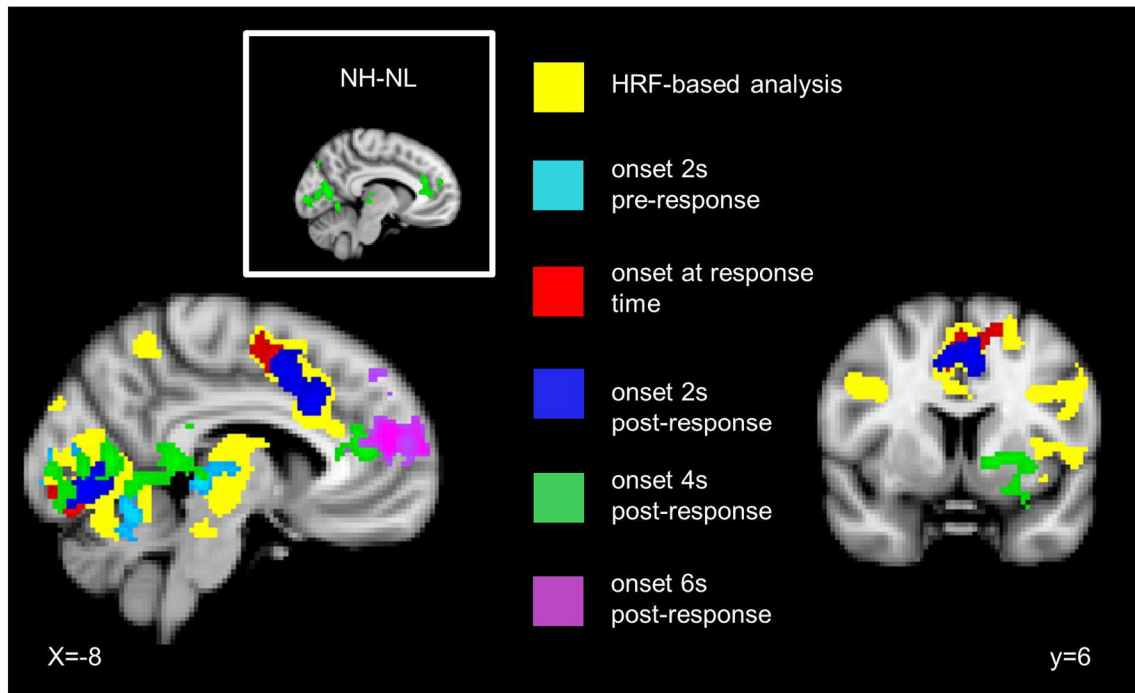


Fig. 6. fMRI activation maps for the FIR-analysis. The configuration \times reward interaction ((HR-LR)-(HN-LN)) is shown in the main images. Colors indicate the onset of the time bins that led to significant activations (see Section 2.3.2 for details). Within the box, the NH-NL contrast is shown. Significant activation in frontomedial cortex was only observed in the time bin with onset 4 s postresponse. The HR - LRcontrast did not yield significant activation. Left hemisphere is on the right.

the posterior angular gyrus (area PGp), and in the retrosplenial cortex, adjacent posterior cingulate cortex and precuneus. The inverse contrast did not yield any significant activation clusters.

The interaction of configuration \times reward ((HR-HN)-(LR-LN)) did not yield significant activation clusters. The reverse interaction contrast ((LR-LN)-(HR-HN)) yielded significant activation clusters throughout visual cortex, including early visual areas, lateral occipital cortex, occipital fusiform gyrus, and large parts of the dorsal and ventral attention networks including bilateral activation along the banks of the intraparietal sulcus and in superior parietal cortex, at the junction of the precentral and superior frontal sulci corresponding to the frontal eye field, in frontomedial cortex corresponding to the supplementary eye field and in the anterior insula and the inferior frontal gyrus. In addition, activation was observed in the anterior cingulate cortex and subcortically in the thalamus bilaterally.

The nature of this interaction is further illustrated by the contrasts HR versus HN and LR versus LN (Fig. 4). Significant activation differences were only observed of the type HN > HR.

Furthermore, we observed increased activation for HN compared with LN in occipital cortex, retrosplenial cortex and striatum.

The additional FIR analysis yielded results that were largely consistent with the model-based analysis. However, additional insights were obtained on the timing of activations. The main effect of configuration yielded activation within the areas activated in the HRF-based analysis. Most of the activation was observed within the two time bins from -2 s until 0 s before the response. For the main effect of reward, an early activation increase was obtained already in the time bin before the response in retrosplenial and orbitofrontal cortices (Fig. 5). While the activation remained largely stationary in the time bins from -2 until 0 s before the response in retrosplenial cortex, it spreads in the postresponse-time bins from orbitofrontal cortex to more dorsal – up to pregenual paracingulate cortex – and to more rostral portions of frontomedial cortex. In addition to the areas observed in the HRF-based analysis, a significant reward \times configuration interaction was observed that spreads from pregenual paracingulate cortex (4 s postresponse) to the more rostral frontomedial cortex (6 s

postresponse). The interaction was at least partly driven by increased activation for highly rewarded novel displays (Fig. 6). In addition, we observed an interaction missed by the HRF-based analysis in the left putamen, reaching into the vicinity of the nucleus accumbens (4 s postresponse).

4. Discussion

We investigated reward modulation of spatial contextual cueing of the target location in visual search. A training session was carried out to establish incidental learning of spatial target-distractor configurations in an inefficient visual search task. During training, specific displays were repeatedly presented either with high or low monetary reward. This training session was followed by an fMRI session, during which the learnt displays were presented without reward to investigate the neural mechanisms that are responsible for modulating search guidance via contextual cueing.

4.1. Reward modulation of contextual cueing

Behaviorally, we replicated a recent report that contextual cueing in visual search can be modulated by associating value with repeated displays in visual search (Tseng and Lleras, 2013). During the training session, participants earned either 1 or 10 Euro Cents for a correct target discrimination response in a visual search task. The reward was signaled by means of a post-cueing procedure after the search had ended. This procedure ensured that participants could not selectively attend with greater effort to high-value displays. We observed that only the highly rewarded displays showed a contextual cueing effect, with faster search times for repeated versus novel displays developing during the training session. While the configuration \times reward \times epoch interaction of the training data narrowly missed significance, the reward-modulated learning during the training session led to persistent contextual cueing only for highly reward displays that was observed several days after training in the test session conducted in the scanner. Note the similarity of the search time advantage in the last epoch of the training session and

the first epoch of the fMRI session, although no reward was given (or signaled) during the scanner session.

Thus, we could replicate the finding of Tseng and Lleras (2013) that reward can modulate contextual cueing of visual search. Instead of workload reduction, as in their study, we used monetary reward, thereby extending the types of reward that are capable of modulating contextual cueing. Tseng and Lleras observed faster development of the search time advantage for rewarded versus non-rewarded repeated displays. In the present experiment, repeated high-reward distractor configurations elicited a strong search advantage, whereas no such advantage was observed for low reward configurations. Importantly, no such search advantage was observed for target locations that were associated with high versus low reward in displays with novel distractor configurations. Thus, we could not confirm a report by Schlagbauer et al. (2014) who attributed their reward modulation effect to probabilistic learning of the target location. Instead, our search time data support the conjecture by Tseng and Lleras (2013) that reward improves the learning of repeated distractor configurations.

Unexpectedly, low-reward displays did not elicit contextual cueing at all. This is remarkable because we have observed a stable contextual cueing effect in experiments without reward manipulation using very similar stimuli and procedures as in the present experiment, both in behavioral lab and magnetic resonance scanner environments (Manginelli et al., 2012, 2013a, 2013b; Manginelli and Pollmann, 2009). The pattern of strong contextual cueing for repeated high reward displays and its absence for low reward displays may indicate that relative rather than absolute reward value may be the driving force behind reward modulation of contextual cueing. Specifically, we can conjecture that in the present context low reward, relative to high reward, acted against the occurrence of learning, unlike what happens in a context wherein reward is not involved, as in previous studies. A potential explanation might take into account that – in the absence of reward – some displays contribute more than others to the overall contextual cueing effect (Schlagbauer et al., 2012; Smyth and Shanks, 2008). To the extent that this reflects a limitation of resources to learn the repeated configurations, it may be that the reward cues in the present study led to a preferential allocation of these resources to the high reward displays.

Contextual cueing was originally described as a form of incidental and implicit learning (Chun and Jiang, 1998). The implicit nature of contextual cueing has subsequently been debated (Smyth and Shanks, 2008; Vadillo, Konstantinidis and Shanks, 2015). Most studies show some differences between subjects or between items in the degree of explicit recognition, if any. However, a general finding is the lack of a correlation between these measures of explicitness and the size of the search facilitation due to contextual cueing (Geyer et al., 2010, 2012; Preston and Gabrieli, 2008). In the present study, no evidence for explicit recognition of repeated displays was observed, although a sensitive test was used that avoided the low power of the simple repeated – novel recognition tests that were used in early contextual cueing studies (e.g. Chun and Jiang, 1998; Manginelli and Pollmann, 2009).

Thus, our work extends the literature on reward modulation of attention (see Chelazzi et al., 2013, for review) in that reward can be associated via incidental learning to spatial configurations. This association can subsequently be used to improve search for the target in learned displays. More generally, the results reported here add nicely to the growing evidence that rewards can alter the attentional priority of spatial information (e.g., see Chelazzi et al., 2014; Doallo et al., 2013; Hickey et al., 2014).

4.2. Neural structures involved in contextual search guidance

The main aim of the present experiment was to investigate how learned associations between reward and spatial target–distractor configurations change the neural processes involved in context-guided visual search. As observed previously (Manginelli et al., 2013a),

reduction of search times due to learning of repeated displays should lead to reduced activation in brain areas involved in visual search, particularly the dorsal network involved in attention shifts (Corbetta et al., 2008; Pollmann and von Cramon, 2000; Wager et al., 2004). This was confirmed in that large parts of occipital cortex and the cortex along the banks of the intraparietal sulcus were less activated during the more efficient search for repeated displays. Frontal components of the attention network, the frontal and supplementary eye-fields, showed no main effect of configuration, but an interaction pattern between configuration and reward, reflecting the selectively shorter search times in the repeated high-reward displays. This interaction pattern was observed pervasively in both the dorsal and ventral attention networks, from occipital cortex up along the banks of the intraparietal sulcus (largely overlapping with the main effect of configuration) and in the frontal and supplementary eye-fields as well as lateral occipital and inferior frontal/insular cortex. Subcortically, the same pattern was observed in the superior colliculi and the thalamus bilaterally.

Displays associated with high reward were expected to elicit increased activation relative to low-reward displays in brain areas involved in reward valuation. Reward value representations have been observed particularly in orbitofrontal neurons (Critchley and Rolls, 1996; Tremblay and Schultz, 1999). In humans, differential monetary reward value was represented in activation strength of ventral frontomedial cortex (Elliott et al., 2008). In keeping with these findings, we observed increased activation in ventral frontomedial cortex for repeated high versus low reward displays. In a meta-analysis of 142 imaging studies, this area was activated more by positive than negative reward (including monetary loss or, importantly, the lower of two possible reward values, as in the present study) and appeared to be more directly related to reward outcome than anticipation (Liu et al., 2011).

Ventral frontomedial cortex has also been found to support value-based decision-making (Gläscher et al., 2012). More specifically, ventromedial prefrontal cortex is particularly involved in value-based choices between previously learned stimulus–reward associations rather than during the learning process itself (Jocham et al., 2011). The results reported here are in agreement with this scenario because in the present study the effects of previously learned reward-associations were investigated.

Moreover, orbitofrontal cortex has been observed to represent relative rather than absolute reward value. This was initially found in monkey orbitofrontal cortex (Tremblay and Schultz, 1999) and later on in human ventral frontomedial cortex (Elliott et al., 2008). As noted above, the difference between a strong reduction of search times for high-reward repeated displays and no reduction at all for low-reward displays suggests that relative rather than absolute reward value drives the cueing effects in the present study.

The ventral striatum might also be expected to subserve reward enhancement of contextual cueing, as it was activated in a large range of reward-based learning studies (Daniel and Pollmann, 2014). However, in a recent study investigating distractive effects of previously rewarded items in visual search, no ventral striatal activation was observed (Anderson et al., 2014). This is in agreement with the absence of ventral striatal activation to previously rewarded configurations in the HRF-based analysis of the present study. We did, however, observe an activation of the putamen, reaching into the vicinity of the nucleus accumbens, in the model free FIR analysis. This activation was observed around 4 s after the response. That it was not observed in the stimulus locked analysis, but in the response locked FIR analysis may indicate that the nucleus accumbens is activated by response-related rather than stimulus-driven processes.

Furthermore, it is noteworthy that ventral striatal activation was observed in the HRF-based analysis when we contrasted novel high reward–low reward displays. In these displays, reward was only associated with target location. Thus, although we did not observe a

behavioral reward modulation for the novel displays, the increased activation in the striatum — as well as in the retrosplenial and occipital cortices — hints at a role of these areas in associating reward value with the target location. This system may thus support the reward modulation of target location probability learning observed by Schlagbauer et al. (2014). However, the question remains why the contrast of high reward versus low reward did not yield the same activation differences for repeated displays. There are at least two possible answers to this question. It may be that target location probability cueing occurs less (or is completely blocked) if repeated target–distractor configurations occur. The alternative account is that we may simply not observe increased activation for repeated high reward over low reward displays because of generally lower activation due the shorter search times for repeated high reward displays.

Another large cluster with increased activation for high versus low-reward displays was found in retrosplenial cortex and adjacent precuneus. The reward-related retrosplenial cluster overlapped with the configuration \times reward cluster. Retrosplenial cortex has dense fiber connections to the medial temporal lobe and the anterior thalamic nuclei. It is known to support spatial navigation, including spatial context memory (Miller et al., 2014), as well as memory retrieval for scenes (Summerfield et al., 2006). A reward modulation of saccade-related activity has been found in monkey area CGp in the posterior cingulate gyrus (McCoy et al., 2003). The present data show that this area is also important for the modulation of contextual cueing by reward.

The model-free analysis based on FIR functions yielded additional insights into the temporal development of activations. The bulk of the activations captured by the main effect of configurations was observed in the time bins from -2 s to 2 s around the response. Since the FIR analysis does not model the lag of the vascular response, this time course is consistent with an interpretation of these activations being generated by visual search processes. In contrast, the main effect of reward generated activations over a more extended time window, starting already during search, but continuing until 4 s postresponse. The activation spreads from orbitofrontal cortex to more dorsal and rostral portions of frontomedial cortex. Between 4–6 s postresponse, the reward response in the pregenual paracingulate and adjacent frontomedial cortex interacted with configuration in that highly rewarded novel (but not repeated) displays elicited increased activation. Again, please note that this activation is consistent with a neural event timing around the time of the response.

Thus, the association of reward value with a specific display, learned in the training session and retrieved in the fMRI session by the repeated presentation of the display, triggered a frontomedial activation increase that persisted for several seconds. The particularly strong signal increase for the highly rewarded novel displays emphasizes the need for further investigations of target location probability learning and its interaction with contextual cueing.

5. Conclusions

Our findings show that reward modulates incidental learning of contexts in visual search. Previously highly rewarded contexts are searched more efficiently even days later and in the absence of reward. This more efficient search is reflected by selectively less involvement of the dorsal attention network involved in overt and covert attention shifts. The incidentally learned reward association leads to increased activation in retrosplenial cortex, angular gyrus and ventromedial prefrontal cortex, areas that are known to be connected to posterior parahippocampal gyrus and to support context memory. Ventromedial prefrontal cortex is also well-known to support value-based decisions. Reward modulation of repeated contexts was particularly reflected by retrosplenial activation. This network, known to support intentional reward learning and spatial memory, also supports utilization of incidentally learned contextual reward cues in the service of optimal visual search.

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