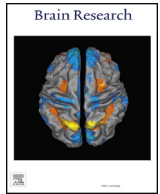




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Research report

Dissociable neural mechanisms underlie value-driven and selection-driven attentional capture

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HIGHLIGHTS

- Stimuli selected repeatedly in the past capture attention.
- The capture effect is driven by visual plasticity acquired over repeated selection.
- There was a more right lateralised pattern of distractor-evoked activation.
- No distractor-evoked activity was found in the caudate tail.
- Selection history and reward history influence attention via dissociable mechanisms.

ARTICLE INFO

Keywords:

Selection history
 Reward history
 Attentional capture
 Visual plasticity
 fMRI

ABSTRACT

Stimuli associated with reward acquire the ability to automatically capture attention. It is also the case that, with sufficient training, former targets can acquire the ability to capture attention in the absence of extrinsic rewards. It remains unclear whether these two experience-dependent attentional biases share a common underlying mechanism. The present study examined the influence of selection history on attentional capture, and compared its neural correlates with those of value-driven attentional capture reported in Anderson et al. (2014a). Participants completed a four-day training in visual search for a specific colour target. In a subsequent test phase, they performed visual search for a shape-defined target in which colour was task-irrelevant. Response times were slower when a former target-colour distractor was present than when it was absent, replicating attentional capture by unrewarded former targets. Neuroimaging results revealed preferential activation by a former target-colour distractor in sensory areas. A more right lateralised pattern of activation was observed, compared to attentional capture by reward cues. No distractor-evoked activity was found in the caudate tail. These results imply that attentional capture by selection history is primarily driven by plasticity in sensory areas, and that reward history and selection history influence attention via dissociable underlying mechanisms.

1. Introduction

The human visual system has a limited capacity for processing information (Desimone and Duncan, 1995). Hence the ability to filter out unnecessary information is vital. Two modes of visual selection – top-down and bottom-up control – facilitate efficient processing. Top-down control guides attention in a goal-directed manner (Wolfe et al., 1989), whereas bottom-up control guides attention based on the physical salience of stimuli (Theeuwes, 1992; Theeuwes, 2010). In addition to these traditional modes, selection history has recently been suggested as another element of attentional control. It refers to prioritisation of items that have been previously attended. Repeated selection as a target and extrinsic rewards predicted by a stimulus are two components of

prior experience that influence the control of attention under this framework (Awh et al., 2012).

A stimulus previously associated with reward can bias attention even when it is not salient and task-irrelevant (referred to as value-driven attentional capture; Anderson et al., 2011). In particular, the caudate tail and extrastriate cortex respond preferentially to a previously reward-associated stimulus when it appears as a distractor, representing a putatively value-driven attentional priority signal (Anderson et al., 2014a; Anderson et al., 2016).

However, reward may not be necessary for a former target stimulus to be capable of capturing attention (Grubb and Li, 2018; Sha and Jiang, 2016). Prior experience alone may be sufficient to influence attentional selection (Awh et al., 2012). Following an extensive training

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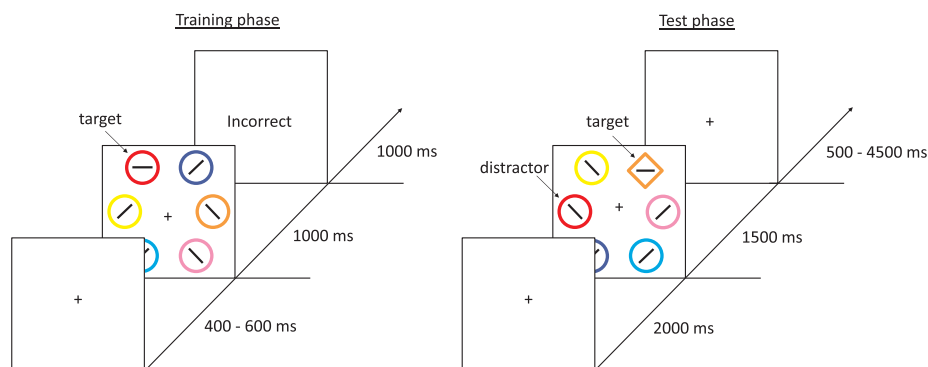


Fig. 1. Sequence of trial events.

that spans multiple days in visual search without extrinsic rewards, task-irrelevant former targets acquire the ability to capture attention (Kyllingsbæk et al., 2001; Kyllingsbæk et al., 2014; Lin et al., 2016; Qu et al., 2017; Schneider and Shiffrin, 1977).

Theories of perceptual learning have suggested that a sense of accomplishment upon successful task performance provides an internal reward signal that reinforces sensory signals related to the presented feature (Seitz and Watanabe, 2005; Watanabe and Sasaki, 2015). Confidence prediction error signals – the discrepancy between the level of confidence in performance on a given trial and the expected level of performance confidence based on previous experiences – generated from an internal monitoring process function as teaching signals that drive learning. The neural substrates implicated in such learning overlap with those implicated in reward learning. The dopaminergic brain regions such as the ventral striatum and ventral tegmental area (VTA) that contain confidence signals project to sensory regions, causing plasticity in those regions (Aron et al., 2004; Daniel and Pollmann, 2012; Guggenmos et al., 2016; Hebart et al., 2016; Roelfsema et al., 2010). This offers a potentially unifying account of value-driven attention and attentional capture driven by selection history.

In contrast, evidence for a dissociable mechanism comes from individuals with depressive symptoms, who exhibited a blunted attentional bias following rewarded but not unrewarded training (Anderson et al., 2014b; Anderson et al., 2017). There may be two distinct influences that contribute to attentional bias to former targets. Reward prediction error refers to the difference between received and predicted rewards. It is positive when greater reward is received than predicted; it is negative when less reward is received than predicted (Schultz, 2007). These error signals serve as teaching signals that enhance stimulus representation (Anderson, 2016; Sali et al., 2014). Stimulus representation can also be enhanced through repeated selection, independently of feedback processing. This is reflected in greater activation in the primary visual cortex post-learning (e.g. Furmanski et al., 2004; Schwartz et al., 2002; Yotsumoto et al., 2008). It is thought that only the former is affected by depressive symptoms.

These studies pose a question whether value-driven attentional capture and selection-driven attentional capture share a common mechanism. The present study addressed this question by examining the neural correlates of selection-driven attentional capture using functional magnetic resonance imaging (fMRI) and directly comparing them to those of value-driven attentional capture reported in Anderson et al. (2014a). Participants completed a four-day lab training in which they searched for a colour-defined target among differently coloured distractors. On the following day, participants were scanned while completing a test phase, which mirrored the design of Anderson et al. (2014a). They searched for a shape singleton target among differently shaped distractors. Occasionally, one of the distractors was rendered in the former target colour.

Objects that are previously reward predictive are more strongly

represented in the caudate tail (Anderson et al., 2014a; Anderson et al., 2016; Kim et al., 2013; Yamamoto et al., 2013). If value-driven and selection-driven attentional capture rely on a common mechanism, the caudate tail and extrastriate cortex would show stronger activation in the present study, similar to the results observed in Anderson et al. (2014a). We expected activations primarily in visual processing areas if they rely on a dissociable mechanism, with selection history being limited to plasticity in sensory cortex.

2. Results

2.1. Behavioural data

2.1.1. Training phase

There was a robust effect of training day on RT, $F(3, 69) = 57.13$, $p < 0.001$, $\eta_p^2 = 0.71$. On each day, participants made significant improvements in RT. There was also a robust effect of training day on accuracy, $F(3, 69) = 10.02$, $p < 0.001$, $\eta_p^2 = 0.30$. Participants made significant improvements in accuracy between Day 1 and Day 2. By Day 3, their performance reached a stable level (Fig. 2).

2.1.2. Test phase

There were significant main effects of run, $F(3, 69) = 57.05$, $p < 0.001$, $\eta_p^2 = 0.71$, and distractor condition, $F(1, 23) = 20.1$, $p < 0.001$, $\eta_p^2 = 0.47$, respectively. RT gradually improved over the test runs and it was significantly slower when a former target distractor was present relative to when it was absent. The interaction between the two factors was not significant, $F(3, 69) = 2.04$, $p = 0.12$, $\eta_p^2 = 0.08$. For accuracy, only the main effect of run was significant, $F(3, 69) = 22.28$, $p < 0.001$, $\eta_p^2 = 0.49$. The main effect of distractor condition and the interaction effect were not significant ($F_s < 0.77$, $p_s > 0.47$) (Fig. 3).

2.2. MRI data

The whole brain analysis comparing trials on which a former target distractor was present versus absent in the contralateral hemifield revealed no significant areas of activation when the voxelwise p was thresholded at 0.005, although trend-wise activations were evident in the visual cortex. These activations were reliable at the cluster level using a more liberal voxelwise p threshold of 0.05, with significant activation by the distractor mostly in visual processing areas, including the right parahippocampal gyrus, right middle occipital gyrus, right lingual gyrus, right cuneus and left inferior parietal lobule when the distractor was present in the left hemifield. When it was present in the right hemifield, the left fusiform gyrus, left middle occipital gyrus and left middle temporal gyrus were significantly more responsive (Fig. 4).

Notably, the pattern of activation observed in the present study appeared more right-hemisphere lateralised than the pattern of distractor-evoked activity observed by reward-associated stimuli in

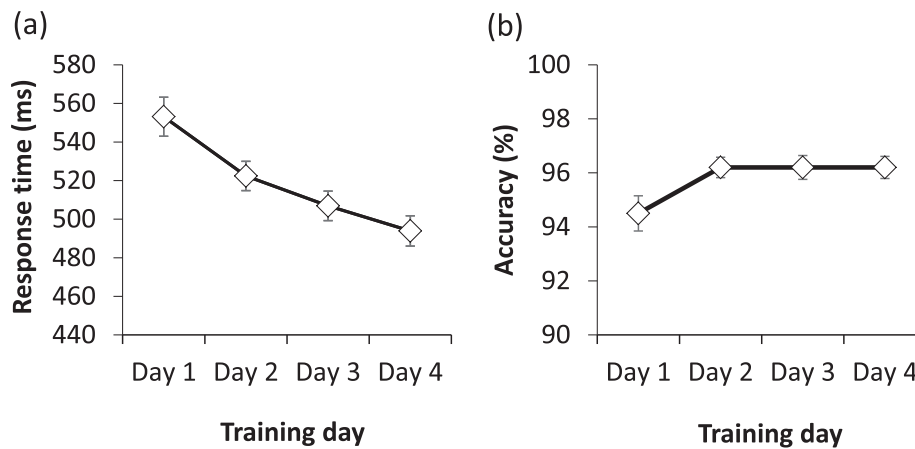


Fig. 2. Mean response time (a) and accuracy (b) in the training phase. Error bars represent the within-subjects SEM.

Anderson et al. (2014a). To formalise this comparison, we contrasted distractor-evoked responses in the present study to those observed in Anderson et al. (2014a) within the regions of the value-driven attention network. We defined the value-driven attention network using a region of interest mask provided by an independent dataset (Anderson, 2017). For each hemisphere, the difference in the peak of the haemodynamic response to distractors in the contralateral hemifield versus distractor-absent trials was computed, with the difference scores subjected to a 2×2 analysis of variance (ANOVA) with hemisphere as a within-subjects factor and feedback (reward vs. no reward) as a between-subjects factor. Relative to Anderson et al.'s (2014a) reward study, the current study showed a significantly more right-lateralised pattern of activation, as revealed by a hemisphere by feedback interaction, $F(1, 39) = 5.18, p = 0.03, \eta_p^2 = 0.12$ (Fig. 5).

To further probe whether selection-driven attentional capture involves the same priority signals underlying value-driven attentional capture, we specifically probed distractor-evoked responses in the caudate tail. The caudate tail is known to respond preferentially to previously reward-predictive objects (Anderson et al., 2014a; Anderson et al., 2016; Kim et al., 2013; Yamamoto et al., 2013), and is thought to reflect a dopaminergic value-based visual priority signal. Hence significant activation in the caudate tail would imply that value-driven and selection-driven attentional capture share a common signalling mechanism. However, using the caudate tail activation provided by Anderson et al. (2014a) as a mask, no significant distractor-evoked activation was found in the caudate tail in the present study, t

(23) = $-0.46, p = 0.65$, corroborating the absence of an effect in this region at the whole-brain level. The Bayes factor for this comparison was 4.15 in favour of the null hypothesis, which is considered strong evidence (Rouder et al., 2009).

3. Discussion

The present study examined the neural mechanisms of attentional capture by selection history using an extensive training procedure that does not involve reward feedback and directly compared the neural correlates of selection-driven and value-driven attentional capture (Anderson et al., 2014a). We found a highly reliable attentional capture effect by a former target distractor, as indicated by slower RTs when it was present relative to when it was absent. This effect was primarily driven by enhanced activity in the visual cortex and did not appear to recruit the caudate tail. It also showed a more right-lateralised pattern of activation than value-driven attentional capture. These results imply that dissociable mechanisms underlie the influence of reward history and selection history on attentional capture.

The contribution of reward history and selection history to value-driven attentional capture has been ambiguous, with some studies failing to demonstrate the influence of selection history (e.g. Anderson and Halpern, 2017; Marchner and Preusschhof, 2018; Qi et al., 2013) and others finding a joint contribution (Grubb and Li, 2018; Sha and Jiang, 2016). Our behavioural data seemingly favour the joint contribution account, at least with sufficient training, but the neural

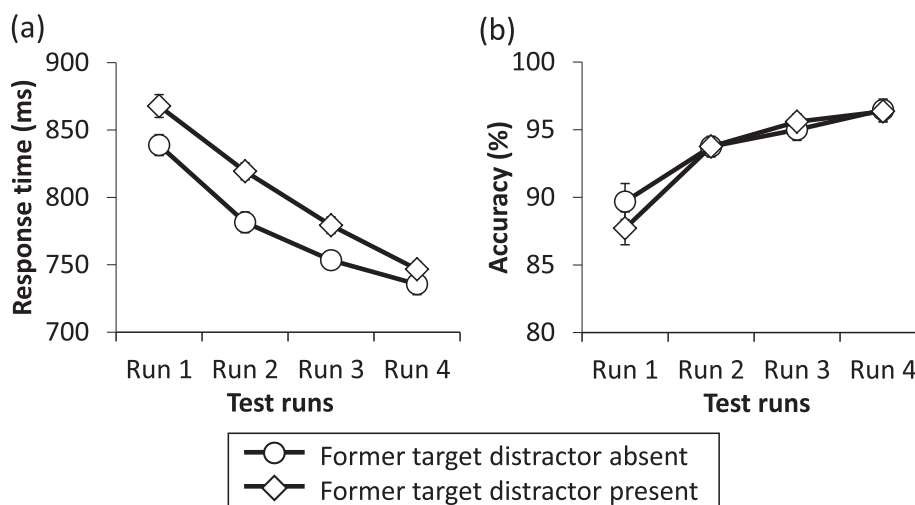


Fig. 3. Mean response time (a) and accuracy (b) in the test phase. Error bars represent the within-subjects SEM. * $p < 0.001$.

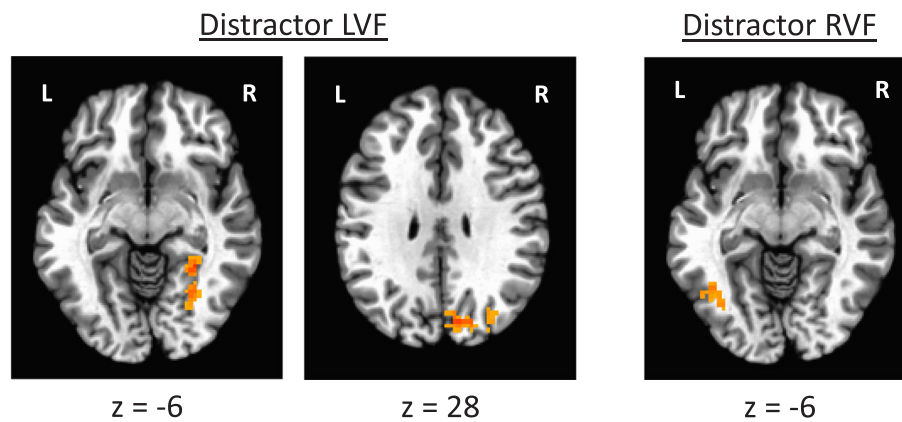


Fig. 4. Cortical representation of selection-driven attentional capture. LVF = left visual field, RVF = right visual field.

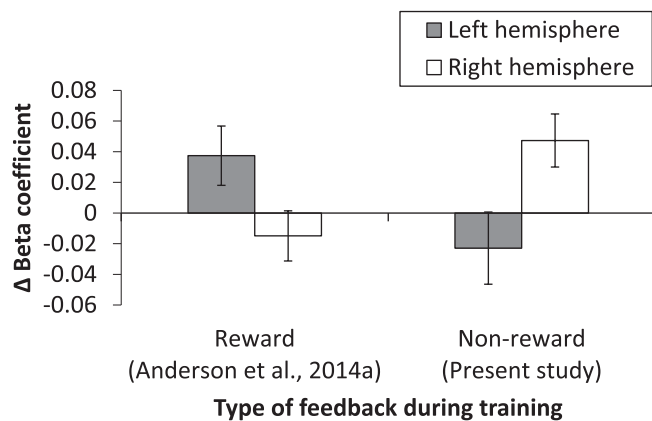


Fig. 5. The interaction between laterality and type of feedback during training on distractor-evoked activity (present in the contralateral hemifield minus absent, y-axis) within the value-driven attention network. Error bars represent the within-subjects SEM.

evidence suggests otherwise; neither the caudate tail nor any other dopaminergic regions responded to former target distractors. Instead of the internal reward account prevalent in the perceptual learning literature, we believe that selection-driven attentional capture in the present study reflects increased sensitivity of neurons in visual areas through repeated goal-directed selection and corresponding top-down feedback signals that drive plasticity (Furmanski et al., 2004; Roelfsema et al., 2010; Schwartz et al., 2002; Yotsumoto et al., 2008).

One possible explanation for the failure to observe a more similar neural profile to value-driven attention may be that the absence of explicit positive feedback during the training phase impeded generation of an internal reward signal. If participants were given explicit feedback about the correctness of their performance, perhaps internal reward signals would have been stronger, reaching a critical threshold for shaping the visual system. However, we believe this is unlikely. Unlike typical perceptual learning tasks, the search task in the training phase was relatively easy; participants should be able to immediately recognise whether their response was correct or not and self-generate feedback. Perceptual confidence that reflects internal reward signals has been observed even in studies that used more advanced perceptual learning tasks without feedback (Daniel and Pollmann, 2012; Guggenmos et al., 2016). It has also been suggested that feedback type – whether explicit or implicit – is negligible in producing attentional capture effects (Grubb and Li, 2018).

Instead, it may be the case that perceptual confidence and performance accuracy are dissociable in the control of attention, with only the act of correctly identifying the target serving to update priorities. In an ideal world, perceptual confidence should correlate with accuracy.

However, an increasing number of studies report that perceptual confidence does not reflect the likelihood of correct performance (Maniscalco et al., 2016; Peters et al., 2017; Vlassova et al., 2014). This may explain why we were unable to observe activations in the caudate tail.

Another possible explanation may be that attentional orienting was indeed reinforced by internal reward signals but their associative strength was susceptible to rapid extinction during the test phase. The possible role of extinction is a commonly recognised limitation of an experimental design that involves separate training and test phases, and a way to directly address this problem is combining training and test phases (Feldmann-Wüstefeld et al., 2015; Feldmann-Wüstefeld et al., 2016; Le Pelley et al., 2015). However, our findings and previous studies provide little support for the extinction account. In the present study, attention was consistently captured by a former target distractor at least through the first three runs of the task. Qu et al. (2017) also demonstrated that perceptual learning effects on attentional capture persisted 3–5 months after training.

Our across-experiments approach allowed us to measure a robust form of selection-driven attentional capture by incorporating substantially more training than the Anderson et al. (2014a) study with monetary reward, providing a strong basis for comparison. In this sense, the fact that no evidence for striatal activation was observed in the present study in spite of highly reliable behavioural evidence for attentional capture is striking. At the same time, this across-experiments approach has important limitations. A salient limitation is the inability to decompose the neural correlates of value-driven attentional capture into distinctly reward-related and selection-related components, which would require a within-subjects approach. Although in the original study a control experiment demonstrated that the neural correlates observed for value-driven attentional capture were not reducible to otherwise comparable selection history without rewards (Anderson et al., 2014a), value-driven attentional capture by definition reflects some combination or interaction between these two factors given the nature of the training phase (in which reward-predictive stimuli are search targets). An interesting question for future research concerns the nature of the relationship between these two sources of priority, which our data and prior behavioural evidence (Anderson et al., 2017) suggest should be at least to some degree dissociable. For example, it is possible that some neural signatures of value-driven attentional priority (e.g., Anderson et al., 2014a; Anderson et al., 2016) reflect the convergence of value-related and selection-related inputs, and it may be possible for value-related and selection-related priority signals to compete with each other under certain circumstances.

A second limitation of the across-experiments approach adopted here is that, although we tried to reproduce the procedures described in Anderson et al. (2014a) as closely as possible, including the timing and distribution of trials, imaging parameters, etc., subtle differences still

exist between the test phase of Anderson et al.'s (2014a) study and the present study. The two studies used different MRI scanners (Siemens MAGNETOM Verio scanner vs. Philips Gyroscan scanner) and different samples (Texas A&M University vs. Johns Hopkins University). However, any influence of these differences should be minimal, as the scan parameters (e.g., voxel size, TR, TE, flip angle) and analytic approach were matched to those of Anderson et al. (2014a), and robust value-driven attentional capture has also been reported using the Texas A&M University sample (Anderson et al., 2017; Anderson and Kim, 2018a; Anderson and Kim, 2018b).

In conclusion, the present study showed that the influence of reward history and selection history on attention are dissociable. Similar to rewarded former target distractors, unrewarded former target distractors are also capable of capturing attention, but the underlying neural mechanisms are distinct. In particular, the topography of distractor-evoked activity is different across the two hemispheres, and the caudate tail appears to be particular to the signalling of value-driven attentional priority. This latter finding, which was corroborated by a Bayes factor analysis, is consistent with evidence from non-human primates demonstrating object-selective responses in caudate tail neurons (Yamamoto et al., 2012) that are modulated by stable object-reward associations (Yamamoto et al., 2013).

4. Experimental procedure

For the purpose of comparing the present study to that of Anderson et al. (2014a), we attempted to replicate the experimental design, MRI acquisition and data analysis used in Anderson et al. (2014a) as closely as possible.

4.1. Participants

Twenty-four healthy participants were recruited from the Texas A&M University community (11 females; mean age 24.2 years). All reported normal or corrected-to-normal visual acuity and colour vision and provided written informed consent. The experimental procedure was approved by the Institutional Review Board of Texas A&M University.

4.2. Apparatus

For the in-lab portion of the experiment, stimulus presentation was controlled by a Dell OptiPlex equipped with MATLAB and Psychtoolbox 3.0. Participants were seated approximately 70 cm from a Dell P2717H monitor. Key responses were entered using a standard keyboard. For the fMRI portion of the experiment, stimulus presentation was controlled by an Invivo SensaVue display system. The eye-to-screen distance was approximately 125 cm. Key responses were entered using a Cedrus Lumina two-button response pad.

4.3. Design

The experiment consisted of a four-day lab visit, followed by a scan visit. During each lab visit, participants completed a training phase. It consisted of 1008 trials, including eight trials at the beginning which were considered warm-up trials. Between each 100 trial block, there was a short break. On the first lab visit, participants completed 36 practice trials prior to the training phase. On the last lab visit, in addition to the training phase, participants practised a test phase which consisted of 42 trials.

During the scan visit, participants completed seven brain scans, including two runs of the training phase so they could familiarise with the scan environment, followed by an anatomical scan and four runs of the test phase. Each run of the training and test phase consisted of 60 and 80 trials, respectively.

4.4. Procedure

4.4.1. Training phase

Each trial of the in-lab training phase began with a fixation cross for either 400, 500 or 600 ms, followed by a search array for 1000 ms and a feedback display for 1000 ms. The search array consisted of one target circle and five distractor circles. Each circle was 3.6° visual angle in diameter. On each side of the display, the middle circle was presented 10.6° from the fixation cross centre-to-centre, and the top and bottom circles were presented 9.8° from the fixation cross centre-to-centre. All circles had a line segment in them. Inside the target, the line was oriented either horizontally or vertically and inside the distractors, the line was tilted 45° either to the left or to the right. For half of the participants, the target circle was always rendered in red and for the other half, it was rendered in green. The target appeared in each stimulus position equally-often across trials, and the order of trials was randomised. Each distractor circle was rendered in one of the following colours, randomly chosen without replacement: blue, cyan, pink, orange, yellow and white. Participants were instructed to search for a target-coloured circle and report the orientation of a line within the circle. They pressed the “n” key and the “m” key for the vertically or horizontally oriented lines inside the circle, respectively, using their right hand. If they responded incorrectly, ‘Incorrect’ was presented and if they responded too slowly or missed the trial ‘Too slow’ appeared on the screen. No feedback was given when participants made a correct response (Fig. 1).

The training phase for the scan visit was similar. Each trial began with a fixation cross for 2000 ms, followed by a search array for 1000 ms, a fixation cross for 1000 or 3000 ms (equally-often), feedback for 1000 ms and an inter-trial-interval (ITI) consisting of a fixation cross for 1000, 3000 or 5000 ms (exponentially distributed). Each circle in the search array was 2.7° visual angle in diameter. On each side of the display, the middle circle was presented 9.1° from the fixation cross centre-to-centre, and the top and bottom circles were presented 8.5° from the fixation cross centre-to-centre. Participants pressed the left button and the right button on the response pad for the vertically or horizontally oriented lines inside the target circle, respectively, using their right hand.

4.4.2. Test phase

Each trial began with a fixation cross for 2000 ms, followed by a search display for 1500 ms and then an ITI consisting of a fixation cross for either 500, 2500 or 4500 ms (exponentially distributed). The search array contained a uniquely shaped target and five differently shaped distractors, appearing in the same positions used in the training phase. If the target was a circle, then distractors were diamonds and vice versa. All distractor shapes had a 45° tilted line segment in them. The target shape had a horizontal or vertical line segment in it. The target appeared in each position equally-often. On half of the trials, one of the distractors appeared in the colour that defined the target in the training phase. The distractor appeared on the side of the screen opposite the target on 3/5 of trials on which it was present, and on the same side on the remaining 2/5 of trials. Trials were presented in a random order. Participants were instructed to find a unique shape and report the orientation of a line within the shape, using the same orientation-to-response mapping as in the in-scanner portion of the training phase. Feedback was not provided (Fig. 1). The timing, distribution, and number of trials were matched to Anderson et al. (2014a), as were the experimental stimuli (e.g., same colours, shapes, line segments, etc.).

4.5. MRI data acquisition

MRI data were acquired with a Siemens 3-Tesla MAGNETOM Verio scanner and a 32-channel head coil at the Texas A&M Institute for Preclinical Studies (TIPS). An anatomical scan was acquired using a T1-weighted magnetisation prepared rapid gradient echo (MPRAGE)

sequence (150 coronal slices, TR = 7.9 ms, TE = 3.65 ms, flip angle = 8°, voxel size = 1 mm isotropic). Whole-brain functional images were acquired using a T2*-weighted echo planar imaging (EPI) sequence (35 axial slices, TR = 2000 ms, TE = 30 ms, flip angle = 70°, image matrix = 80 × 80, field of view = 240 mm, slice thickness = 2.5 mm with a 0.5 mm gap), using the same parameters as Anderson et al. (2014a). The first three volumes were discarded to allow stabilisation of magnetic fields. The total number of volumes acquired was 245 for each training phase run and 203 for each test phase run.

4.6. MRI data processing

Data from one participant were excluded from the analysis due to scanner failure. Preprocessing and analysis were conducted using the AFNI software package (Cox, 1996). All functional images from the test phase were slice time corrected and motion corrected using the first image that immediately follows the anatomical scan as a reference. They were then co-registered to the anatomical image of each participant and warped to the Talairach brain (Talairach and Tournoux, 1988) using 3dQwarp. The images were then converted into percent signal change normalised to the mean of each run and spatially smoothed using a 5 mm full width half maximum Gaussian kernel.

The preprocessed data were subjected to a general linear model (GLM) with the following regressors of interest, following the procedures of Anderson et al. (2014a): (1) target on the left, distractor absent, (2) target on the right, distractor absent, (3) target on the left, distractor on the left, (4) target on the left, distractor on the right, (5) target on the right, distractor on the left, (6) target on the right, distractor on the right. The regressors were modelled using finite impulse response (FIR) functions beginning at the onset of the search display. Regressors of non-interest included six motion parameters and scanner drift. To compare the peak of the haemodynamic response to each condition of interest, the resulting beta weight estimates were averaged 4–6 s post search display onset and submitted to a priori paired samples *t*-tests.

Two paired samples *t*-tests were conducted on the peak beta weight estimates. We compared trials on which a former target distractor was present versus absent in the contralateral hemifield, separately for each of the two hemifields (as in Anderson et al., 2014a). We focused these analyses on trials on which the target was presented in the ipsilateral hemifield, thereby isolating the response to task-irrelevant stimuli in the contralateral hemifield as a function of selection history (i.e., regressors 4 vs. 1 and 5 vs. 2 as described above). The results were corrected for multiple comparisons using the AFNI programme 3dClustSim, with the smoothness of the data estimated using the ACF method (clusterwise $\alpha < 0.05$).

4.7. Analysis of behavioural data

Only correct responses were included in the analyses of mean response times (RTs) and RTs faster than 200 ms or exceeding 2.5 standard deviations of the mean were trimmed. RT and accuracy from the lab training phase were subjected to a repeated-measures ANOVA, with training day (1–4) as a within-subjects factor. RT and accuracy from the test phase were also subjected to a repeated-measures ANOVA, with run (1–4) and distractor condition (former target distractor present vs. absent) as factors.

5. Declarations of interest

None.

Author contributions

BAA and HK conceived of the study and designed the experiments.

HK collected the data. BAA and HK analysed the data. BAA and HK wrote and edited the manuscript.

Funding sources

The reported research was funded through a start-up package to BAA through Texas A&M University and NARSAD Young Investigator Grant 26008 to BAA.

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