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# Motivation and short-term memory in visual search: Attention's accelerator revisited

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## ABSTRACT

A cue indicating the possibility of cash reward will cause participants to perform memory-based visual search more efficiently. A recent study has suggested that this performance benefit might reflect the use of multiple memory systems: when needed, participants may maintain the to-be-remembered object in both long-term and short-term visual memory, with this redundancy benefitting target identification during search (Reinhart, McClenahan & Woodman, 2016). Here we test this compelling hypothesis. We had participants complete a memory-based visual search task involving a reward cue that either preceded presentation of the to-be-remembered target (pre-cue) or followed it (retro-cue). Following earlier work, we tracked memory representation using two components of the event-related potential (ERP): the contralateral delay activity (CDA), reflecting short-term visual memory, and the anterior P170, reflecting long-term storage. We additionally tracked attentional preparation and deployment in the contingent negative variation (CNV) and N2pc, respectively. Results show that only the reward pre-cue impacted our ERP indices of memory. However, both types of cue elicited a robust CNV, reflecting an influence on task preparation, both had equivalent impact on deployment of attention to the target, as indexed in the N2pc, and both had equivalent impact on visual search behavior. Reward prospect thus has an influence on memory-guided visual search, but this does not appear to be necessarily mediated by a change in the visual memory representations indexed by CDA. Our results demonstrate that the impact of motivation on search is not a simple product of improved memory for target templates.

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## 1. Introduction

Selective attention is sensitive to motivation. People will detect and discriminate targets with greater accuracy and

speed when they are motivated by the potential for reward (e.g., Hickey, Chelazzi, & Theeuwes, 2010; Hickey, Kaiser, & Peelen, 2015; Kiss, Driver, & Eimer, 2009; Kristjansson, Sigurjonsdottir, & Driver, 2010), and the association of

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reward to stimuli impacts how these objects are perceived and attended (e.g., Anderson, Laurent, & Yantis, 2011; Della Libera & Chelazzi, 2006, 2009; Krebs, Boehler, & Woldorff, 2010; Raymond & O'Brien, 2009; Sawaki, Luck, & Raymond, 2015). This influence is pervasive and robust (see Anderson, 2016; Chelazzi, Perlato, Santandrea, & Della Libera, 2013; Pessoa, 2009, for review), but very little is known about how it is instantiated. One possibility is that the effect of motivation on attention is mediated by memory. Research suggests that visual objects stored in short-term (Desimone & Duncan, 1995) and long-term memory (Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006; Summerfield, Rao, Garside, & Nobre, 2011) can act to bias processing in visual cortex such that attention is drawn to remembered items during search (see Olivers, Peters, Houtkamp, & Roelfsema, 2011 for review). Reward may leverage this mechanism, impacting attentional deployment indirectly through a boost to mnemonic target representations.

Recently, Reinhart and colleagues (Reinhart & Woodman, 2014; Reinhart, McClenahan, & Woodman, 2016) have reported several experiments designed to investigate this hypothesis in the context of visual search. This work has relied on the *memory-guided visual search paradigm*, where participants are given information about target-defining characteristics that they must remember in order to subsequently complete a visual search task (Carlisle, Arita, Pardo, & Woodman, 2011; Reinhart & Woodman, 2015; Woodman, Carlisle, & Reinhart, 2013). The paradigm has been used extensively in event-related potential (ERP) studies of memory's role in attentional control, largely because maintenance of target information can be tracked in an ERP component known as contralateral delay activity (CDA). This sustained and load-sensitive negativity appears contralateral to the target cue and has been compellingly linked to visual short-term memory (Ikkai, McCollough, & Vogel, 2010; Schneider, Mertes, & Wascher, 2015; Vogel & Machizawa, 2004). Results show that large cue-elicited CDA predicts fast responses during visual search, suggesting that a high-quality VWM representation of the target improves search performance. At the same time, the CDA reduces when target information is repeated several trials in a row, even as search performance improves (Carlisle et al., 2011; Woodman et al., 2013). With this decrease in CDA comes a corresponding change in an anterior ERP component – the P170 – that has been linked to the emergence of long-term memory representations (Voss, Schendan, & Paller, 2010; Woodman et al., 2013). This pattern has accordingly been interpreted as a 'handing off' of information from short-term visual memory to long-term store. Templates at either level of representation appear to effectively guide search, such that performance is maintained or even improved through the process (Reinhart & Woodman, 2014; Reinhart et al., 2016; Woodman et al., 2013).

Reinhart and colleagues (Reinhart & Woodman, 2014; Reinhart et al., 2016) have suggested that motivation's influence on attention might be largely implemented through the reinstatement of attentional templates in short-term memory after the initial hand-off of target representations has completed. By this, these redundant target representations in both short-term and long-term memory act as 'attention's accelerator', benefitting search by speeding

target identification. Support for this idea comes from experiments employing a modified version of the memory-based search task that includes a cue at the beginning of each trial. This infrequently informs participants that correct performance will result in a cash reward. In line with the broader literature, results showed a reduction of CDA amplitude as the target repeats. Strikingly, however, when a trial is preceded by the reward cue, the CDA re-emerges to pre-repetition strength and behavior and electrophysiology show a corresponding improvement in search performance.

The idea that motivational effects on search are mediated by visual short-term memory is compelling and consistent with extant results, but the relationship between CDA reinstatement and search performance is, of course, correlational, and as such there are valid alternative interpretations. One possibility is that cue-elicited variance in CDA does not cause the observed change in search performance, but that both happen to co-vary with other motivational factors. If this were the case, it might become evident if a reward-cue were to impact search without having any preceding influence on the CDA.

In the current experiment, we extend existing work in order to test the idea that motivation-elicited CDA reinstatement is directly responsible for subsequent improvements in visual search behavior. We did so by making a simple change to the experimental design employed by Reinhart and colleagues. In that earlier work, the reward cue preceded the encoding stage of the memory-guided visual search paradigm. That is, participants were told that reward was available, and then informed of the target-defining characteristic that must be remembered to complete the search task. In the current study, we added a reward retro-cue condition, where we first told participants of the target-defining characteristic and subsequently about the availability of reward.

We considered three possible outcomes for the experiment. One was that the reward retro-cue might have impact equivalent to that of the reward pre-cue. Both would accordingly reinstate the CDA and benefit search performance. This outcome would provide support for the notion that motivation acts on search through the reactivation of attentional templates in short-term memory. An alternative was that the retro-cue would have no impact, leaving both the CDA and search performance unchanged. This was the least welcome outcome, as it would provide limited perspective on the relationship between reward, memory, and attentional control. The final possibility was that both pre-cue and retro-cue might benefit search, but that the CDA would only be impacted by the pre-cue. This would challenge the proposed link between reinstatement of CDA and the impact of motivation on search performance.

## 2. Methods

### 2.1. Participants

Sixteen participants (9 female) provided written informed consent before taking part in the experiment (mean age = 23.06 years; SD = 2.08 years). All were right-handed and had normal or corrected-to-normal vision, and none reported

any neurological or psychiatric disorder. Participants were paid €6 per hour plus an additional sum based on behavioral performance during the experiment (see below). The study was approved by the local ethics committee of the University of Trento and was conducted in accordance with the Declaration of Helsinki.

## 2.2. Stimuli and procedure

The experiment was run on a 23.6-inch VIEWPixx LCD monitor (100 Hz) with a viewing distance of 60 cm. Stimulus presentation was controlled by an NVIDIA GeForce GTX 650 graphics accelerator and luminance values were set by means of a Minolta CS-100A meter. The display background was dark gray with a luminance of 10 cd/m<sup>2</sup> (RGB: 80, 80, 80) and the fixation dot (.29° visual angle diameter) remained present at the center of the screen throughout the experiment. Each trial involved three primary stimulus events: the target array, the reward cue, and the visual search array. Stimuli were presented using Opensesame (Mathot, Schreij, & Theeuwes, 2012).

The target array contained a red (RGB: 255, 102, 102) and a green (RGB: 80, 179, 80) Landolt-C stimulus presented to the left and right of fixation with a luminance of 25 cd/m<sup>2</sup> and a lateral offset of 1.43° visual angle (see Fig. 1). Each Landolt-C was composed of a colored outer circle (1.43° diameter), an inner circle in background color (.86° diameter), and a small gap in background color (.38°). The gap could appear on 8 positions corresponding to Landolt-C orientations of 0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°. Participants were instructed to memorize the orientation of either the green or red C with target color counterbalanced across participants. Orientation always differed between the two objects in the target array.

The position and orientation of the memory target was repeated for sets of 5 trials. After the last trial of each set, a new target position was randomly determined and target orientation was selected from the 7 orientations not employed in the preceding set. In half of the trials, the target display was preceded by a reward pre-cue, and in all trials the target display was followed by a reward retro-cue. This meant that the retro-cue was redundant in conditions where the pre-cue was also displayed, and this design feature was adopted to equate sensory processing in the delay interval across pre-cue and retro-cue conditions. Reward cues were presented as a change of the black fixation dot to light blue (RGB: 0, 178, 178) or yellow (RGB: 163, 163, 0; 25 cd/m<sup>2</sup> in both cases), with the assignment of cue colors to reward magnitude counterbalanced across participants. In each of the first 4 trials in a set of 5, the chance of a high-magnitude reward cue was about 5% (1094 low-reward trials vs 58 high-reward trials). These were employed to ensure participants remained on task. In the 5th target presentation trials, the probability of the high-magnitude reward cue increased to 50% (i.e., 144 high-reward and 144 low-reward trials).

The visual search array followed the offset of the retro-cue and was composed of 12 Landolt-C stimuli with the same size as those in the target display. The Cs were arranged in a circle with a radius of 4.15° visual angle. One was presented in target color, another in distractor color, and the rest were gray (RGB:

158, 158, 158; 25 cd/m<sup>2</sup>). In 50% of trials, the search target appeared at one of two positions on the vertical meridian of the display with the distractor at one of the lateral positions. In the remaining trials, the target was presented at a lateral position and the distractor was presented on the vertical. Participants searched for the Landolt-C presented in target color and compared its gap orientation to the memorized target. The orientation of the memorized Landolt-C and the relevant Landolt-C in the search array was the same in 50% of trials. They responded by pressing one key on a standard computer keyboard when the search target orientation matched the memory target orientation and another key when this was not the case ('s' and 'l', counterbalanced across participants). Task instructions emphasized both speed and accuracy.

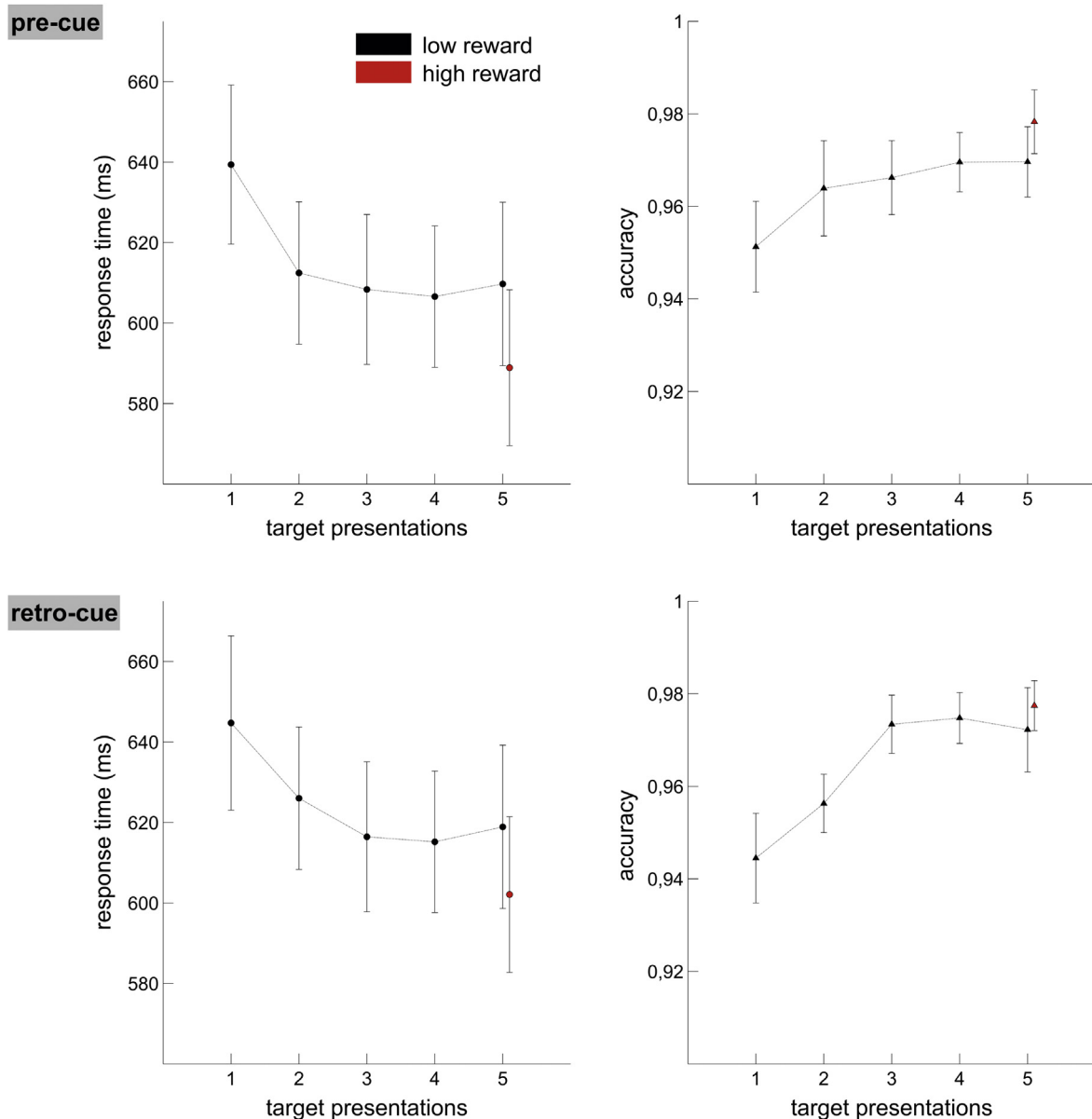
Reward feedback ('+50', '+1', or 'xx' for errors) was overlaid on the visual search display above fixation 200 msec after response. It was possible to earn up to 11,338 points through the course of the experiment. Participants received a basic payment of 18 € for participation, plus an additional 1 € for each 1000 points earned in the course of the experiment (rounded up to a full euro value). On average, participants scored 11,075 points (SD = 254.6) and they consequently received a financial bonus of 11–12 € for their performance. The experiment consisted of 8 blocks of 180 trials with a 2-min break between each block. During the break the total number of points earned to that point in the experiment was centrally displayed.

## 2.3. EEG recording and ERP preprocessing

EEG was recorded from 62 Ag/AgCl electrodes arranged according to the 10/20 system. Two additional electrodes were placed on the left and right mastoids and all impedances were kept below 10 K $\Omega$  during recording. EEG was amplified with a BrainAmp amplifier (BrainProducts GmbH, Munich, Germany) using an online reference of Cz and sampled at 1 kHz. During recording a .016 Hz high-pass filter was applied.

Data were analyzed with the EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) toolboxes for the MATLAB® environment. Data were filtered offline with a high-pass FIR kernel at .25 Hz (13,801 points; transition band width .2391 Hz; –6 dB at .13 Hz) and a low-pass FIR kernel at 20 Hz (661 points; transition band width 5 Hz; –6 dB at 22.5 Hz) and subsequently re-referenced to the average signal recorded from both mastoid electrodes. EEG was epoched into intervals beginning 1000 msec before onset of the target array and ending 3000 msec after. Independent component analysis (ICA; Bell & Sejnowski, 1995) was calculated from a subset of the epoched data (every third trial) and components corresponding to eye blinks and generic data discontinuities were identified using the ADJUST plugin to EEGLAB (Mognon, Jovicich, Bruzzone, & Buiatti, 2010). Epochs that continued to show artifacts after this process were subsequently detected and removed using EEGLAB's automated epoch rejection parameters. Conditional ERPs were calculated based only on trials with correct performance, and in all cases were baseline corrected on the 200 msec interval preceding onset of the pre-cue (i.e., the interval from 600 to 400 msec prior to onset of the target array in conditions where the pre-cue was absent).





**Fig. 2 – Behavioral results.** Response times (msec) decreased with the number of target repetitions in both the pre-cue and the retro-cue condition. Additionally, high-reward cues were associated with faster responses in the 5th target presentation trials. Response accuracy increased with the number of target repetition in both cue conditions and was also increased after high-compared to low-reward cues in the 5th target presentation trials. Bars depict the standard error of the mean (SE).

### 3.2. ERP data

#### 3.2.1. Target-array N2pc and CDA

We began ERP analysis by examining waveforms elicited by the to-be-remembered target array. We extracted contralateral and ipsilateral signals in reference to the position of the memory target, subsequently subtracting the ipsilateral from the contralateral ERP to generate a difference wave. N2pc (Luck & Hillyard, 1994a, 1994b) was measured at PO7/8, where it was maximal across conditions, as the mean amplitude of the difference from 251 to 261 msec post-stimulus. This interval corresponded to the middle of the N2pc as observed across experimental conditions. To identify this point, we

found the time at which the PO7/8 difference wave had a negative area of 50%. Because the negative voltage difference extended outside the range of the N2pc (i.e., became the CDA), calculation of negative area was truncated at 300 msec post-stimulus.

To test the impact of target repetition on N2pc, we conducted an ANOVA with within-subject factors for *repetition* (target presentation 1–5) and *cue-type* (reward pre-cue vs reward retro-cue). The target-array N2pc did not reliably vary as a function of target repetition,  $F(4,60) = 1.759$ ,  $\epsilon = .685$ ,  $P = .174$ ,  $\eta^2_p = .105$ , or across cue conditions,  $F(1,15) = .129$ ,  $P = .725$ ,  $\eta^2_p = .009$ , and these factors did not interact,  $F(4,60) = 2.2$ ,  $\epsilon = .663$ ,  $P = .11$ ,  $\eta^2_p = .128$ . A second ANOVA was



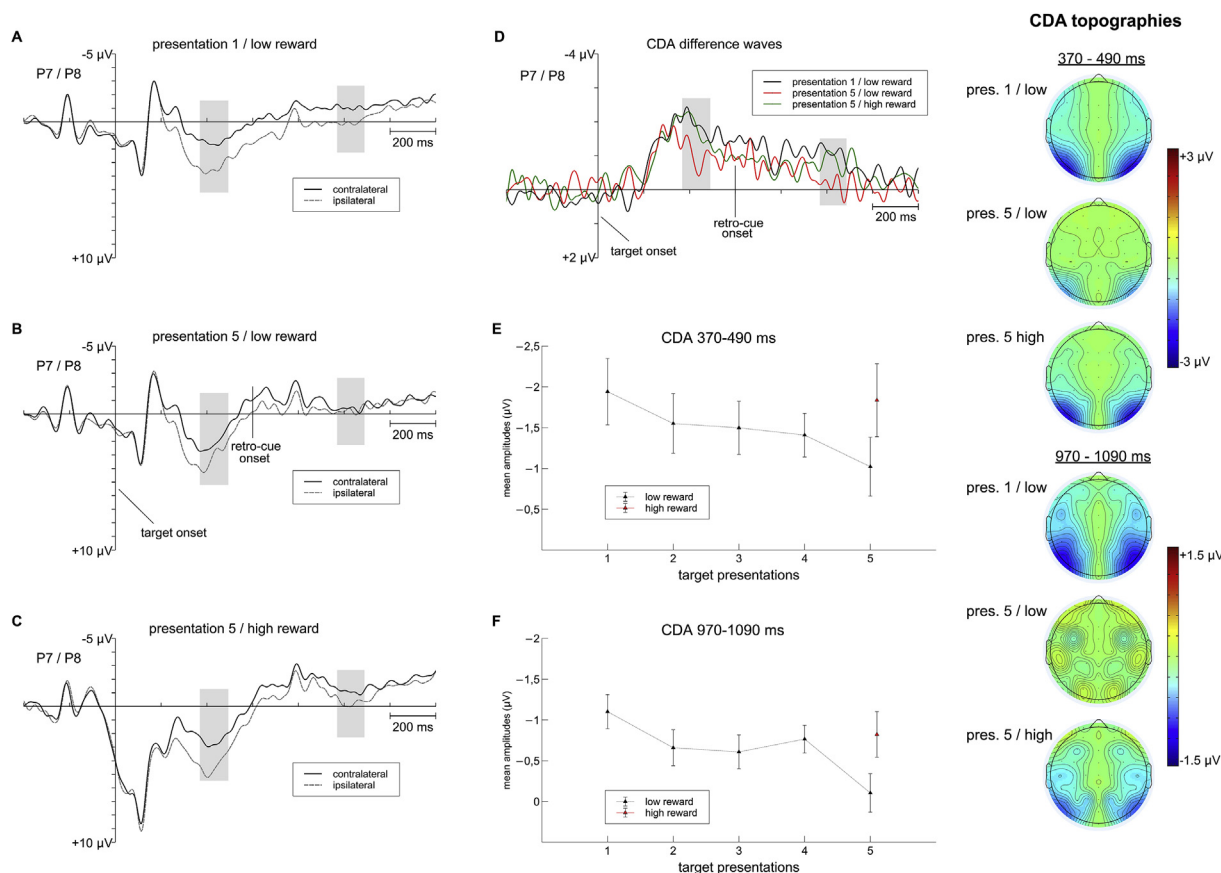
conducted to examine the impact of the reward-magnitude indicated by the pre-cue on the 5th target presentation and this had a within-subject factor for *reward pre-cue magnitude* (low vs high). No effect emerged from this analysis,  $F < 1$ .

The CDA elicited by the target display was examined both before and after the presentation of the retro-cue (see Figs. 3 and 4). The CDA was maximal at P7/8 across conditions, and early CDA was measured at these electrode sites as the mean amplitude of the difference wave 370–490 msec after onset of the target array. This interval corresponded to the 120 msec time window centered at the peak of the overall CDA effect in the grand average. The peak was measured as the time point in the 300–600 msec post-stimulus interval when the negative area under the grand average difference curve at P7/8 reached 50%. Early CDA was analyzed with an ANOVA including within-subject factors for *repetition* and *cue-type*. The early CDA decreased with the number of target repetitions,  $F(4,60) = 4.052$ ,  $\epsilon = .551$ ,  $P = .023$ ,  $\eta^2_p = .213$ , but did not differ between the cue conditions,  $F(1,15) = 1.681$ ,  $P = .214$ ,  $\eta^2_p = .101$ , and these factors did not interact,  $F < 1$ .

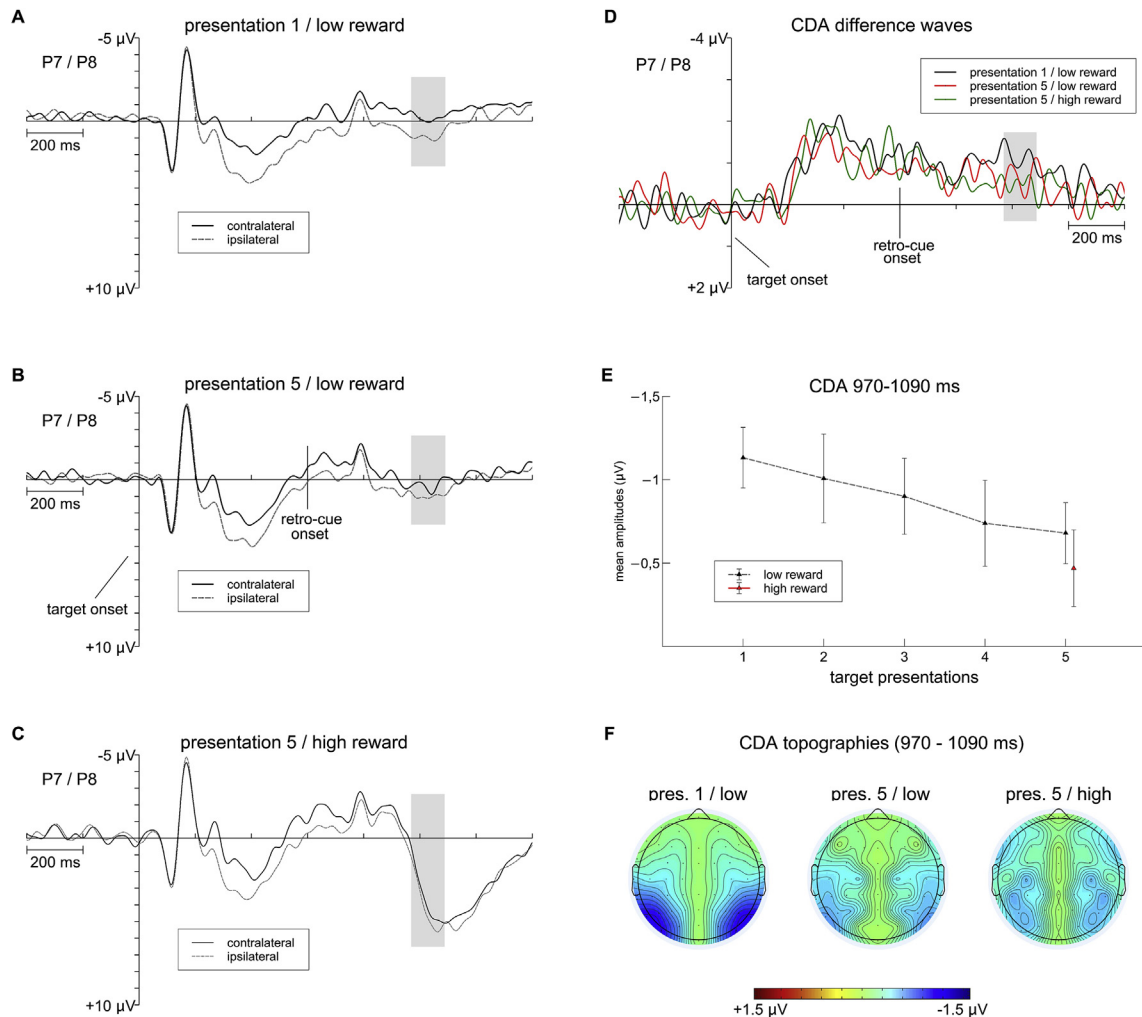
As in analysis of the N2pc, a subsequent ANOVA examined the impact of the reward pre-cue on the 5th target presentation and had a within-subject factor for *reward pre-cue*

*magnitude* (low vs high). Results showed that the early CDA was larger following a high-magnitude reward pre-cue,  $F(1,15) = 5.718$ ,  $P = .03$ ,  $\eta^2_p = .276$ . This replicates results from Reinhart et al. (2016) and Reinhart and Woodman (2014).

Based on the time window used for the analyses of early CDA, late CDA was measured at P7/8 from 970 to 1090 msec after onset of the target array (i.e., 370–490 msec after the onset of the retro-cue). ANOVA analysis of late CDA paralleled analysis of the early CDA: one ANOVA examined all trials and had factors for *repetition* and *cue-type*, and a second ANOVA was limited to the 5th target presentation and had within-subject factors for *reward* and *cue-type*. As was the case for early CDA, the late CDA decreased with the number of target repetitions,  $F(4,60) = 5.182$ ,  $\epsilon = .583$ ,  $P = .008$ ,  $\eta^2_p = .257$ , but did not differ reliably between the cue conditions,  $F(1,15) = 3.587$ ,  $P = .077$ ,  $\eta^2_p = .193$ , and these factors did not interact,  $F(4,60) = 1.186$ ,  $\epsilon = .747$ ,  $P = .326$ ,  $\eta^2_p = .073$ . In the 5th target repetition trials, late CDA did not differ as a function of *cue-type*,  $F(1,15) = .291$ ,  $P = .6$ ,  $\eta^2_p = .019$ , and revealed no main effect of *reward*,  $F(1,15) = 2.219$ ,  $P = .157$ ,  $\eta^2_p = .129$ . However, these factors importantly interacted,  $F(1,15) = 5.149$ ,  $P = .038$ ,  $\eta^2_p = .256$ . Follow-up analysis showed that late CDA increased when a pre-cue indicated the potential for high-magnitude



**Fig. 3 – Contralateral delay activity (CDA) in the pre-cue condition.** (A–C) depict the contralateral and ipsilateral portions of posterior ERPs for the 1st target presentation trials and the 5th target presentation trials (high- vs low-reward). (D) depicts the difference functions (contralateral minus ipsilateral) for the conditions shown in (A–C). (E, F) Show the decrease of the CDA effect with the number of target repetitions and the increased CDA as a function of high-reward in both the early (E) and late (F) CDA time window. Topographies of these CDA effects are depicted in the right corner of the figure. Bars depict the standard error of the mean (SE).



**Fig. 4 – Contralateral delay activity (CDA) in the retro-cue condition. (A–C)** Depict the contralateral and ipsilateral portions of posterior ERPs for the 1st target presentation and the 5th target presentation trials (high- vs low-reward). **(D)** Shows the difference functions (contralateral minus ipsilateral) for the conditions shown in (A–C). **(E)** Indicates the course of the CDA effect with the increasing number of target repetitions and the reward effect in the 5th target presentation trials for the late CDA time window. Respective topographies of the CDA effects are given in **(F)**. Bars depict the standard error of the mean (SE).

reward relative to low-magnitude reward,  $F(1,15) = 5.593$ ,  $P = .032$ ,  $\eta^2_p = .272$ , but was unaffected when this information was conveyed by a retro-cue,  $F < 1$ .

The reward pre-cue thus caused the CDA to return to pre-repetition amplitude, but the retro-cue did not.

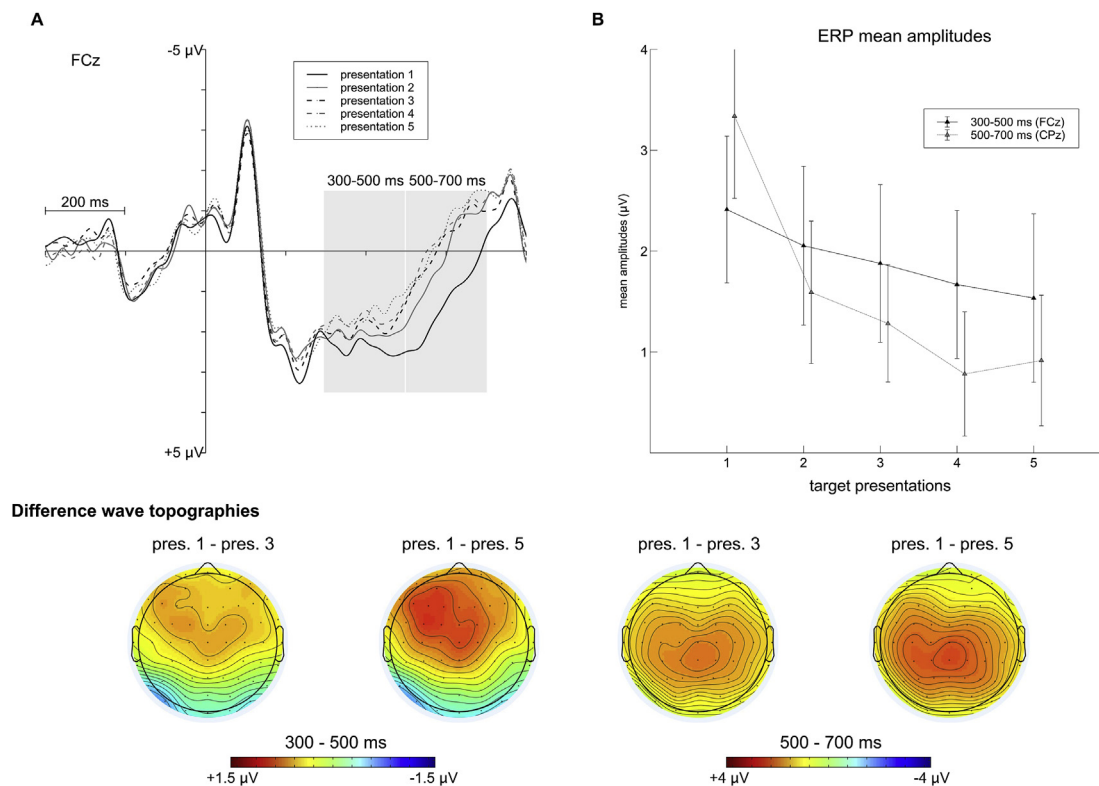
### 3.2.2. Target-array P170 and P3

Prior studies of the P170 suggest that the component is long-lasting and characterized by a topographic shift over time from anterior to posterior (e.g., Reinhardt & Woodman, 2014, Figure 6). With this in mind we measured ‘early P170’ from 170 to 240 msec following target-array onset at FCz and ‘late P170’ at the same location but in a time window from 300 to 500 msec. Note that for the sake of consistency with prior literature investigating memory-guided visual search we refer to this activity as ‘late P170’, but this component could very well be relabeled N400.

Target repetition had a still later effect on the P3 that, to our knowledge, has not been examined in prior work on short-term to long-term memory hand-off. We examined this effect at electrode location CPz in the 500–700 msec interval. Early P170, late P170, and P3 were each analyzed with separate ANOVAs with factors for repetition and cue-type.

Early P170 appears to vary as a function of target repetition (Fig. 5), but this effect was not reliable in our sample,  $F(4,60) = 1.317$ ,  $\epsilon = .574$ ,  $P = .283$ ,  $\eta^2_p = .081$ , all other  $F$ s  $< 1$ . In contrast, a negative shift in the late P170 reliably increased as a function of target repetition,  $F(4,60) = 3.638$ ,  $\epsilon = .806$ ,  $P = .017$ ,  $\eta^2_p = .195$ , all other  $F$ s  $< 1$ . A similar shift in the P3 was reliable,  $F(4,60) = 20.658$ ,  $\epsilon = .541$ ,  $P < .001$ ,  $\eta^2_p = .579$ , but cue-type had no effect on this component,  $F < 1$ , and these factors did not interact  $F(4,60) = 1.278$ ,  $\epsilon = .7$ ,  $P = .294$ ,  $\eta^2_p = .078$ .

This broadly replicates prior studies of the hand-off of target templates from short-term to long-term memory, with



**Fig. 5 – P170 and positive slow wave. (A)** Depicts the sustained ERP effect related to the target repetitions starting after P170 component at channel FCz. The course of this effect is shown in **(B)**, both for the 300–500 msec (at FCz) and the 500–700 msec (at CPz) time window. The corresponding topographies are presented on the bottom of the figure. Bars depict the standard error of the mean (SE).

a negative shift in anterior positive components emerging as the target is repeated.

### 3.2.3. Target-array CNV

Prior to the onset of the search display a prominent contingent negative variation (CNV) component emerged over frontal midline electrode locations (Fig. 6). This is consistent with the CNV's known sensitivity to motivational effects and its role in the investment of attentional resources on an upcoming task (e.g., Silvetti, Nunez Castellar, Roger, & Verguts, 2014).

In the retro-cue condition, the relatively rare high-magnitude reward cue elicited a large P3 that overlapped with early CNV. To minimize the potential for confound, we limited analysis of the CNV to 1400–1600 msec after target display onset for both the pre-cue and retro-cue conditions. At this latency the retro-cue-elicited P3 was substantially diminished at the frontal electrode sites where CNV emerged (see Fig. 6).

CNV in the pre-cue and retro-cue conditions were separately analyzed with ANOVAs with within-subject factors for reward. To keep trial numbers comparable between the high- and low-reward conditions, only 5th target presentations were examined. The CNV was larger when either the pre-cue,  $F(1,15) = 24.509$ ,  $P < .001$ ,  $\eta^2_p = .62$ , or retro-cue indicated the potential for high-magnitude reward,  $F(1,15) = 7.491$ ,  $P = .015$ ,  $\eta^2_p = .333$ . An additional ANOVA with factors for both reward and cue-type failed to identify a difference in the effect of reward between the cue conditions, as reflected in a not-

significant interaction between the factors,  $F(1,15) = 1.028$ ,  $P = .327$ ,  $\eta^2_p = .064$ .

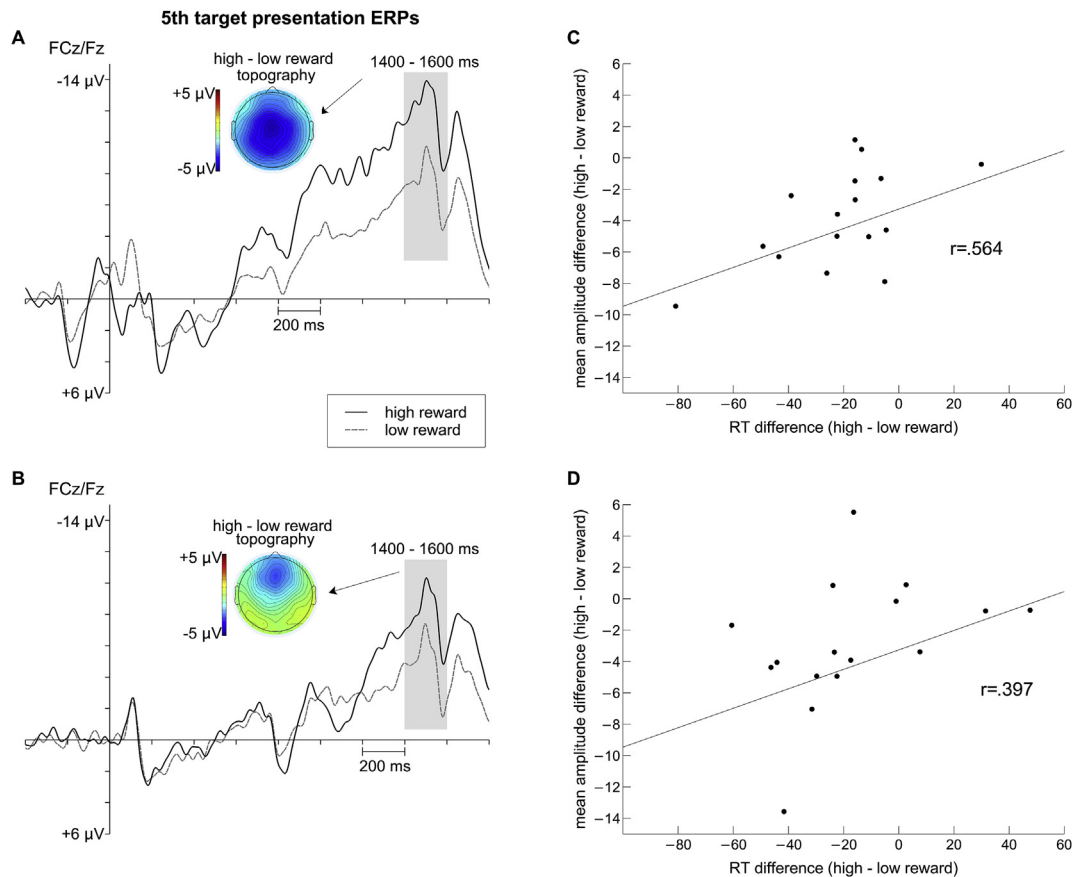
We approached this analysis with the expectation that CNV variance would reflect engagement and preparation for the search task, and thus that participants with greater reward-elicited CNV variance might also show improved visual search performance. To test this, we calculated the impact of reward prospect on the CNV and correlated this with the impact of reward prospect on search RT. Correlations were statistically assessed using permutation tests employing 10,000 combinations, an approach which reduces sensitivity to outlier values. As illustrated in Fig. 6C and D, the effect of a reward cue on the CNV was positively correlated to the effect of a reward cue on RTs, both for pre-cues,  $r = .563$ ,  $P = .017$ , and retro-cues,  $r = .397$ ,  $P = .002$ .

Preparatory and attentional mechanisms reflected in the CNV thus appear involved in the instantiation of motivational effect on visual search and are sensitive to reward-prospect indicated by both pre-cues and retro-cues in this design.

### 3.2.4. Search-array N2pc/SPCN

Calculation of search-array N2pc was similar to calculation of target-array N2pc: we extracted contralateral and ipsilateral ERPs at electrodes PO7/8 – now in reference to the position of search target – and subtracted the ipsilateral from the contralateral ERP to generate a difference wave. To equate trial counts across conditions we only examined 5th target presentation trials. Mean N2pc amplitude was calculated from

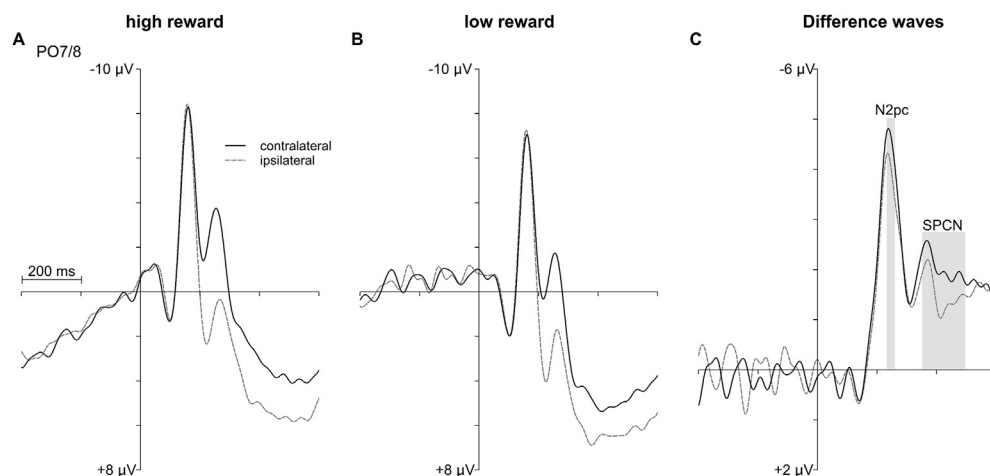




**Fig. 6 – Reward effect on contingent negative variation (CNV).** The sustained frontal negativity for high-compared to low-reward trials is indicated in (A) for the pre-cue condition and in (B) for the retro-cue condition. The respective correlations between the reward effect on CNVs and the effect of reward on search response times are depicted in (C) for the pre-cue and (D) for the retro-cue.

240 to 250 msec. As in analysis of the target array, this corresponded to the middle of the N2pc as observed across experimental conditions, defined as the time when the PO7/8 difference wave had negative area of 50%, with analysis truncated at 300 msec post-stimulus (see Fig. 7).

An ANOVA with within-participant factors for cue-type (pre- vs retro-cue) and reward (high- vs low-reward) revealed that the search-array N2pc was larger following cues indicating the potential for high-magnitude reward,  $F(1,15) = 6.08$ ,  $P = .026$ ,  $\eta^2_p = .288$ , and varied marginally as a function of cue-



**Fig. 7 – Search display N2pc and SPCN.** An increased contralateral negativity is shown for the high-reward (A) and the low-reward condition (B), both in the time window of N2pc and later SPCN elicited after search display onset. The respective difference waves (C) show that these effects were increased following a high-reward compared to a low-reward cue.

type,  $F(1,15) = 3.918$ ,  $P = .066$ ,  $\eta^2_p = .207$ , but that these factors did not interact,  $F(1,15) = .191$ ,  $P = .668$ ,  $\eta^2_p = .013$ .

Our results showed evidence of subsequent lateral ERP activity corresponding to the sustained posterior contralateral negativity (SPCN; Jolicoeur, Brisson, & Robitaille, 2008). Mean SPCN amplitude was calculated at PO7/8 from 350 to 500 msec after search display onset (Kiss, Van Velzen, & Eimer, 2008). As was the case for the earlier N2pc, the SPCN was larger after high-magnitude reward cues,  $F(1,15) = 7.699$ ,  $P = .014$ ,  $\eta^2_p = .339$ , varied marginally as a function of cue-type,  $F(1,15) = 4.358$ ,  $P = .054$ ,  $\eta^2_p = .225$ , but these factors did not interact,  $F(1,15) = .007$ ,  $P = .936$ ,  $\eta^2_p = .0004$ .

We conducted an additional analysis in order to directly contrast the effect of pre-cues and retro-cues on the CDA with the effect of pre-cues and retro-cues on lateral attention-related activity expressed in N2pc and SPCN. To this end, we first calculated the mean effect of reward on the combined N2pc and SPCN for each of the pre-cue and retro-cue conditions, before subsequently measuring the mean effect of reward on the late CDA for each of the pre-cue and retro-cue conditions. An ANOVA with factors for *reward*, *cue-type*, and *component* (N2pc/SPCN vs CDA) revealed a main effect of reward,  $F(1,15) = 10.668$ ,  $P = .005$ ,  $\eta^2_p = .416$ , and, critically, a 3-way interaction,  $F(1,15) = 4.911$ ,  $P = .042$ ,  $\eta^2_p = .247$ . This demonstrates that the interaction between *reward* and *cue-type* observed in analysis of late CDA is reliably different than results observed in analysis of target-array N2pc/SPCN, where no such interaction appears.

#### 4. Discussion

Motivation, such as that induced by the prospect of reward, has a benefit on visual search, but the neural mechanisms that underlie this effect are not well characterized. One possibility is that motivation boosts the representation of target templates in memory. Stronger mnemonic representations of targets may help search performance by guiding attention to likely targets or by speeding the process of target identification.

Reinhart and colleagues (Reinhart & Woodman, 2014; Reinhart et al., 2016) recently built from this general idea to develop a compelling, specific, and testable hypothesis linking motivation to search via its impact on memory. Work from these authors and others has shown that target templates stored in short-term visual memory are ‘handed off’ to long-term memory when target characteristics are repeated (Carlisle et al., 2011; Reinhart et al., 2016; Woodman et al., 2013). Because representations in either long-term or short-term memory can guide search, performance is sustained throughout this process. Reinhart and colleagues’ proposal is that once target templates have been transferred to long-term memory in this way, task motivation can cause their reinstatement in short-term memory. As a result, targets are redundantly represented in both long-term and short-term memory and this double-barreled attentional template benefits performance during search by speeding target identification.

In support of this proposal, these authors point to results from a series of ERP experiments showing that reward cues

preceding the encoding of target information cause a re-emergence of CDA. This is followed by efficient search, as expressed both in overt behavior and electrophysiology. This suggests a causative relationship, but the alternative is that these two effects independently co-vary with a third factor. This would become evident if a situation could be created where the reward-cue impacts search performance without having a corresponding effect on CDA.

Here we show such a disconnect between CDA re-emergence and search performance. Reinhart and colleagues (Reinhart & Woodman, 2014; Reinhart et al., 2016) cued reward-magnitude at the beginning of each trial before participants were asked to remember target characteristics. We added to this design a reward retro-cue condition where participants were first asked to remember target characteristics before being subsequently told about the opportunity for high-magnitude reward. In our reward pre-cue condition, we replicate earlier results: when the CDA was diminished following target repetition, a cue indicating potential for high-magnitude reward caused it to re-emerge to pre-repetition strength and participants showed improved search performance. But in our reward retro-cue condition we see the same performance benefit for high-reward cues in the absence of any reward effect on the CDA.

Pre-cues did have an overall benefit on search performance, leading to faster RTs, lower error rates, and a marginally-significant increase in search-elicited N2pc. But, critically, these effects did not reliably vary as a function of the magnitude of reward indicated by the cue. These null interactions are, of course, difficult to interpret. There is the possibility that reward magnitude had an impact on the cueing effect, but our experiment lacked the statistical power to detect it. We did not observe even a remote trend toward such an interaction in analysis of RT, accuracy, or search-array N2pc ( $F = .238$ ,  $F = .181$ , and  $F = .191$ , respectively), but the possibility remains. An alternative is that the pre-cue rather acted as a temporal cue, warning participants of the impending presentation of the target array. This allowed participants to better process the target, regardless of the semantic information conveyed by the warning signal.

More convincing than these null findings is our active demonstration of the independence of reward effects on the CDA and search N2pc/SPCN. In a 3-factor analysis, we find that the representation of target templates in short-term memory, as expressed in CDA, was sensitive to reward prospect only when this was indicated by a pre-cue, whereas the subsequent attentional selection of the search target, as expressed in N2pc/SPCN, improved when either a pre-cue or a retro-cue indicated the potential for high-magnitude reward. This pattern would be impossible if variance in the short-term mnemonic representation of target templates was the primary vehicle through which motivation impacted attentional selection of the target.

In approaching this study, we were interested in the possibility that CDA would show sensitivity to motivational information provided after the to-be-remembered stimulus had already been encoded. It is unclear in the literature if visual short-term memory is sensitive to cognitive influences like motivation or reward association throughout maintenance, or if the quality of mnemonic representation is defined solely by

the quality of initial stimulus encoding (Infanti, Hickey, & Turatto, 2015). Our reward retro-cue had no influence on the CDA, which suggests that a stimulus representation, once encoded, cannot be subsequently 'boosted' in visual memory by an increase in task motivation. However, our results also show that such a retro-cue had an impact on search performance that was statistically indistinguishable from the effect of an equivalent pre-cue. Thus the current results make it quite clear that reward's impact on subsequent search performance is not contingent on its ability to impact the CDA.

Furthermore, results show that both high-reward pre-cues and high-reward retro-cues caused a broad and long-lasting CNV amplitude increase. The CNV has been traditionally linked to task-specific motor preparation, with generators in primary and supplementary motor cortex (e.g., Leuthold & Jentzsch, 2001; Walter, Cooper, Aldridge, McCallum, & Winter, 1964), but in recent years has come to be considered a broader reflection of preparation across the cognitive system (see Brunia, van Boxtel, & Böcker, 2012, for review). We not only found that the CNV increased in response to both high-reward pre-cues and retro-cues, but that the magnitude of this effect predicted how high-reward cues impacted search performance. Those participants who showed a strong increase in CNV in response to cues indicating the potential for high-magnitude reward thus also showed a strong benefit of the cue on visual search performance, and this correlation was of similar magnitude regardless of whether analysis focused on the effect of pre-cues or retro-cues. This means that the CNV was a surprisingly accurate predictor of motivational effects on visual search in this experiment, in contrast to the CDA, which was not. This is interesting in the context of the current study because medial-frontal areas were shown to contribute to the CNV effect, including anterior cingulate cortex (ACC) (Nagai et al., 2004). Alongside other prefrontal cortical areas, the ACC is a primary target site for dopaminergic signals from the striatum carrying information about reward expectancy and availability (Haber, Fudge, & McFarland, 2000; Williams & Goldman-Rakic, 1993), and existing work has shown modulation of medial-frontal CNV activity related to reward expectation (Plichta et al., 2013; Silvetti et al., 2014). This raises the possibility that motivation's impact on visual search may involve the preparatory release of cognitive resources via ACC.

This does not imply that visual short-term memory never mediates motivational effects on attention. Reward prospect and outcome have pervasive influence on neural systems, and it seems reasonable visual short-term memory will be one of the many systems impacted. But existing observations of correlation between CDA and visual search performance do not necessarily demonstrate this principle. There is the ripe opportunity for further research to investigate if, when and how motivation leverages visual short-term memory for the optimization of attentional selection.

To sum, in a set of recent studies Reinhart and colleagues (Reinhart & Woodman, 2014; Reinhart et al., 2016) suggested that motivational effects in visual search are mediated by changes to the representation of target templates in visual short-term memory. The idea is that when these representations are redundantly activated in long-term memory and visual short-term memory – as reflect in amplitude of the P170

and CDA ERP components – visual search becomes better. But here we show that an increase in CDA amplitude is not a necessary precondition to improved search performance. This challenges the idea that visual short-term memory plays a core role in instantiating motivational effects on visual search.

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