

COGNITIVE NEUROSCIENCE

R

M G^{1,2,3} F^{1,4} Y^{1,4} and S L^{1,2,3}

¹Department of Psychology and Beijing Key Laboratory of Behavior and Mental Health, Peking University, 5 Yiheyuan Road, Haidian, Beijing 10087, China

²PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing, China

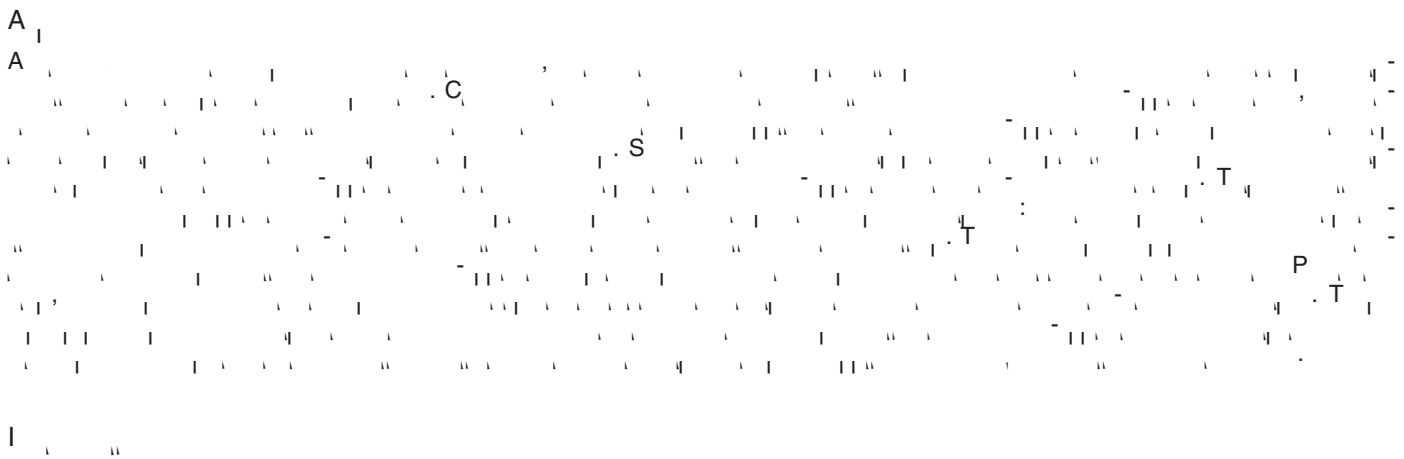
³Key Laboratory of Machine Perception (Ministry of Education), Peking University, Beijing, China

⁴Department of Psychological and Brain Sciences, Johns Hopkins University, Baltimore, MD, USA

Keywords: active suppression, priority map, reward salience, working memory

Edited by John Foxe

Received 23 September 2015, revised 31 December 2015, accepted 12 January 2016



Visual attention selects information based on a spatial map where the priority of attentional allocation is determined according to the competitive interactions between bottom-up and top-down mechanisms (Theeuwes, 1991; Itti & Koch, 2001; Corbetta & Shulman, 2002; Fecteau & Munoz, 2006; Bisler & Goldberg, 2010). This priority map weights the information in different locations and guides attention toward the peak of the map. It has been shown that a physically salient item has privileged access to attentional selection (Theeuwes, 1991). The enhanced neural activity induced by the salient item in its topologically corresponding location in early visual cortex is considered as the bottom-up signal that modifies the priority map (Itti *et al.*, 1998; Li, 2002). Meanwhile, top-down factors such as target template and search mode can also influence the generation of attentional priority, and reduce (Folk *et al.*, 1992; Bacon & Egeth, 1994) or even reverse the bottom-up salience effect (Einhäuser *et al.*, 2008). More specifically, the active maintenance of the task-relevant information in working memory (WM) has been shown to bias the stimulus' representation in the fronto-parietal network to

compete for selection (Olivers *et al.*, 2011; Ptak, 2012). Moreover, optimal allocation of attention not only requires successful target selection, but also efficient distractor suppression. Recent studies have shown that foreknowledge of distractor identity can facilitate visual search performance by serving as a 'template for rejection' (Woodman & Luck, 2007; Arita *et al.*, 2012). This top-down influence driven by suppression of a distractor can gate the sensory representation and override the effect of bottom-up salience (Geng & DiQuattro, 2010; Geng, 2014). As suggested by neurophysiological investigations, such successful attentional suppression is linked to increased neural activity in the frontal areas that initiates the inhibitory control, and reduced neural activity in the parietal areas that represents the priority map (Hasegawa *et al.*, 2004; Ipata *et al.*, 2006).

In the natural environment, directing attention to the information that leads to reward or avoids punishment posits motivational importance. It has been shown that visual attention is prioritized for motivationally significant locations or objects (Engelmann & Pessoa, 2007; Liston & Stone, 2008; Kiss *et al.*, 2009), even if they are irrelevant to the task at hand (Della Libera & Chelazzi, 2009; Peck *et al.*, 2009; Hickey *et al.*, 2010; Anderson *et al.*, 2011; LePelle *et al.*, 2015). These behavioural effects are associated with changes

Correspondence: Dr S. Li, ¹Department of Psychology, as above.
E-mail: sli@pku.edu.cn

in neural activity in lateral intraparietal area that encode the value of the stimulus (Platt & Glimcher, 1999; Sugrue *et al.*, 2004) and persist when the reward-conditioned stimulus is task-irrelevant (Peck *et al.*, 2009). According to a modified theory of attentional control, reward association based on past experience becomes integrated into the priority map as an independent modulator to guide where attention is directed (Awh *et al.*, 2012). Nevertheless, it remains unclear whether the priority of reward salience could be reversed by top-down factors when it serves as distractor. Studies have mainly characterized the reward salience-driven capture effect as being difficult to be overridden by top-down control (Hickey *et al.*, 2011; Hickey & van Zoest, 2012; Le Pelletier *et al.*, 2015). By contrast, indirect evidence indicates that suppression of reward salience in visual search includes observation of the Pz component, an event-related potential (ERP) that is linked to inhibitory control (Hickey *et al.*, 2009; Sawaki & Luck, 2010), that appears contralateral to a reward-associated distractor in fast-response trials (Qi *et al.*, 2013), and that the encoding accuracy in object-selective visual cortex for reward-associated objects decreases when there were distractors (Hickey & Peelen, 2015). Despite the presence of these neural signatures for the suppression of items with reward salience, it remains unclear whether inhibitory processing of reward salience can lead to facilitated behavioural performance as shown for physical salience (Geng & DiQuattro, 2010).

Previous findings have demonstrated that the performance benefit obtained through distractor suppression was critically related to the top-down knowledge of distractor identity held in WM (Woodman & Luck, 2007; Arita *et al.*, 2012) and inhibitory activity during WM maintenance (Dhawan *et al.*, 2013). In the experiments conducted by Woodman and colleagues (Woodman & Luck, 2007; Arita *et al.*, 2012), a WM-guided visual search paradigm was used. In this paradigm, the memorized item always shared an identical feature with the distractors in subsequent search display, and the observers were instructed to ignore the items with the WM-matching feature. Although the WM-matching distractors needed to be ignored, they remained task-relevant and must be memorized during the delay. In this set-up, the reaction time for the matching distractor condition was faster than for the non-matching distractor condition, indicating that the WM template of a distractor plays an important role in facilitating top-down suppression. In our previous work, combining reward learning and change detection paradigms, we have shown improved WM performance for the items that shared previously reward-associated features (Gong & Li, 2014). Therefore, we hypothesize that, if the reward-associated feature is to be suppressed voluntarily, its enhanced WM representation can be used by top-down control to facilitate the suppression. To test this idea, we modified the WM-guided visual search paradigm (Woodman & Luck, 2007; Arita *et al.*, 2012) and combined it with electroencephalogram (EEG) measurements, aiming to examine whether the reward-associated feature can be effectively suppressed and to unravel the underlying mechanism of the suppression.

Experiment 1 – “”

Materials and methods

Participants

Twenty-two observers (11 males; mean age, 22.09 years) participated in Experiment 1. All participants completed two sessions (training and test) on two successive days and were paid for their participation. They were students from Peking University with normal or corrected-to-normal vision, and gave written informed con-

sent. The study was approved by the Committee for Protecting Human and Animal Subjects, Department of Psychology, Peking University.

Stimuli

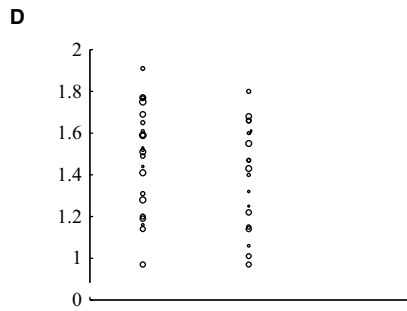
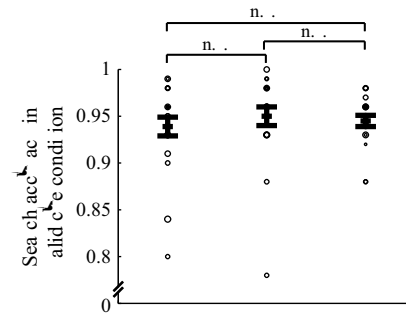
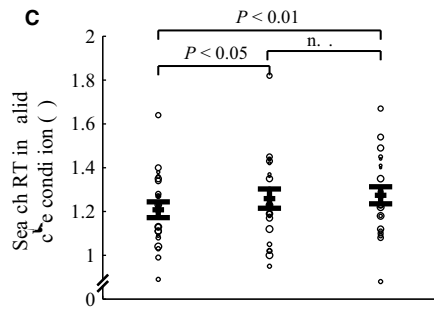
Ten colours were selected (including red and green) for Experiment 1 (15 cd/m²). Stimuli were displayed on a black background of a cathode ray tube (CRT) monitor (refresh rate: 60 Hz).

Procedure

Training session. As shown in Fig. 1A, each trial started with the presentation of a central fixation cross, followed by a search display. The search display around the fixation point was composed of eight white bars (1.3° × 0.1°) that were located inside different coloured circles (2.6° × 2.6°). The bars were shown at equal eccentricities (6°). The search target was a uniquely orientated bar with a horizontal (0°) or vertical (90°) orientation, whereas the other seven bars were tilted by 45° to either the left or the right. The target bar appeared only inside a red or a green circle with equal probability (50%). The observers were instructed to identify the orientation of the target bar by pressing a button (left and right arrow keys) with the index and middle fingers of their right hand. On-screen feedback was provided to the observers immediately after a correct response to indicate both the reward for the current trial and the total earnings. A blank screen appeared after an incorrect response. Importantly, the red and green circles were associated with a high probability (80%) of a high reward (¥ 0.5) and a low reward (¥ 0.1), respectively (or vice versa). The assignment of the colours to the reward magnitudes was counterbalanced across observers who were naïve to this association. However, they were told that the payment in the training session was based on individual performance. There were 800 trials in the training session.

Test session. As shown in Fig. 1B, each trial started with a central fixation cross. The cue display was shown with a centrally positioned coloured circle (2.25° × 2.25°), followed by the search display composed of a ring of 12 circles. Each circle (2.25° × 2.25°) in the search display enclosed an orientated bar (0.96° × 0.1°) and located at equal eccentricities (7°) around the fixation point. Six circles appeared in each hemifield. The circles within one hemifield were in the same colour. The search target was a uniquely orientated bar with horizontal or vertical orientation, whereas the other 11 bars were tilted by 15° to either the left or the right. The observers were instructed to identify the orientation of the target bar by pressing a button (left and right arrow keys).

There were two cue conditions. In the valid cue condition, the observers were instructed to ignore half of the circles that matched the cued colour and appeared in one hemifield of the search display, as the target would never appear in these circles. The cued colour could be associated with high or low reward (i.e. HRC or LRC) during a training session, or was randomly chosen from two of the non-rewarded colours (control colours, CCs) for each observer. The remaining six CCs were used only in the search display. In the neutral cue condition, none of the colours in the search display matched the cued colour, and hence the colour cue was not informative for the target location. The four cue colours were repeated with equal probability in the cue display for both the valid cue and neutral cue conditions, and each of them was randomly paired with one of the six CCs in the search display. There were 320 trials for the valid cue and neutral cue condition, respectively.



Data analysis

Reaction time (RT) and accuracy were measured during the training and test session. To compute search RT, error trials and outliers (trials with RTs exceeding ± 3 SD) were excluded. Repeated measures analyses of variance (ANOVAs) were performed with Bonferroni correction for multiple comparisons.

Results

As indicated by a paired *t*-test, RT in the training session was significantly shorter when the target bar appeared inside the circle rendered in the HRC than in the LRC ($t_{21} = 2.21$, $P < 0.05$), whereas no significant difference was observed for search accuracy ($t_{21} = 0.71$, $P = 0.49$).

We then analysed the behavioural data from the test session. For the valid cue condition, as illustrated in Fig. 1C, a main effect of reward was found across cue colours (HRC, LRC and CCs; $F_{2,42} = 6.76$, $P < 0.01$, $\eta_p^2 = 0.24$). RT was significantly faster when the cue was in the HRC than in the LRC (mean difference = -0.05 s, SE = 0.018 s, $P < 0.05$) or CCs (mean difference = -0.07 s, SE = 0.018 s, $P < 0.01$). No significant difference was found between the LRC and CCs (mean difference = -0.015 s, SE = 0.02 s, $P = 1.0$). No significant effect on search accuracy was observed, either ($F_{2,42} = 1.0$, $P = 0.38$, $\eta_p^2 = 0.05$). These results suggest that search performance was facilitated when the known distractors' critical feature had been associated with high reward.

Before drawing an conclusion on the underlying inhibitor mechanism, we tested the possibility of whether reward facilitated the visual search because of the arousal effect. We analysed the data from the neutral cue condition: if the reward-induced increase in arousal level can account for the observed behavioural effect, we should expect to find similar facilitation when the HRC was shown in the cue display, as compared with other conditions. However, the results showed no influence of reward colour on search RT ($F_{2,42} = 1.29$, $P = 0.29$, $\eta_p^2 = 0.06$) or accuracy ($F_{2,42} = 1.71$, $P = 0.19$, $\eta_p^2 = 0.07$). We also split the data according to the colour of the target circle while the trials with the distractors in the reward-associated colours were excluded. The repeated-measures ANOVA revealed a main effect of target colour as shown in Fig. 1D (HRC, LRC and CCs; RT: $F_{2,42} = 3.62$, $P < 0.05$, $\eta_p^2 = 0.15$; accuracy: $F_{2,42} = 4.05$, $P < 0.05$, $\eta_p^2 = 0.16$), but the Bonferroni *post-hoc* analysis showed no advantage of the HRC in either RT or accuracy relative to the LRC or CCs (for all comparison, RT: $P > 0.06$; accuracy: $P > 0.13$), except a superior search accuracy for the LRC than for CCs (mean difference = -0.032 , SE = 0.011, $P < 0.05$). These results suggest that the observed reward effect was unlikely a reflection of the general elevation in arousal level.

The benefit in overall RT in Experiment 1 suggests an effective suppression over the high reward-associated distractors. Nevertheless, the spatial symmetry of the search display made it easy for the observers to deploy a space-based, rather than a feature-based, inhibitor strategy. In Experiment 2, we minimized this possible confounding factor by randomizing the locations of the items in cued and non-cued colours. We also added a change detection task to ensure the active maintenance of the cued colour in WM throughout the trial, avoiding a diminished cue effect by simple exposure (Downing, 2000). To help elucidate the neural mechanism underlying the reward effect at the behavioural level, we recorded EEG signals while the observers performed the behavioural task in Experiment 2.

Experiment 2 – ERP

Materials and methods

Participants

Twenty-eight (16 males; mean age, 22.18 years) observers participated in Experiment 2. None of the observers had participated in Experiment 1. All participants completed two sessions (training and test) on two successive days and were paid for their participation. They were students from Peking University with normal or corrected-to-normal vision, and gave written informed consent. The study was approved by the Committee for Protecting Human and Animal Subjects, Department of Psychology, Peking University.

Stimuli

Eight colours were selected for Experiment 2 (10.5 cd/m^2) to equalize the visual display of stimuli in monitors from the behavioural and EEG labs. Stimuli were displayed on a black background of a CRT monitor (refresh rate: 75 Hz).

Procedure

The training session in Experiment 2 was identical to that in Experiment 1. During the test session (Fig. 2A), each trial started with a central fixation cross. Then an arrow ($0.6^\circ \times 0.3^\circ$) was presented centrally and pointed either leftward or rightward, indicating the location of the to-be-remembered cue colour. The cue display consisted of two coloured squares ($0.6^\circ \times 0.6^\circ$) appearing on both sides of the fixation cross (3° in distance) along the horizontal axis. The search display was presented after a blank screen and consisted of eight items (i.e. Landolt-C) that were randomly positioned within a virtual circle ($6.1^\circ \times 6.1^\circ$) centered at the fixation point. The search target was a unique Landolt-C with a gap on the top or the bottom, while the remaining seven items were Landolt-Cs with a gap on the left or the right. An equal number of items were presented in two different colours. The observers were instructed to identify the gap on the target Landolt-C by pressing a button (up and down arrow keys). Only the valid cue condition was included. The observers were asked to ignore the search items that matched the cued colour to enable fast and accurate responses. The HRC, LRC and two CCs were selected as the candidates of the cue colour. The remaining four CCs were used only in the search display. The HRC and LRC were separately paired with two CCs in the cue display. These four colours were repeated with equal probability in the cue display, and each of them was randomly paired with one of the four remaining CCs in the search display. Following the response and a delay, a memory display appeared with two coloured squares. The observers were asked to indicate whether the square at the cued position had changed its colour by pressing a button (left and right arrow keys). The test session comprised nine blocks, with 80 trials for each block.

Data analysis

Behavioural analysis. RT and accuracy were measured during the training and test sessions. Trials with RT longer than 2500 ms were excluded from the analysis as the long-RT trials tended to show a residual effect in the EEG signal after the correction of ocular artefacts with independent component analysis (ICA). We also excluded trials with error responses. Repeated-measures ANOVAs were performed with Bonferroni correction for multiple comparisons.

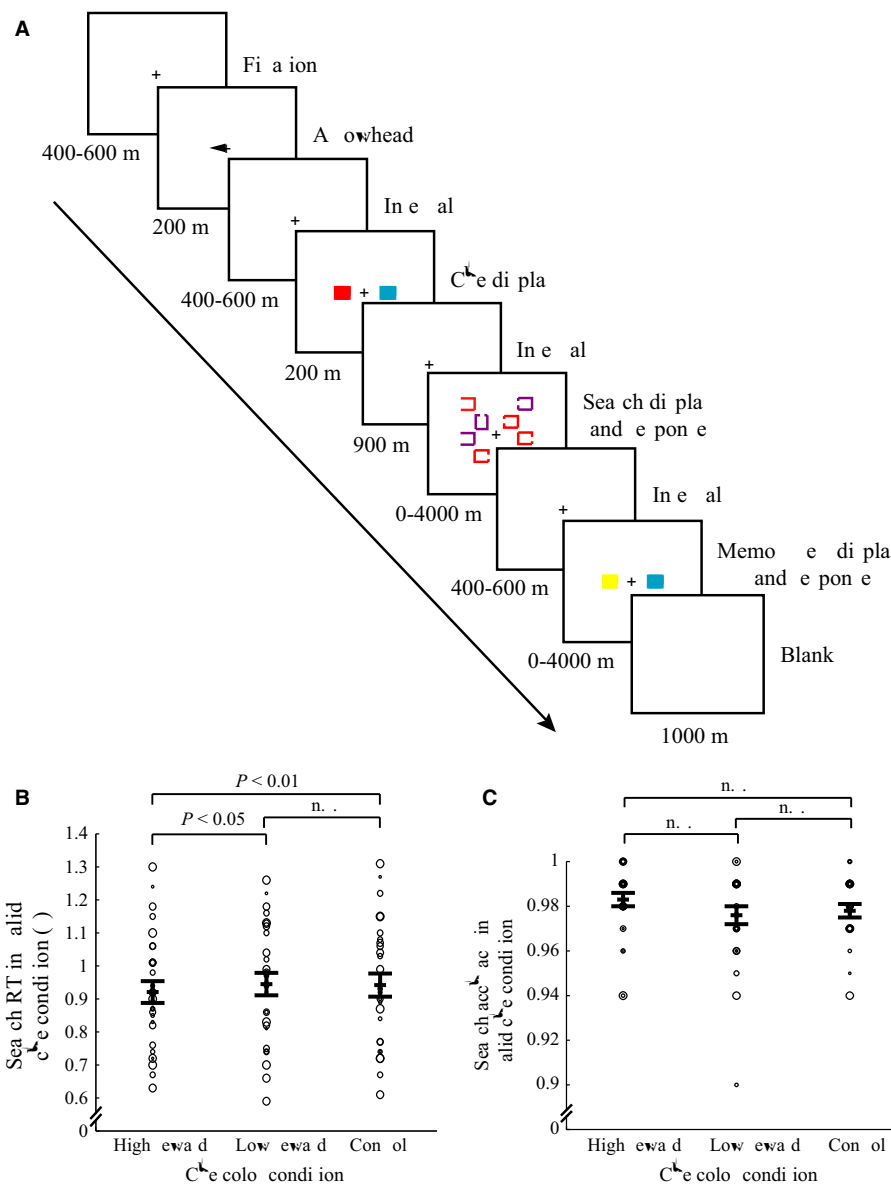


FIG. 2. Test task and results in Experiments 2. (A) Observers searched for a target Landolt-C with a unique gap (on the top or bottom) and reported whether the cued position had changed its colour in the memory test display. Half of the Landolt-Cs in the search display that matched the colour of the cued square were to be ignored during the search. (B) Search RT and (C) accuracy across three cue colours. Each point on the scatter plot shows an individual observer's data. Error bars represent the standard error of the mean.

EEG recording and ERP analysis. EEG data were acquired from a 64-channel EEG cap positioned according to the international 10-20 system (Brain Products, Munich, Germany). Electrode impedance was kept below 5 kΩ for scalp channels. The electrooculograms were recorded with electrodes placed lateral to the external canthus of the left eye and above the right eye. An external electrode placed on the tip of the nose served as the on-line reference. The electrode AF was chosen to be the ground electrode. EEG data were recorded at a sampling rate of 1000 Hz and were re-referenced off-line with the averaged mastoids.

Conventional off-line analysis was performed using BRAIN VISION ANALYZER 2.0. Ocular artefacts were semi-automatically corrected using ICA. In addition to the automatically calculated electrooculogram variance for each ICA component, the semi-automatic mode allowed us to visually identify the relevance of the ICA components to eye movement and reject them based on their scalp topographies

(i.e. ocular activity projects strongly over the frontal sites). The EEG signal from each electrode was filtered using a finite impulse response (low-frequency cutoff: 0.016 Hz; high-frequency cutoff: 100 Hz; decay of stop band: 24 dB per octave). The continuous EEG data were separated into epochs from -200 to 800 ms around the onset of cue and search displays. A 200-ms pre-stimulus epoch was used as the baseline period. Artefact rejection was performed before averaging to discard epochs with signals exceeding $\pm 70 \mu\text{V}$. The ERPs were averaged across observers for visual inspection of the components, which may differ across three cue colour conditions. The averaged waveforms were separately computed for contralateral (electrodes contralateral vs. ipsilateral to the location of the cue colour). The peak point of each ERP component was individually identified with a semi-automatic peak detection program. The mean amplitude of each ERP component was calculated by averaging 11 points centered at the peak point within separate time

windows for P1 (70–150 ms), N1 (120–220 ms), P2 (160–280 ms) and P3 (220–350 ms) components. Repeated-measures ANOVAs with two factors (cue colour: HRC, LRC and CCs; contralateralit y) were performed for each group of paired electrodes: the frontal (F1/F2, F3/F4, F5/F6, FC1/FC2, FC3/FC4, FC5/FC6), central (C1/C2, C3/C4, C5/C6), central-parietal (CP1/CP2, CP3/CP4, CP5/CP6), parietal (P1/P2, P3/P4, P5/P6) and parieto-occipital (PO3/PO4, PO7/PO8, O1/O2) regions. Contralateralit y was not considered for the midline electrodes. All reported P values were Bonferroni corrected.

Time–frequency analysis. Time–frequency analyses on single trial EEG data were performed using EEGLAB software (Delorme & Makeig, 2004). The Morlet wavelet transformation was applied to the epochs from –1500 ms before to 2000 ms after the cue onset. Baseline power from –200 to 0 ms relative to the cue onset was removed. There were 200 linearl y spaced time points and 100 log-spaced frequencies ranging from 1 to 30 Hz, with two cycles at the lowest frequency increasing linearl y to eight cycles at the highest frequency. The variation in the number of cycles was adopted to make a compromise between temporal and frequency resolutions. Event-related spectral perturbations (ERSPs) were calculated for each channel and averaged across trials, after which the ERSPs were individuall y estimated b y the regional mean value of the grouped electrodes in the frontal region (F, F1, F2, F3, F4, FC, FC1, FC2, FC3, FC4) across cue conditions. Repeated-measures ANOVAs with one factor (cue colour: HRC, LRC and CCs) were performed for each frequency at each time point. To make comparison between conditions while avoiding the problem of circular analysis (Kriegeskorte *et al.*, 2009), we adopted the method of leave-one-out cross-validation. EEG data were divided into nine independent epochs according to the number of blocks during the test session. ERSPs were calculated separatel y for each epoch and each observer. We reduced the number of output frequency to 30 (linearl y spaced) for computational efficienc y while leaving all other parameters unchanged. We chose eight epochs as the training set and one epoch as the test set. The training set was anal ysed to define a region of interest (ROI) ($P < 0.01$, uncorrected), and the corresponding time and frequency information within the ROI was used for the retrieval of data points from the test set. This process was repeated nine times until all combinations of assigning blocks as training and test sets were examined. For each observer, the ERSPs were averaged across repetitions for each cue condition.

Source reconstruction. Source reconstruction was performed on the preprocessed epochs between 0 and 350 ms after cue onset, using statistical parametric mapping (SPM8). The differential wave between the HRC and LRC was individuall y calculated for the subsequent analysis of distributed source reconstruction with the following procedure (Litvak *et al.*, 2011). The data modalit y (i.e. EEG) was initiall y defined, followed b y the confirmation of sensor locations and fiducials available in SPM8. The possible sources were generated using the normal cortical mesh in a head model in Montreal Neurological Institute (MNI) space. The link between sensor locations and MNI coordinates was established b y means of co-registration. To compute the activit y that would have been reflected on the sensors b y each dipole on the cortical mesh, the forward model was calculated using the boundar y element model. Group inversion was then used to estimate the hyperparameters of multiple sparse priors, ensuring that the reconstructed activit y were from the same sources across observers (Litvak & Friston, 2008). No prior information about dipole locations and orientations was provided. The estimated solutions for sources were written to the contrast

images for each observer. The resultant mean of the explained variance across observers was 92.14% (25 of 28 observers had the explained variance above 90%), providing a firm foundation for the further connectivit y analysis. The general linear model was conducted to determine the reward-modulated sources ($P < 0.05$, family-wise error corrected). The effects of reward were evident in multiple clusters within different brain areas. Each cluster consisted of a set of closel y located coordinates. We chose the coordinate with the maximal t -value (i.e. an index of reward effect) from a cluster to represent a specific brain region. These coordinates were then used as the prior mean locations for the to-be-modelled sources in the connectivit y analysis.

Dynamic causal modelling (DCM). The DCM used the spatial priors from source reconstruction and specified the neuronal models with constraints on physiological plausibilit y (David *et al.*, 2006). B y adopting the approach of a single equivalent current dipole, the parameters of the predetermined extrinsic connectivit y were estimated. To be consistent with the reconstruction analysis, the window of interest was defined from 0 to 350 ms after cue onset. We also defined the comparison between the HRC and LRC conditions to model the dynamics of the reward effect. The averaged waveforms for each observer were computed using singular value decomposition, with the multi-channel EEG data being modelled with six principal eigenvectors to increase computational efficienc y (Harter, 1990). The optimal model was selected with Bayesian model selection (BMS) b y performing a group-level fixed-effect analysis (FFX) on the summed log-evidence for each model across individuals (Stephan *et al.*, 2010). The same analysis was also performed on the grand-averaged data. One model was defined to be superior to other models with a difference in log-evidence above 3 (Penn *et al.*, 2004). Statistical analyses were performed to test the individuall y estimated posterior means for the possible experimental effect on each connection.

Results

Behavioral results

The training performance showed no significant difference between the HRC and LRC conditions (RT: $t_{27} = 0.79$, $P = 0.44$; accurac y: $t_{27} = 0.12$, $P = 0.56$). The results of the test session were similar to Experiment 1 (Fig. 2B). We observed a significant main effect of cue colour ($F_{2,54} = 5.76$, $P < 0.01$, $\eta_p^2 = 0.18$). The observers responded significantl y faster when the cued colour was in the HRC than when it was in the LRC (mean difference = -0.023 s, SE = 0.009 s, $P < 0.05$) or the CCs (mean difference = -0.022 s, SE = 0.006 s, $P < 0.01$). No significant difference was found between the LRC and the CCs (mean difference = -0.002 s, SE = 0.008 s, $P = 1.0$). Anal yses of search accurac y ($F_{2,54} = 2.20$, $P = 0.12$, $\eta_p^2 = 0.07$; Fig. 2B) and memor y accurac y ($F_{2,54} = 0.62$, $P = 0.54$, $\eta_p^2 = 0.02$; Fig. 2C) revealed no significant difference across conditions. These results confirmed the facilitation of search performance when the known distractors were in previousl y high reward-associated colour.

Anterior P2 and posterior P3 components

We anal ysed the ERP waveforms time-locked to the cue displac ement and search displac ement, and contrasted the ERP waveforms across three cue colour conditions. No significant differences were found between conditions for the ERP waveforms elicited b y the search displac ement.

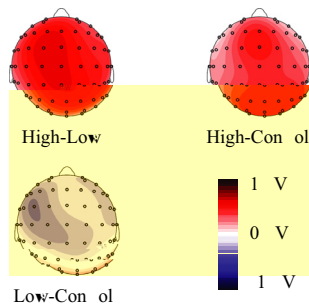
As shown in Fig. 3, when time-locked to the onset of the cue display, the first ERP component that differed across cue colours was P2 (a.k.a. P2a) (Potts & Tucker, 2001; Voss & Paller, 2009). Analyses of P2 amplitude revealed significant effects of cue colour in the frontal ($F_{2,54} = 8.22, P < 0.01, \eta_p^2 = 0.23$), central ($F_{2,54} = 8.19, P < 0.01, \eta_p^2 = 0.23$) and centro-parietal ($F_{2,54} = 9.011, P < 0.01, \eta_p^2 = 0.25$) regions. P2 was larger when the cue was in the HRC than in the LRC (frontal: mean difference = 0.399, SE = 0.125, $P < 0.05$; central: mean difference = 0.368, SE = 0.117, $P < 0.05$; centro-parietal: mean difference = 0.394, SE = 0.122, $P < 0.05$) or the CCs (frontal: mean difference = 0.421, SE = 0.132, $P < 0.05$; central: mean difference = 0.424, SE = 0.128, $P < 0.01$; centro-parietal: mean difference = 0.517, SE = 0.136, $P < 0.01$). No significant difference was found between the LRC and the CCs ($P > 0.9$ across all regions). Moreover, P2 amplitude was larger at the contralateral than ipsilateral side in the central ($F_{1,27} = 4.46, P < 0.05, \eta_p^2 = 0.14$) and centro-parietal ($F_{1,27} = 10.18, P < 0.01, \eta_p^2 = 0.27$) regions. No significant interaction was observed between the two factors ($P > 0.5$ across all regions).

As shown in Fig. 4, the second ERP component that differed across cue colours was P3 (a.k.a. P3b) (Polich, 2007). Analyses of P3 amplitude revealed significant effects of cue colour in the centro-parietal ($F_{2,54} = 11.85, P < 0.01, \eta_p^2 = 0.31$), parietal ($F_{2,54} = 10.62, P < 0.01, \eta_p^2 = 0.28$) and parieto-occipital ($F_{2,54} = 8.54, P < 0.01, \eta_p^2 = 0.24$) regions. Significantly larger P3 amplitude was elicited for the cue in the HRC than the cue in the LRC (centro-parietal: mean difference = 0.414, SE = 0.143, $P < 0.05$; parietal: mean difference = 0.36, SE = 0.136, $P < 0.05$;

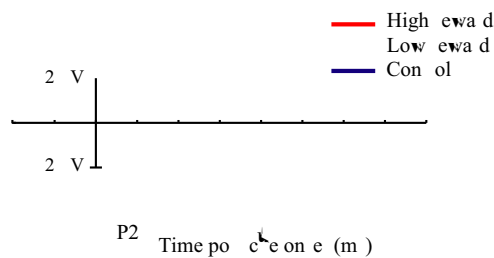
parieto-occipital: mean difference = 0.299, SE = 0.121, $P = 0.059$) or the CCs (centro-parietal: mean difference = 0.72, SE = 0.173, $P < 0.01$; parietal: mean difference = 0.613, SE = 0.148, $P < 0.01$; parieto-occipital: mean difference = 0.46, SE = 0.107, $P < 0.01$). No significant difference was observed between the LRC and the CCs ($P > 0.07$ across all regions). Neither a main effect of contralateralit ($P > 0.7$ across all regions) nor an interaction was found between cue colour and contralateralit ($P > 0.37$ across all regions).

The observed reward effects time-locked to the cue display suggest that the task-relevant cue information is better processed if it was associated with higher reward. The anterior P2 has been linked to the matching degree between the sensory input and the stored memory representation (Voss & Paller, 2009), whereas posterior P3 is commonly associated with attention and memory processing (Polich, 2007). Given the necessity of maintaining this task-relevant cue information in WM for the upcoming visual search, the reward effects on anterior P2 and posterior P3 components may reflect an enhanced WM representation of the HRC in the fronto-parietal network (Ptak, 2012). Reward effects were also observed to covary between ERP components, as indicated by the cross-region covariance between the amplitudes of frontal P2 and centro-parietal P3 across observers, which was only evident under the HRC condition ($r = 0.42, P < 0.05$). This result sheds light on the possible information flow passed from frontal to parietal regions, which resembles the top-down modulation that regulated the expression of HRC in the prior map (Ipata *et al.*, 2006; Zanto *et al.*, 2011). However, we failed to observe the effect of reward on lateralized activity, such

A 180 - 200 ms



A reward effect in frontal region



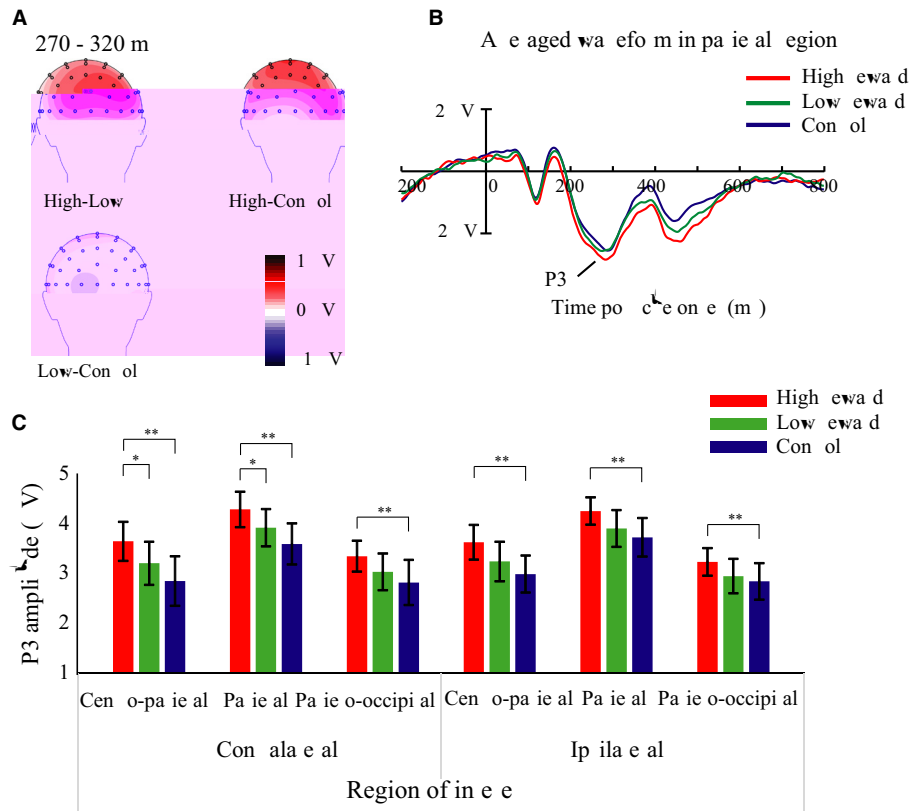


FIG. 4. ERP results of posterior P3. (A) The grand-averaged scalp topograph of the P3 component elicited by the cue display. (B) The grand-averaged ERP waveforms of the averaged parietal electrodes. (C) Contralateral and ipsilateral P3 amplitudes of the centro-parietal, parietal and parieto-occipital regions across three cue colours. Error bars represent the standard error of the mean (* $P < 0.05$, ** $P < 0.01$).

as N2pc difference waveforms between the hemifields contralateral and ipsilateral to the cue colour (Kiss *et al.*, 2009). This is probably due to two reasons: first, the cue colours in all conditions were pre-attended by an arrow that rendered the attention level less different between the HRC, LRC and CCs; second, the spatial information of the cue colour was irrelevant to where the target and distractor would appear in the search arrays, thus making it unnecessary for attention to vary across hemifields. The lack of the lateralized activity suggests further that the anterior P2 and posterior P3 reflect WM-related attentional processing that is based on feature rather than space.

Frontal theta oscillation

To further confirm the enhanced WM representation for the HRC during the cue display, we conducted a time–frequency analysis that focused on frontal theta oscillation. The frontal theta oscillation is considered as an important neural signature for WM processing (Raghavachari *et al.*, 2001; Hsieh & Ranganath, 2014), including active maintenance and manipulation (Itthipuripat *et al.*, 2013). Recent advances in the understanding of frontal theta have extended its potential role in signalling a need for enhanced cognitive control (Cavanagh & Frank, 2014), which echoes well with the literature of WM-based top-down processes (Olivers *et al.*, 2011). The statistical parametric map of the F -test (Fig. 5) visualized the reward-induced power changes in the frequency range from 5.8 to 7.6 Hz, at 197–343 ms after cue onset. This result showed a reward effect within the theta range over the frontal region. Similar range of frequency and time interval were found by cross-validation (5–9 Hz, 153–

406 ms after cue onset). Within the ROI defined by the independent training set, a main effect of cue colour in the test set was observed ($F_{2,54} = 4.18$, $P < 0.05$, $\eta_p^2 = 0.13$). The Bonferroni *post-hoc* analysis revealed a significant difference between HRC and LRC (mean difference = 0.268, SE = 0.079, $P < 0.01$), whereas no significant differences were obtained for the other comparisons (HRC vs. CCs: mean difference = 0.117, SE = 0.089, $P = 0.61$; LRC vs. CCs: mean difference = -0.151 , SE = 0.108, $P = 0.52$).

Taken together, these results not only support the strengthened representation of a high reward-associated item in WM that confirms our previous findings about the reward-induced improvement in WM representation (Gong & Li, 2014), but also reveals the instantiation of increased top-down control that overrides Pavlovian biases (Cavanagh *et al.*, 2013). Taken together, these findings lead to the idea that the reward-enhanced WM representation during the preparatory phase before the search arrays contributes to the activation of a top-down suppression mechanism.

Top-down modulations from frontal regions

DCM analysis was conducted to characterize the temporo-spatial dynamics between the reward-related ROIs that were defined based on source reconstruction (Fig. 6A): bilateral anterior temporal lobe (ATL; left: $t_{27} = 10.51$, $P < 0.01$, right: $t_{27} = 8.13$, $P < 0.01$), bilateral lateral prefrontal cortex (LPFC; left: $t_{27} = 6.92$, $P < 0.01$, right: $t_{27} = 7.07$, $P < 0.01$) and cingulate gyrus (CG; $t_{27} = 8.53$, $P < 0.01$). Nine unilateral or bilateral candidate models within these ROIs (Fig. 6B) were tested with the assumption that the experimental manipulation had influenced the forward (F-model), backward

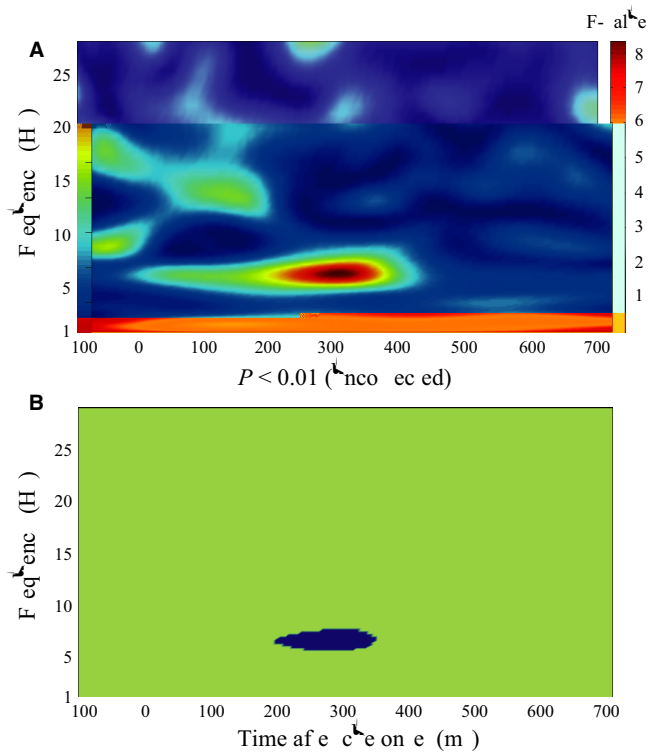


FIG. 5. Reward effects observed in frontal theta oscillation. (A) Statistical parametric map of the F-statistic revealed a reward effect in the theta range between 5.8 and 7.6 Hz, at 197–343 ms after cue onset for the frontal electrodes. (B) The map with threshold at $P < 0.01$ (uncorrected).

(B-model) or both pathways (FB-model). BMS revealed strong evidence in favour of the bilateral FB-model (Fig. 6C), exceeding that of the second best model by a relative Bayes factor of 679.02.

As shown in Fig. 6D, estimation of the reward modulation on the effective connectivity for the optimal model revealed stronger couplings in the backward pathways from ILPFC to IATL ($t_{27} = 2.76$, $P < 0.05$), from CG to rATL ($t_{27} = 3.19$, $P < 0.01$) and from rLPFC to CG ($t_{27} = 2.36$, $P < 0.05$). A trend of significant modulation was observed from CG to IATL ($t_{27} = 1.88$, $P = 0.07$). None of the forward modulations approached significance ($P > 0.13$ for all comparisons). The significant reward effects on the feedback connectivity demonstrate an important role of top-down modulation for the observed behavioural facilitation. The feedback modulation that occurred during WM maintenance agrees with the idea of a 'template for rejection' in guiding the cognitive control to implement suppression over reward-associated distractors (Woodman & Luck, 2007; Arita *et al.*, 2012).

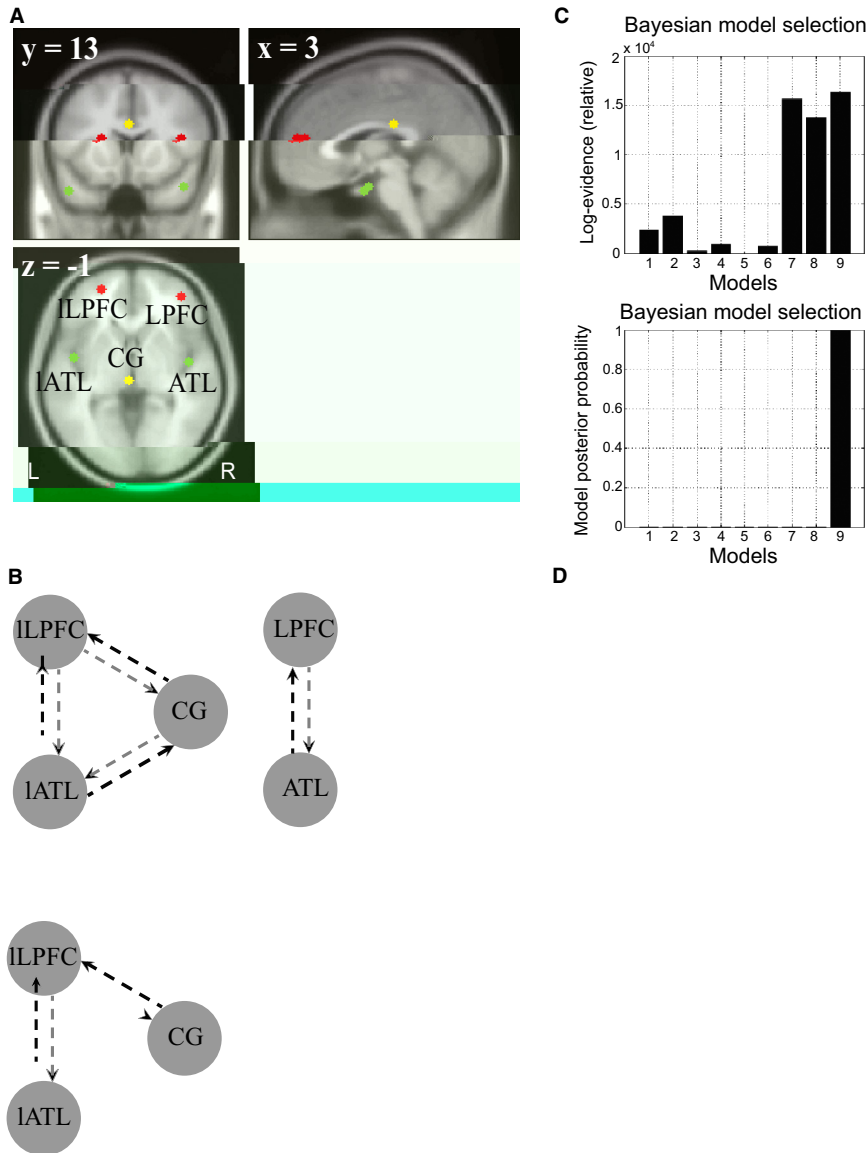
D

Our results demonstrate that, after associating a colour with reward, the performance of a visual search task is facilitated when this colour is cued as a critical feature of distractor before the onset of the search display. The behavioural results are accompanied by increased theta oscillation over the frontal region and enhanced top-down modulation from frontal to anterior temporal regions during the delay period. To conclude with a mechanistic interpretation of our results, two important questions need to be addressed.

First, why can reward association facilitate distractor suppression? Provided that reward salience and physical salience exert a similar influence on attentional selection (Della Libera & Chelazzi, 2009;

Hickey *et al.*, 2010; Anderson *et al.*, 2011; LePelle *et al.*, 2015), it is reasonable to ascribe the main trigger of the active suppression in our study to the increased salience of the distractors in the HRC. According to the signal suppression hypothesis of controlled attention capture (Sawaki & Luck, 2010, 2011; Sawaki *et al.*, 2012), the prioritized signal generated by reward salience can be counteracted by top-down suppression. However, this apparent account is not sufficient to clarify the source for the strengthened top-down suppression of distractors in HRC. Importantly, we found a neural signature of frontal theta oscillation that suggests an enhanced WM representation for the HRC and the increased need for cognitive control under the HRC condition. On the one hand, this result is consistent with recent findings showing that previously established reward association can enhance the representation of reward-related items in either WM (Gong & Li, 2014) or long term memory (Muraama & Kitagami, 2014), presumably accompanied by automatic activation of the stored reward association in these memory systems (Logan, 1988; Moores *et al.*, 2003). On the other hand, this result coincides with the finding that the conflict between goal-directed attention and Pavlovian biases predicts an increase in cognitive control (Cavanagh *et al.*, 2013). Moreover, given the idea that the WM content can be used to avoid attention towards WM-matching items (Woodman & Luck, 2007; Arita *et al.*, 2012), we suggest that the reward salience facilitates the suppression mechanism through its enhanced WM representation and guides top-down attention based on task instruction. The WM representation and task instruction can jointly contribute to produce a stronger top-down signal that modifies the priority of the items with reward salience.

Second, how does reward association facilitate distractor suppression? In our experiments, the suppression effects were generated by proactive control, in which the instructed task goal and rule (i.e. searching for a unique orientation or Landolt-C while ignoring the items in the cued colour) were actively maintained in WM to guide top-down attention. While the proactive strategy was manipulated to render direct suppression over a reward-associated distractor (i.e. without directing attention to it in the first place), the reactive strategy (i.e. initial capture plus rapid rejection) may also be recruited for effective target selection. Concerning the non-informativeness of the cue colour in predicting distractor location and the reward salience-driven attentional effect for the items in the HRC, we believe that both proactive and reactive control could play roles in the observed facilitation effect. More specifically, observers' attention may be initially orientated to the items in either the CCs or the HRC. In the former case, direct suppression may take place to prevent further attraction by the HRC because in observers' priority maps, the items in the HRC were marked with lower priority as compared with the currently fixed colour. In the latter case, rapid rejection may operate to compensate for the HRC-induced RT costs due to misallocation of attention (Peck *et al.*, 2009; Hickey *et al.*, 2010; Anderson *et al.*, 2011). Both accounts are consistent with previous theoretical notions (Braver, 2012; Geng, 2014), and well aligned with our DCM results that demonstrate direct frontal suppression (i.e. from IPFC to IATL) and indirect suppression mediated by cingulate cortex that is responsible for conflict detection (i.e. from rPFC to rATL via CG) (van Veen *et al.*, 2001; Padmala & Pessoa, 2011). In addition, while ATL is generally thought to be critical for the processing of semantic memory, recent studies on ATL have observed its role in representing associative pairings (Eifuku *et al.*, 2010), and in encoding and maintenance of stimuli with emotional significance (Olson *et al.*, 2013). Therefore, it is likely that the activation of ATL in the present study reflected its response to the learned reward association, which can be further



modulated b PFC to guide optimal behaviour. Taking the behavioural and electrophysiological evidence together, we suggest two coexisting pathways (i.e. direct suppression and rapid rejection) that work together to modify the prioritization map and facilitate the suppression of reward-associated distractors. Importantly, our findings provide the first neural evidence that reward association modulates the top-down control through its enhanced WM representation before the onset of the visual search display, leading to a more efficient deployment of task strategy when search items appear.

Several previous studies have reported the reward-related suppression effect at behavioural and neural levels. However, the behavioural evidence was obtained depending on extra antecedents. For example, suppression over a high reward-associated distractor is possible when it served as a distractor during the learning period

(Della Libera & Chelazzi, 2009), or when the reward-associated distractors shared a critical feature with the cued target template, regardless of reward magnitude (Lee & Shomstein, 2014). While neural evidence was shown for inhibition-related evoked potential (i.e. Pd component) in fast-response trials (Qi *et al.*, 2013) and with decreased encoding accuracy in sensor cortex in the presence of a reward-associated distractor (Hickey & Peelen, 2015), no corresponding evidence for suppression was observed at the behavioural level. In comparison with these studies, our findings have two major advances. First, we disentangled the antecedents based on learning history and target-distractor relationship from our design, providing consistent behavioural and electrophysiological evidence in support of attentional suppression over reward salience. Second, we offered mechanistic accounts for 'when and how' the stronger suppression

was found for the distractors in the HRC relative to the LRC and CCs, unravelling the neural mechanism that contributes to the modification of priority for the items with reward salience. However, we believe that further investigations with functional magnetic resonance imaging could complement our findings with greater spatial resolution.

The behavioural results from Experiment 1 showed that visual search was not influenced by the cued colour in the neutral cue condition, suggesting that our findings were unlikely to be due to an arousal effect caused by the reward-associated distractors. Under the neutral cue condition, the lack of benefit in search RT for the target in the reward-associated colour seems contradictory to the prediction of the reward-induced priority in attentional selection (Awh *et al.*, 2012). However, in our design, the cued HRC matched the colour of half of the distractors in the search display. This set-up reduced the expression of reward salience as compared with the capture effect driven by a singleton distractor in HRC (Hicke *et al.*, 2010; Anderson *et al.*, 2011). More importantly, in both Experiments 1 and 2, observers were required to engage in a feature-based serial search, thus enforcing the search process to be dominated by a top-down mechanism. This manipulation differed fundamentally from previous studies that used singleton-based parallel search controlled by bottom-up attention (Theeuwes *et al.*, 2010). The interpretation of search mode echoes well with the latest behavioural finding on suppression over physical salience (Gaspelin *et al.*, 2015), suggesting that our results are not contradictory to the previous findings of value-driven attentional capture (Hicke *et al.*, 2010; Anderson *et al.*, 2011).

To summarize, our results agree with the proposal that reward association modifies attentional priority based on a factor other than bottom-up physical salience and top-down task goal (Awh *et al.*, 2012; Chelazzi *et al.*, 2014). The present study showed an alternative form of modification on the priority map by reward salience through distractor suppression. Our findings suggest that reward association can modify the priority map during active distractor suppression and benefit behavioural performance, as a result of the interaction between a top-down inhibition mechanism and enhanced WM representation of the reward-associated feature. These findings demonstrate a flexible role of learned reward association on cognitive control (Pessoa, 2009), and could advance our understanding of inhibition-related clinical syndromes, such as attention deficit/hyperactivity disorder, drug addiction and depression.

C 

The authors declare no competing financial interests.

A 

This work was supported by the National Natural Science Foundation of China (31230029, 31470974, 31271081, J1103602), the National High Technology Research and Development Program of China (863 Program) (2012AA011602), and the Program for New Century Excellent Talents in University, State Education Ministry.

A 

ANOVA, analysis of variance; ATL, anterior temporal lobe; BMS, Bayesian model selection; CC, control colour; CG, cingulate gyrus; DCM, dynamic causal modelling; EEG, electroencephalogram; ERP, event-related potential; ERSF, event-related spectral perturbation; HRC, high reward colour; ICA, independent component analysis; LPFC, lateral prefrontal cortex; LRC, low reward colour; MNI, Montreal Neurological Institute; ROI, region of interest; RT, reaction time; WM, working memory.

R

- Anderson, B.A., Laurent, P.A. & Yantis, S. (2011) Value-driven attentional capture. *Proc. Natl. Acad. Sci USA*, **108**, 10367–10371.
- Arita, J.T., Carlisle, N.B. & Woodman, G.F. (2012) Templates for rejection: configuring attention to ignore task-irrelevant features. *J. Exp. Psychol. Human*, **38**, 580–584.
- Awh, E., Belopolsky, A.V. & Theeuwes, J. (2012) Top-down versus bottom-up attentional control: a failed theoretical dichotomy. *Trends Cogn. Sci.*, **16**, 437–443.
- Bacon, W.F. & Egeth, H.E. (1994) Overriding stimulus-driven attentional capture. *Percept. Psychophys.*, **56**, 485–496.
- Bisley, J.W. & Goldberg, M.E. (2010) Attention, intention, and priority in the parietal lobe. *Annu. Rev. Neurosci.*, **33**, 1–21.
- Braver, T.S. (2012) The variable nature of cognitive control: a dual mechanisms framework. *Trends Cogn. Sci.*, **16**, 106–113.
- Cavanagh, J.F. & Frank, M.J. (2014) Frontal theta as a mechanism for cognitive control. *Trends Cogn. Sci.*, **18**, 414–421.
- Cavanagh, J.F., Eisenberg, I., Guitart-Masip, M., Hu, S., Q., & Frank, M.J. (2013) Frontal theta overrides pavlovian learning biases. *J. Neurosci.*, **33**, 8541–8548.
- Chelazzi, L., Eštočinová, J., Calletti, R., Gerfo, E.L., Sani, I., Della Libera, C. & Santandrea, E. (2014) Altering spatial priority maps via reward-based learning. *J. Neurosci.*, **34**, 8594–8604.
- Corbetta, M. & Shulman, G.L. (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.*, **3**, 201–215.
- David, O., Kiebel, S.J., Harrison, L.M., Mattout, J., Kilner, J.M. & Friston, K.J. (2006) Dynamic causal modeling of evoked responses in EEG and MEG. *Neuroimage*, **30**, 1255–1272.
- Della Libera, C. & Chelazzi, L. (2009) Learning to attend and to ignore is a matter of gains and losses. *Psychol. Sci.*, **20**, 778–784.
- Delorme, A. & Makeig, S. (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods*, **134**, 9–21.
- Dhawan, S., Deubel, H. & Jonikaitis, D. (2013) Inhibition of saccades elicits attentional suppression. *J. Vision*, **13**, 9.

- Hicke, C., Chelazzi, L. & Theeuwes, J. (2011) Reward has a residual impact on target selection in visual search, but not on the suppression of distractors. *Vis Cogn.*, **1**, 117–128.
- Hsieh, L.T. & Ranganath, C. (2014) Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. *Neuroimage*, **90**, 721–729.
- Ipata, A.E., Gee, A.L., Gottlieb, J., Bisler, J.W. & Goldberg, M.E. (2006) LIP responses to a popout stimulus are reduced if it is overtly ignored. *Nat. Neurosci.*, **9**, 1071–1076.
- Ithipipat, S., Wessel, J.R. & Aron, A.R. (2013) Frontal theta is a signature of successful working memory manipulation. *Exp. Brain Res.*, **224**, 255–262.
- Itti, L. & Koch, C. (2001) Computational modelling of visual attention. *Nat. Rev. Neurosci.*, **2**, 194–203.
- Itti, L., Koch, C. & Niebur, E. (1998) A model of saliency-based visual attention for rapid scene analysis. *IEEE T. Pattern. Anal.*, **11**, 1254–1259.
- Kiss, M., Driver, J. & Eimer, M. (2009) Reward priority of visual target singletons modulates event-related potential signatures of attentional selection. *Psychol. Sci.*, **20**, 245–251.
- Kriegeskorte, N., Simmons, W.K., Bellgowan, P.S. & Baker, C.I. (2009) Circular analysis in systems neuroscience: the dangers of double dipping. *Nat. Neurosci.*, **12**, 535–540.
- LePelle, M.E., Pearson, D., Griffiths, O. & Beesley, T. (2015) When goals conflict with values: counterproductive attentional and oculomotor capture by reward-related stimuli. *J. Exp. Psychol. Gen.*, **144**, 158–171.
- Lee, J. & Shomstein, S. (2014) Reward-based transfer from bottom-up to top-down search tasks. *Psychol. Sci.*, **25**, 466–475.
- Li, Z. (2002) A saliency map in primary visual cortex. *Trends Cogn. Sci.*, **6**, 9–16.
- Liston, D.B. & Stone, L.S. (2008) Effects of prior information and reward on oculomotor and perceptual choices. *J. Neurosci.*, **28**, 13866–13875.
- Litvak, V. & Friston, K. (2008) Electromagnetic source reconstruction for group studies. *Neuroimage*, **42**, 1490–1498.
- Litvak, V., Mattout, J., Kiebel, S., Phillips, C., Henson, R., Kilner, J., Barnes, G., Oostenveld, R., Daunizeau, J., Flandin, G., Penn, W. & Friston, K. (2011) EEG and MEG data analysis in SPM8. *Comput. Intell. Neurosci.*, **2011**, 852961.
- Logan, G.D. (1988) Toward an instance theory of automatization. *Psychol. Rev.*, **95**, 492–527.
- Moore, E., Laiti, L. & Chelazzi, L. (2003) Associative knowledge controls deployment of visual selective attention. *Nat. Neurosci.*, **6**, 182–189.
- Murayama, K. & Kitagami, S. (2014) Consolidation power of extrinsic rewards: reward cues enhance long-term memory for irrelevant past events. *J. Exp. Psychol. Gen.*, **143**, 15–20.
- Olivers, C.N., Peters, J., Houtkamp, R. & Roelfsema, P.R. (2011) Different states in visual working memory: when it guides attention and when it does not. *Trends Cogn. Sci.*, **15**, 327–334.
- Olson, I.R., McCoy, D., Klobusick, E. & Ross, L.A. (2013) Social cognition and the anterior temporal lobes: a review and theoretical framework. *Soc. Cogn. Affect. Neurosci.*, **8**, 123–133.
- Padmala, S. & Pessoa, L. (2011) Reward reduces conflict by enhancing attentional control and biasing visual cortical processing. *J. Cognitive Neurosci.*, **23**, 3419–3432.
- Peck, C.J., Jangraw, D.C., Suzuki, M., Efe, R. & Gottlieb, J. (2009) Reward modulates attention independent of action value in posterior parietal cortex. *J. Neurosci.*, **29**, 11182–11191.
- Penn, W.D., Stephan, K.E., Mechelli, A. & Friston, K.J. (2004) Comparing dynamic causal models. *Neuroimage*, **22**, 1157–1172.
- Pessoa, L. (2009) How do emotion and motivation direct executive control? *Trends Cogn. Sci.*, **13**, 160–166.
- Platt, M.L. & Glimcher, P.W. (1999) Neural correlates of decision variables in parietal cortex. *Nature*, **400**, 233–238.
- Polich, J. (2007) Updating P300: an integrative theory of P3a and P3b. *Clin. Neurophysiol.*, **118**, 2128–2148.
- Potts, G.F. & Tucker, D.M. (2001) Frontal evaluation and posterior representation in target detection. *Cognitive Brain Res.*, **11**, 147–156.
- Ptak, R. (2012) The frontoparietal attention network of the human brain: action, saliency, and a priority map of the environment. *Neuroscientist*, **18**, 502–515.
- Qi, S., Zeng, Q., Ding, C. & Li, H. (2013) Neural correlates of reward-driven attentional capture in visual search. *Brain Res.*, **152**, 32–43.
- Raghavachari, S., Kahana, M.J., Ritscher, D.S., Caplan, J.B., Kirschen, M.P., Bourgeois, B., Madsen, J.R. & Lisman, J.E. (2001) Gating of human theta oscillations by a working memory task. *J. Neurosci.*, **21**, 3175–3183.
- Sawaki, R. & Luck, S.J. (2010) Capture versus suppression of attention by salient singletons: electrophysiological evidence for an automatic attention-to-me signal. *Atten. Percept. Psycho.*, **48**, 1455–1470.
- Sawaki, R. & Luck, S.J. (2011) Active suppression of distractors that match the contents of visual working memory. *Vis. Cogn.*, **17**, 956–972.
- Sawaki, R., Geng, J.J. & Luck, S.J. (2012) A common neural mechanism for preventing and terminating the allocation of attention. *J. Neurosci.*, **32**, 10725–10736.
- Stephan, K.E., Penn, W.D., Moran, R.J., den Ouden, H.E., Daunizeau, J. & Friston, K.J. (2010) Ten simple rules for dynamic causal modeling. *Neuroimage*, **49**, 3099–3109.
- Sugrue, L.P., Corrado, G.S. & Newsome, W.T. (2004) Matching behavior and the representation of value in the parietal cortex. *Science*, **304**, 1782–1787.
- Theeuwes, J. (1991) Cross-dimensional perceptual selectivity. *Percept. Psychophys.*, **50**, 184–193.
- Theeuwes, J., Olivers, C.N.L. & Belopolsky, A. (2010) Stimulus-driven capture and contingent capture. *Wiley Int. Rev. Cogn. Sci.*, **14**, 872–881.
- van Veen, V., Cohen, J.D., Botvinick, M.M., Stenger, V.A. & Carter, C.S. (2001) Anterior cingulate cortex, conflict monitoring, and levels of processing. *Neuroimage*, **14**, 1302–1308.
- Voss, J.L. & Paller, K.A. (2009) An electrophysiological signature of unconscious recognition memory. *Nat. Neurosci.*, **12**, 349–355.
- Woodman, G.F. & Luck, S.J. (2007) Do the contents of visual working memory automatically influence attentional selection during visual search? *J. Exp. Psychol. Human*, **33**, 363–377.
- Zanto, T.P., Rubens, M.T., Thangavel, A. & Gazzaniga, A. (2011) Causal role of the prefrontal cortex in top-down modulation of visual processing and working memory. *Nat. Neurosci.*, **14**, 656–661.