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Neural evidence for automatic value-modulated approach behaviour

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ABSTRACT

Reward learning has the ability to bias both attention and behaviour. The current study presents behavioural and neural evidence that irrelevant responses evoked by previously reward-associated stimuli are more robustly represented in the motor system using a combined go/no-go and flankers task. Following a colour-reward association training, participants were instructed to respond to a central target only in a response-relevant context, while ignoring flankers that appeared either in a high-value or low-value colour. The motor cortex and cerebellum exhibited reduced activation to low-value flankers in a response-irrelevant context, consistent with goal-directed response suppression. However, these same regions exhibited similar activation to high-value flankers regardless of their response relevance, indicating less effective suppression, and the resulting interaction in motor cortex activation was strongly predicted by the influence of the flankers on behaviour. These findings suggest that associative reward learning produces a general approach bias, which is particularly evident when it conflicts with task goals, extending the principle of value-driven attention to stimulus-evoked responses in the motor system.

1. Introduction

Multiple inputs demand attention in a visually cluttered environment, as the human visual system can only process a subset of such input at any one moment in time (Desimone and Duncan, 1995). Two attentional control mechanisms are responsible for selecting stimuli for further processing (Corbetta et al., 2008; Corbetta and Shulman, 2002). Top-down attentional control selects stimuli in a goal-driven manner (Wolfe et al., 1989). Bottom-up attentional control is guided by physical salience of stimuli (Theeuwes, 1992, 2010). In addition to these two mechanisms, selection history has been proposed as a third category of attentional control mechanism to explain selection of stimuli that are neither physically salient nor task-relevant (Awh et al., 2012). One of the components of selection history is reward history. Through associative reward learning, a stimulus feature acquires the ability to capture attention even when it is physically non-salient and task-irrelevant (referred to as value-driven attention; Anderson et al., 2011).

Associative reward learning facilitates approach behaviour towards reward-associated stimuli (Berridge and Robinson, 1998; Krieglmeyer et al., 2010), and attention to reward cues is believed to play a role in this process (Anderson, 2017; Berridge, 2012). This biasing influence of reward on behaviour has been argued to be at least partly automatic, playing a role in the addiction process (Anderson, 2016b; Robinson and Berridge, 1993). However, the mechanisms by which associative reward learning biases behaviour towards, or more generally in favour of, reward-associated stimuli remains unclear (see Anderson, 2017). In the present study, we sought to examine the relationship between associative reward learning, value-driven attention, and automatic biases in response processing in the motor system. Specifically, we probed whether stimulus-evoked responses in the motor system are automatically influenced by reward history, causing the suppression of task-irrelevant responses to be less effective when the eliciting stimulus has high value.

There is good reason to predict that value-driven attention would have consequences for the strength of stimulus-evoked responses in the motor system, especially when this evoked response conflicts with task goals. The allocation of attention potentiates the sensory processing of stimuli (Jehee et al., 2011; Pessoa et al., 2003; Serences and Boynton, 2007), and in a stop-signal task, competition in the sensory processing of a go and stop signal predicts whether the go response is inhibited in the motor cortex (Boehler et al., 2009). When task-irrelevant distractors compete for attention with a stop signal, response inhibition is impaired (Verbruggen et al., 2014), and the same is true when greater attentional control is required to overcome distractor interference in response selection (Verbruggen et al., 2004). Task-irrelevant information that is consistent with either the need to respond or withhold from responding biases behaviour accordingly (Chmielewski et al., 2016a, 2016b; Kramer et al., 1994; Ridderinkhof et al., 1999), along with stimulus-evoked brain activity during the response selection stage (Chmielewski and Beste,

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2016; Krebs et al., 2011). To the degree that high-value stimuli draw attention, responses evoked by such stimuli might more robustly activate the motor system, and the ability to modulate such responses in accordance with task goals might be reduced with distraction.

Neurophysiological evidence also points to a possible relationship between value-driven attention and stimulus-evoked activity in the motor system. Striatal dopamine plays an important role in both the learning (Anderson et al., 2017) and signalling (Anderson et al., 2016c) of value-driven attentional priority as well as the control of motor behaviour (Bromberg-Martin et al., 2010; Dirnberger and Jahanshahi, 2013; Redgrave et al., 2010; Strafella et al., 2003). In particular, the orienting of attention to a reward-predictive stimulus is correlated with dopamine release in the posterior putamen (Anderson et al., 2016c), which has been strongly implicated in the control of well-learned behaviour (e.g., Bapi et al., 2006; Jueptner et al., 1997; Lehericy et al., 2005). Consistent with this relationship, incentive salience, which encompasses both motivated approach behaviour and biased attentional processing (Berridge, 2012), is thought to rely critically on the striatal dopamine system (Peciña and Berridge, 2013; Pitchers et al., 2017; Wyvell and Berridge, 2000). This shared reliance on striatal dopamine signalling lends further support to the possibility that reward-associated stimuli not only receive more robust representation in perceptual systems (Anderson, 2016a), but also generate a more robust response signal that is less effectively suppressed in a response-irrelevant context.

One of the hallmarks of value-driven attentional capture is its robustness to conflicting task goals (Anderson et al., 2011), which speaks to both its automaticity and translational relevance to issues such as addiction (Anderson, 2016a, 2016b). Correspondingly, we were particularly interested in how reward learning might bias responses evoked by task-irrelevant stimuli in the motor system when such responses explicitly conflict with task goals. An experimental paradigm that we recently developed is well-suited to this specific research question. In this combined go/no-go and flankers task, responses are required only when targets appear in a go colour (Anderson et al., 2012; Anderson and Folk, 2014); task-irrelevant flankers can appear in either the go colour (response-relevant) or a no-go colour (response-irrelevant). The flankers are associated with either the same response as the target (compatible) or the opposite response as the target (incompatible). A reverse-compatibility effect is observed when the flankers are response-irrelevant: response times (RTs) to targets are slower when the flankers are compatible than when they are incompatible. That is, the response-irrelevant flankers are associated with a behavioural profile consistent with the inhibition of their associated response, slowing down responses to targets that signal the need for this same response. This inhibitory process is supported by activation of the default mode network (Anderson et al., 2016a).

Importantly, this reverse-compatibility effect is reduced or eliminated when the flankers are associated with high value. In Anderson et al. (2016b), participants first learned to associate colours with varying amounts of reward. In the combined go/no-go and flankers task that followed, response-irrelevant flankers were rendered in the colours previously associated with reward. Responses evoked by the flankers rendered in the high-value colour were less subject to goal-contingent inhibitory control as reflected in the reverse-compatibility effect, providing behavioural evidence that high-value stimuli evoke robust responses in the motor system regardless of task goals.

While there is a wealth of behavioural evidence that stimuli previously associated with reward attract attention (Anderson, 2016a) and potentiate approach-oriented behaviour (Anderson, 2017), the neural mechanisms underlying the automatic approach component remain unclear. In particular, whether the automatic influence of reward history on information processing extends to stimulus-evoked responses in the motor system is not known. In the present study, we probed the neural correlates of value-dependent modulations of motor responses using the combined go/no-go and flankers task developed by Anderson et al. (2016b).

We expected to replicate Anderson et al. (2016b) results in behaviour: responses evoked by high-value flankers would be less subject to task-contingent modulation, influencing behaviour similarly regardless of response-relevance, whereas those generated by low-value flankers would be more effectively suppressed in a response-irrelevant context, selectively producing a robust reverse compatibility effect in this context. We were especially interested in whether this pattern would be evident in the motor cortex and cerebellum, given their role in motor control (Glover, 2004; Glover et al., 2012; Jahfari et al., 2015; Ramnani, 2006; Stinear et al., 2009) and reward processing (Derosiere et al., 2017a, 2017b; Hosp et al., 2011; Ramnani et al., 2004). Specifically, we predicted a robust interaction between flanker value and response-relevance (cued vs uncued) in flanker-evoked motor activity, such that low-value but not high-value flanker-evoked activity would be significantly reduced in a response-irrelevant context.

2. Methods

2.1. Participants

Thirty healthy participants (13 females; mean age 23 years, $SD = 4.48$ years) were recruited from the Texas A&M University community. All reported normal or corrected-to-normal visual acuity and normal colour vision, and gave written informed consent. They were compensated with money earned in the experimental task. All procedures were reviewed and approved by the Texas A&M University Institutional Review Board. A sensitivity power analysis using the resulting sample size of $n = 26$ (see below) at power $\beta = 0.80$ and $\alpha = 0.025$ (corrected for the two a priori ROIs) allowed detection of effect sizes as small as $\eta^2_p = 0.093$.

Data from the main ROI analyses are provided as supplemental material. The full dataset, including the raw MRI data, are available upon request made to the corresponding author, and will be provided under the provision that the data be used strictly for academic research purposes and not be shared with others without the express written approval of the corresponding author. Data sharing for this article complies with the requirements of the funding agencies and the stipulations of the Texas A&M University IRB approvals.

2.2. 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.

2.3. Design

The study required a lab visit and a scan visit. Participants completed a training phase in the lab and a test phase in the scanner on the following day. The training phase consisted of three runs of 60 trials. Participants completed a 48-trial practice session prior to the training phase. After the training phase, they practised the test phase for 48 trials.

During the scan visit, participants completed nine brain scans. The scans began with a training phase run to allow participants to familiarise with the scan environment and reinstate the study context, followed by three test phase runs, an anatomical scan, another training phase run and three test phase runs. Each training phase run consisted of 60 trials and each test phase run consisted of 48 trials.

2.4. Materials

2.4.1. Training phase

The training phase consisted of a fixation display, a search array and a

feedback display. The fixation display contained a fixation cross in the centre of the screen. The search array included one colour-defined target circle and five non-target circles. The target circle was rendered in red or blue, equally-often. One of the target colours was associated with a high reward (35¢) on 80% of trials and a low reward (5¢) on the remaining 20% (high-value colour). The other (low-value) colour target always yielded a low reward. The colour-reward contingency was counterbalanced across participants. Each non-target circle appeared in one of the following colours, randomly chosen on each trial without replacement: blue, cyan, pink, orange, yellow and white. All circles had a line segment in them. Inside the target, the line segment was tilted either horizontally or vertically. The line segment was tilted 45° either to the left or to the right inside the non-target circles. The feedback display showed the amount earned on the current trial along with the total amount earned in the experiment.

For the in-lab training phase, the fixation cross subtended 1° of visual angle in width and height. 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. For the fMRI training phase, the fixation cross subtended 0.8° of visual angle in width and height. Each circle 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.

2.4.2. Test phase

The test phase consisted of a fixation display, a cue display, a flanker display and a target display. The fixation display contained a fixation cross in the centre of the screen. The cue display contained a colour word cue presented in the centre of the screen. The word always appeared in the colour indicated by the word and determined the response-relevant colour on that trial. The flanker display consisted of a fixation cross in the centre and two identical letter flankers each on the left and right of the fixation cross. The flankers appeared either in the cued (response-relevant) colour or uncued (response-irrelevant) colour. In the target display, on target-present trials, a target letter replaced the fixation cross in the centre while the flankers remained on screen (the fixation cross remained in place of the target on target-absent trials). Target-present trials were included to obtain a behavioural measure of flanker-evoked inhibition, and target-absent trials were included to obtain a pure measure of flanker-evoked motor responses in the brain (as in Anderson et al., 2016a). The target letter could be either compatible or incompatible with the flanker-associated response. The cue, flanker and target appeared in either red or blue in colour. The letters for the flankers and target were A and X. The flankers were task-irrelevant and did not predict the upcoming target.

The fixation cross was 0.8° visual angle in width and height. The size of each flanker and target letter was 2° × 1.8° in width and height, respectively. The fixation-to-flanker distance was 2.7° centre-to-centre.

2.5. Procedure

2.5.1. Training phase

Each trial of the training phase began with a fixation cross for 1.8 s, followed by a search array for 1.2 s, a fixation cross for 0.6–3 s, feedback for 1.5 s and a fixation cross for 0.9–4.5 s (Fig. 1). Each colour target appeared in each of the six stimulus positions equally-often in each run, and trials were presented in a random order. Participants searched for the target circle and reported the orientation of a line within the target. For the in-lab training phase, they pressed the "n" key and the "m" key on the standard keyboard for a vertical or horizontal line using their right hand. For the fMRI training phase, they pressed the left button for a vertical line and the right button for a horizontal line on the response pad using their right hand (index and middle finger, respectively). They were only rewarded for correct responses that were registered within the 1.2 s that the search array was presented; incorrect responses or responses that were too slow resulted in a 0¢ increment in the feedback display.

2.5.2. Test phase

Each trial began with a fixation cross for 1.8–4.2 s, followed by a colour word cue for 1.5 s, a fixation cross for 2.1–4.5 s and two flankers and a fixation cross in the centre for 0.2 s. On target-absent trials, the fixation cross remained on screen for another 0.2 s. On target-present trials, a target letter replaced the fixation cross. The trial ended with a fixation cross for 1.4 s (Fig. 1). On target-present trials, if the target colour matched the cue colour, participants identified the target letter by pressing the left button for A and the right button for X using their right hand. If the colours did not match or on target-absent trials, participants had to withhold responding. Out of the 48 trials in each run, two-thirds of the trials were target-present trials and the remaining one-third were target-absent trials. On target-present trials, the target was presented in

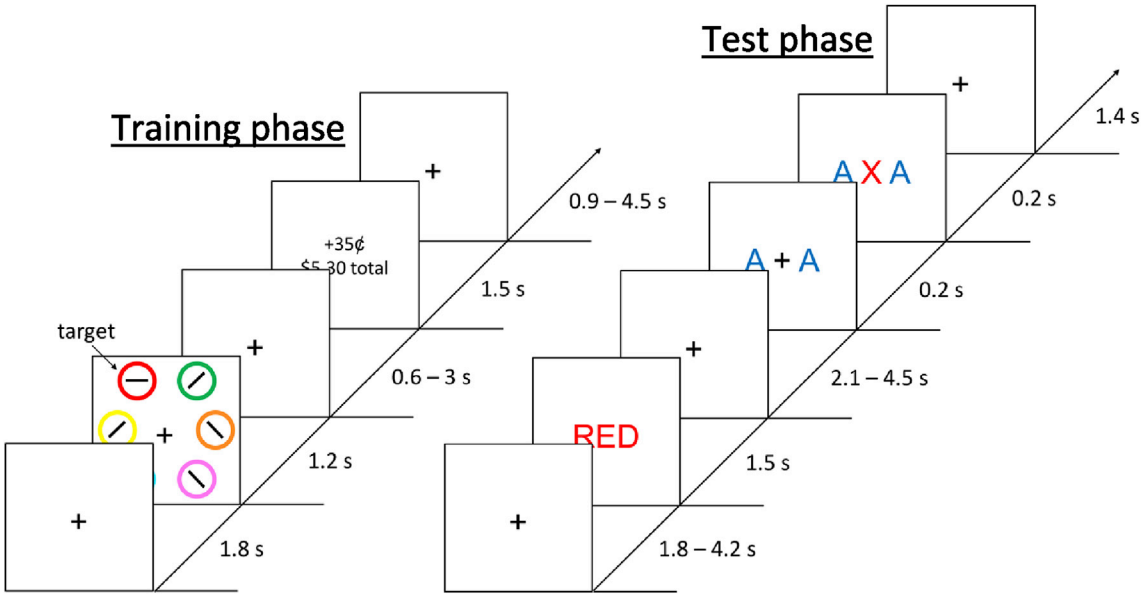

Fig. 1. Sequence of trial events.

the cued and uncued colour equally-often (each one-third of trials). For each target condition, the flanker colour, cue colour, flanker identity, and target identity (on target-present trials) were fully crossed and counterbalanced, and trials were presented in a random order.

2.6. MRI data acquisition

MRI data were acquired with a Siemens 3-T MAGNETOM Verio scanner and a 32-channel head coil at the Texas A&M Institute for Preclinical Studies (TIPS). An anatomical image was acquired using a magnetisation prepared rapid gradient echo (MPRAGE) T1-weighted sequence (150 coronal slices, TR = 7.9 ms, TE = 3.65 ms, flip angle = 8°, voxel size = 1 mm isotropic). Whole-brain functional T2*-weighted images were acquired using a multiband echo planar imaging (EPI) sequence (56 axial slices, TR = 600 ms, TE = 29 ms, flip angle = 52°, image matrix = 96 × 96, field of view = 240 mm, slice thickness = 2.5 mm with no gap). All functional scans began with dummy pulses to allow stabilisation of magnetic fields. The total number of volumes acquired was 826 for each training phase run and 778 for each test phase run.

2.7. MRI data processing

Data from four participants were discarded prior to data analysis because they fell asleep during brain scanning. Preprocessing and analysis were conducted using the AFNI software package (Cox, 1996). All functional images from the test phase were first motion corrected using the first image that immediately follows the anatomical scan as a reference. They were co-registered to the anatomical image of each participant and warped to the Talairach brain (Talairach and Tournoux, 1988) using 3dQwarp. Finally, the images were converted into percent signal change normalised to the mean of each run and spatially smoothed to a resulting 5 mm full width half maximum using 3dBlurToFWHM.

2.7.1. The preprocessed images were subjected to two separate general linear models (GLMs)

The first GLM included the following regressors of interest, collapsed across target conditions: flankers in (1) cued and (2) uncued colour crossed with flanker value (high, low), resulting in four regressors of interest in total. The second GLM focused on target-absent trials to avoid a possible confounding effect of target-related processing (e.g., the actual execution of a motor response), which obscures response bias signals arising from the flankers (see Anderson et al., 2016a). It included the following regressors of interest: flankers in (1) cued and (2) uncued colour on target-absent trials crossed with flanker value, resulting in four regressors of interest in total. All regressors of interest were modelled using 16 finite impulse response (FIR) functions beginning at the onset of the flanker display. Regressors of non-interest were six motion parameters, scanner drift and the onset of the colour word cue. The second GLM included additional regressors of non-interest for all types of target-present trials: flankers in (1) cued and (2) uncued colour, with target in cued colour and flankers in (3) cued and (4) uncued colour, with target in uncued colour, separately for trials on which the flankers appeared in the high- and low-value colour.

To compare the peak of the haemodynamic response to the conditions of interest, we extracted the maximum beta weight estimates from a time window of 3–6 s post flanker display onset and conducted a 2 × 2 repeated measures analysis of variance (ANOVA) on the extracted peak beta weight estimates. The ANOVA included flanker colour-response mapping (cued, uncued) and flanker value (high, low) as factors. The results were thresholded at voxelwise $p < 0.01$ and corrected for multiple comparisons using the AFNI programme 3dClustSim, with the smoothness of the data estimated using the ACF method (clusterwise $\alpha < 0.05$, cluster size $k > 25$).

To probe the influence of flanker-evoked response bias signals on the motor system, we defined functional regions of interest (ROIs) in the contralateral motor cortex and ipsilateral cerebellum, extracted the mean beta weight estimates from these ROIs for each participant, and conducted the same ANOVA on these extracted values. To define the ROIs, a GLM was performed using a procedure similar to those described above. The regressors of interest were: trials on which a target was present and (1) a response was made and (2) no response was made. Regressors of non-interest were six motion parameters, scanner drift, colour word cue onset and target-absent trials. The resulting peak beta weight estimates were then subjected to a paired samples *t*-test using a leave-one-subject-out approach that preserves independence to identify target response-related regions (Esterman et al., 2010). Each subject-specific ROI was defined as the cluster of the most reliable 150 voxels plus ties that overlapped with the corresponding anatomical labels in the Talairach Daemon. Note that statically identical results were obtained using cluster sizes of 50, 100, and 200.

2.8. Behavioural data analysis

Only correct trials were included in the RT analysis. RTs exceeding 2.5 standard deviations of the mean were trimmed (Anderson et al., 2014). For the in-lab training phase, RT data were subjected to a 2 × 3 ANOVA with target value (high, low) and training run (1–3) as within-subjects factors. For the fMRI training phase, RT data were subjected to a 2 × 2 ANOVA with target value (high, low) and training run (1–2) as factors. RT, accuracy, and inverse efficiency score (IES) data were subjected to a 2 × 2 × 2 ANOVA with flanker value (high, low), flanker colour-response mapping (cued, uncued) and flanker-target compatibility (compatible, incompatible) as within-subjects factors. IES was computed by dividing RT by proportion of correct responses (Townsend and Ashby, 1978). Errors occurred when participants pressed the incorrect key on cued target trials, failed to respond within the timeout limit on cued target trials (i.e., misses), or responded when they should not have on uncued target trials (i.e., false alarms). When appropriate, we report Greenhouse-Geisser corrected *p*-values and degrees of freedom. For the fMRI session, behavioural data from the participants who fell asleep during brain scanning were excluded.

2.9. Correlation analysis

To probe the nature of the reverse compatibility effect observed in the behavioural data in more depth, we computed correlations between behavioural performance during the test phase and (a) the effect of reward on performance in the training phase and (b) flanker-evoked responses during the test phase. Learning bias during the training phase was computed by first subtracting RTs to high-value target trials from those to low-value target trials, separately for the in-lab portion and fMRI portion, and then averaging the two resulting bias scores. Higher scores reflect a bias towards high-value targets.

The influence of flanker value on the reverse compatibility effect was computed using RTs from uncued flanker trials. We subtracted RTs on compatible trials from those on incompatible trials, separately for high-value flanker trials and low-value flanker trials. We then subtracted the resulting difference score for low-value flanker trials from that for high-value flanker trials. The final score represents the magnitude of the effect for low-value flankers relative to high-value flankers. The higher the score, the bigger the reverse compatibility effect for low-value flankers.

The interaction between flanker value and flanker colour-response mapping for flanker-evoked activity within the motor cortex and cerebellum ROIs was calculated similarly, replacing flanker-target compatibility with flanker colour-response mapping. The higher the score, the bigger the effect of flanker colour-response mapping for low-value flankers relative to high-value flankers (i.e., the bigger the interaction effect evident in Fig. 6).

With these scores, we computed correlations between (1) learning bias and the behavioural interaction, (2) the behavioural interaction and the interaction observed in the motor cortex and (3) the behavioural

interaction and the interaction observed in the cerebellum.

3. Results

3.1. Behavioural data

3.1.1. Training phase

For the in-lab training phase, there was a significant main effect of training run, $F(1.63, 47.34) = 14.17$, $p < 0.001$, $\eta^2_p = 0.33$ and target value, $F(1, 29) = 5.05$, $p = 0.03$, $\eta^2_p = 0.15$ (Fig. 2). Participants were generally faster to respond to high-value targets and made significant improvements in overall speed from the first run to the second run. The interaction effect was not significant, $F(2, 58) = 1.41$, $p = 0.25$. The main effect of target value persisted to the fMRI training phase, $F(1, 25) = 4.6$, $p = 0.04$, $\eta^2_p = 0.16$. The main effect of run and the interaction effect were not significant ($Fs < 0.05$, $ps > 0.31$).

3.1.2. Test phase

The three-way interaction for RT was not significant, $F(1, 25) = 1.28$, $p = 0.27$. Given our a priori hypotheses, which were informed by prior behavioural findings using this paradigm (Anderson et al., 2016b), we examined performance separately for high-value and low-value flanker trials. On low-value flanker trials, neither the main effect of flanker colour-response.

Mapping nor the main effect of flanker-target compatibility was significant ($Fs < 2.35$, $ps > 0.13$). However, there was a significant interaction between the two factors, $F(1, 25) = 4.77$, $p = 0.04$, $\eta^2_p = 0.16$. Planned contrasts revealed a significant reverse-compatibility effect for low-value flankers when rendered in the uncued colour, indicative of response inhibition; RTs were slower when the target and flankers were compatible than when they were incompatible, $t(25) = 3.13$, $p < 0.01$, $d = 0.62$. On high-value flanker trials, all effects were not significant ($Fs < 3.57$, $ps > 0.07$; Fig. 3).

The three-way interaction for accuracy was also not significant, $F(1, 25) = 2.11$, $p = 0.16$ (see Table 1). The only significant effect for accuracy was the main effect of flanker colour-response mapping on low-value flanker trials, $F(1, 25) = 5.57$, $p = 0.03$, $\eta^2_p = 0.18$. False alarms were rare (overall false alarm rate = 2.4%). For IES, the critical three-way interaction was marginally significant, $F(1, 25) = 4.22$, $p = 0.05$, $\eta^2_p = 0.14$. Planned contrasts revealed that the interaction effect originates from a difference between compatible and incompatible conditions on low-value flanker trials in which the flankers appeared in the uncued colour, $t(25) = 3.12$, $p = 0.01$, $d = 0.65$, consistent with the effects observed in RT.

3.2. Neuroimaging data

The voxel-wise whole brain analysis revealed a significant main effect of flanker colour-response mapping. Bilateral superior parietal lobule, inferior parietal lobule, inferior frontal gyrus, left superior temporal gyrus, left middle frontal gyrus, left middle occipital gyrus, left fusiform gyrus, left putamen, left precentral gyrus, right precuneus and cerebellum showed greater activation to cued flankers than uncued flankers (Fig. 4). No other effects produced significant clusters at the whole-brain level.

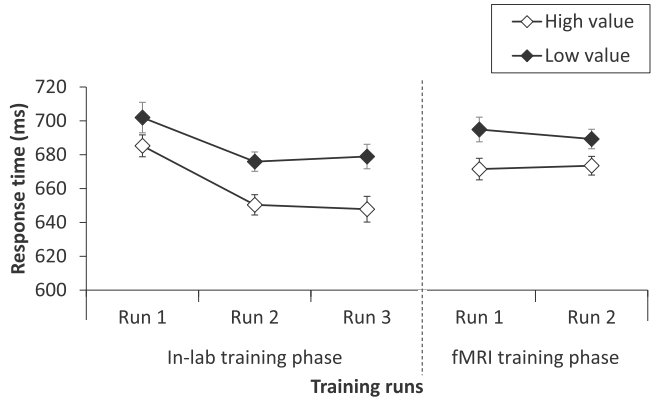

Fig. 2. Mean response times in the training phase. Error bars represent the within-subjects SEM.

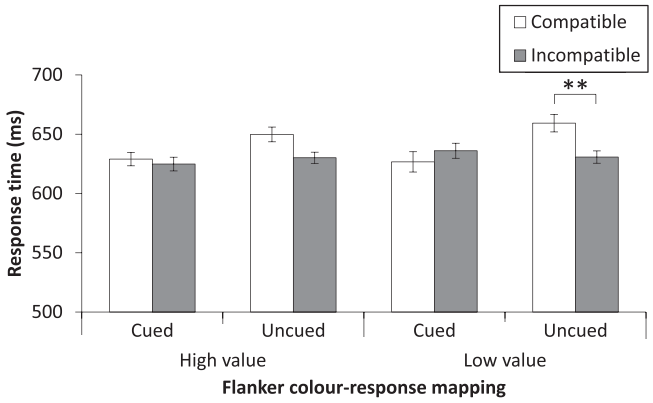

Fig. 3. Mean response times in the test phase. Error bars represent the within-subjects SEM. $^{**}p < 0.01$.

Focusing on target-absent trials revealed a significant interaction between flanker colour-response mapping and flanker value in the right inferior parietal lobule. To probe the nature of this interaction, we extracted peak beta weight estimates for each condition using a leave-one-subject out procedure to define the region in order to preserve independence (Esterman et al., 2010). On low-value flanker trials, significantly less activation was observed when the flankers were uncued, $t(25) = 4.50$, $p < 0.001$, $d = 0.9$. On high-value flanker trials, slightly more activation was observed for uncued flankers, $t(25) = 2.17$, $p = 0.04$, $d = 0.43$ (Fig. 5). The left motor cortex, overlapping with our a priori ROI, also exhibited a significant interaction at the whole-brain level.

The ROI analysis revealed a significant interaction between flanker colour-response mapping and flanker value in the motor cortex, $F(1, 25) = 9.51$, $p < 0.01$, $\eta^2_p = 0.28$, and cerebellum, $F(1, 25) = 7.10$, $p = 0.01$, $\eta^2_p = 0.22$ (File S1). Consistent with the pattern observed in the right inferior parietal lobule, both regions showed reduced activation when the flankers were response-irrelevant only on low-value flanker trials (Fig. 6).

3.3. Correlations

Learning bias during the training phase was positively correlated with individual differences in the interaction between flanker value and compatibility on uncued flanker trials in the test phase, $r = 0.44$, $p = 0.03$. This indicates that a stronger bias towards high-value stimuli during the training phase was associated with a stronger influence of reward on the reverse compatibility effect (greater reduction for high-value flankers) during the test phase. The strength of this behavioural interaction also significantly predicted the interaction observed in the motor cortex, $r = 0.66$, $p < 0.001$, linking the two indicators of inhibitory control. This same correlation between brain and behaviour did not reach significance in the cerebellum, $r = 0.26$, $p = 0.2$, although it was in the same direction.

As a measure of internal reliability, we correlated the peak of the haemodynamic response across the two conditions in which inhibition was not predicted: high- and low-value flankers presented in the cued colour, separately for each ROI. We focused on these trials given the substantial but reliable individual differences in inhibitory control as revealed by the prior correlations. The peak of the haemodynamic response to high- and low-value flankers presented in the cued colour were highly correlated in both the motor cortex, $r = 0.74$, $p < 0.001$, and

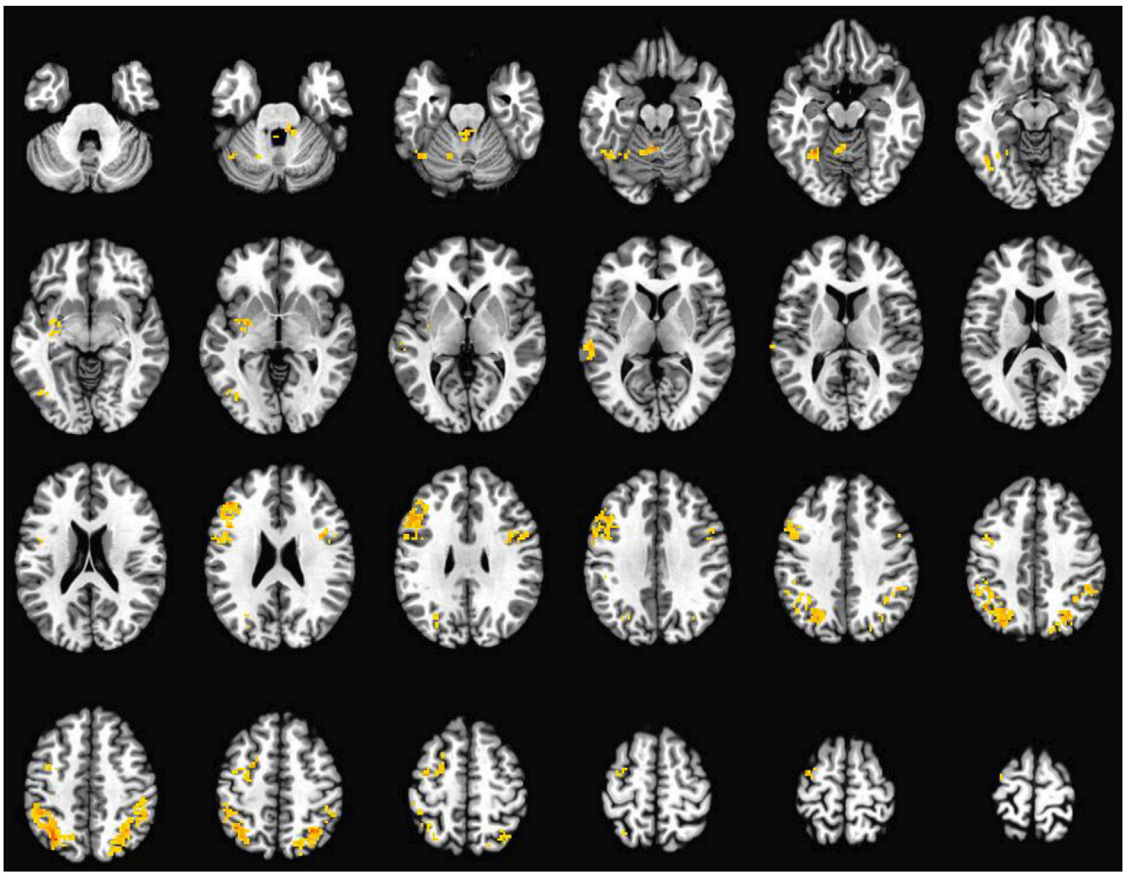

Fig. 4. Brain regions showing greater activation to cued flankers compared to uncued flankers.

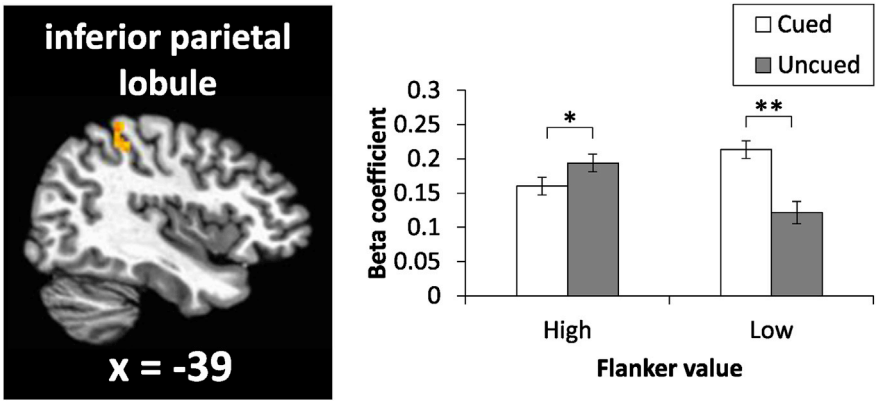

Fig. 5. The interaction between flanker value and flanker colour-response mapping in the right inferior parietal lobule. *$p < 0.05$, **$p < 0.01$.

cerebellum, $r = 0.78$, $p < 0.001$, suggesting that our experiment design produced reliable estimates of flanker-evoked brain activation.

4. Discussion

The present study provided evidence that associative reward learning has consequences for stimulus-evoked responses in the motor system. Responses evoked by low-value stimuli were suppressed or otherwise reduced in a response-irrelevant context, whereas those generated by high-value stimuli remained robust regardless of context. This pattern was evident in the right inferior parietal lobule, motor cortex and cerebellum. A correlation between the influence of reward history on flanker-evoked responses in the motor cortex and the reverse compatibility effect confirmed a relationship between our neuroimaging results and actual motor behaviour.

Successful goal-directed behaviour entails careful monitoring of the current situation. Doing so requires cognitive operations such as attending to task-relevant information, maintaining this information in working memory and planning an appropriate response (Benn et al., 2014). The frontoparietal network which includes the prefrontal cortex, premotor cortex and posterior parietal cortex flexibly configures functional connectivity depending on task demands, allowing it to support a variety of operations (Cole et al., 2013; Zanto and Gazzaley, 2013). Behavioural goal representations from the premotor cortex are stored in the dorsolateral prefrontal cortex (DLPFC), which prevents interference from distractors and facilitates shifting of attention to task-relevant

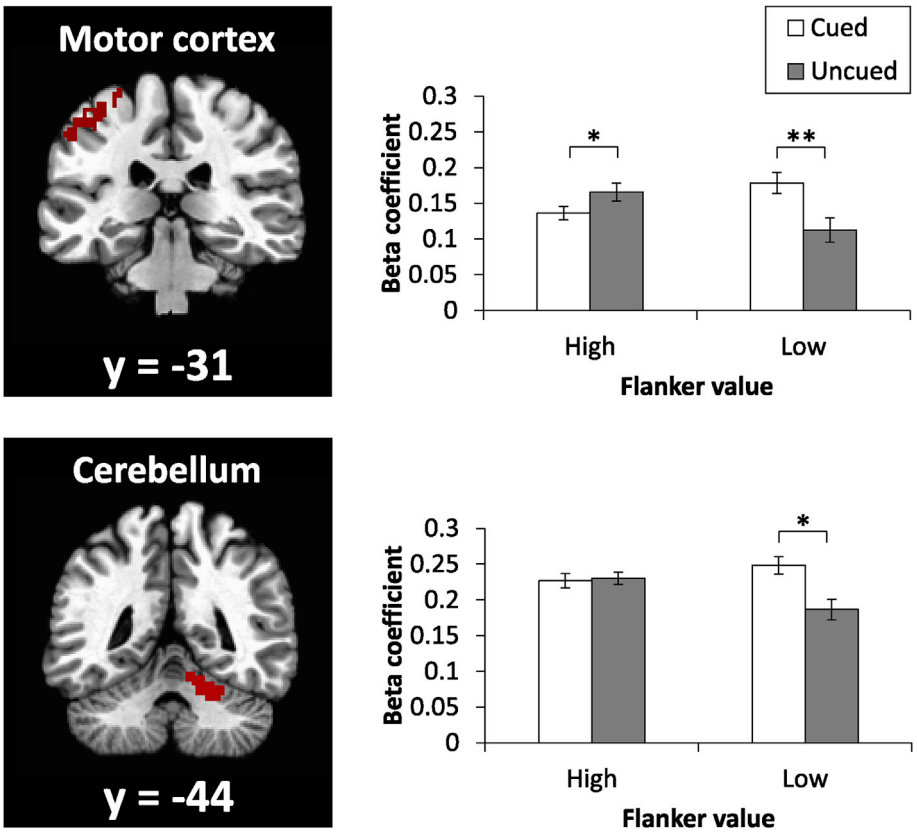

Fig. 6. The interaction between flanker value and flanker colour-response mapping in the motor cortex and cerebellum ROIs. *$p < 0.05$, **$p < 0.01$.

Table 1
Mean proportion correct in the test phase.

		Flanker-target compatibility			
		High value		Low value	
		Compatible	Incompatible	Compatible	Incompatible
Flanker colour-response mapping	Cued	0.94 (0.015)	0.95 (0.013)	0.95 (0.012)	0.94 (0.014)
	Uncued	0.93 (0.012)	0.92 (0.017)	0.91 (0.012)	0.92 (0.011)

Values in parentheses represent the within-subjects SEM.

stimuli (Niendam et al., 2012; Ptak, 2012). The frontoparietal network is also implicated in response planning and control (Fridman et al., 2006; Glover, 2004; Glover et al., 2012). These are consistent with the frontal and parietal regions observed in the cued versus uncued flankers contrast. Flankers rendered in the cued colour attracted attention in a goal-directed manner, facilitating target identification in a response-relevant context.

The present study offers a window into what happens when task goals and learned value compete in the process of response selection. On cued flanker trials, when the flankers were presented in the response-relevant colour, goal-directed attention resulted in the robust representation of both high- and low-value stimuli in the motor system. This fits with several prior studies demonstrating that task goals can overshadow effects of prior reward learning when the two are in alignment (e.g., Anderson and Halpern, 2017; Anderson et al., 2012, 2013). In contrast, when the flankers were presented in the uncued (response-irrelevant) colour, high-value flankers continued to evoke a similarly-strong signal in the motor system, whereas the response evoked by low-value flankers was significantly reduced, and the same pattern was evident in the inferior parietal lobule. This pattern is consistent with preferential attention to the high-value flankers regardless of task relevance (e.g., Anderson, 2016a; Anderson et al., 2011), with stronger stimulus-evoked activity more effectively competing with the goal to withhold responses to the uncued colour (see Xu et al., 2017). Importantly, the present study demonstrates that this influence of value-biased competition extends to stimulus-evoked activity in the motor system, and correlates with the value-modulated influence of the flankers on actual motor responses. This pattern is broadly consistent with the idea that associative reward learning produces an automatic approach tendency (Chen and Bargh, 1999; Krieglmeyer et al., 2010), such that value-associated stimuli come to trigger a corresponding motor response that more robustly competes for selection-for-action even when this response conflicts with current goals (Anderson, 2017; Hoofs et al., 2018).

As previously mentioned, high-value flankers were also associated with increased activation of the right inferior parietal lobule in a response-irrelevant context. One potential interpretation of this finding is that high-value flankers consistently evoked elevated attentional priority even when response-irrelevant, consistent with previous studies of the neural correlates of value-driven attentional capture (Anderson et al., 2014; Barbaro et al., 2017; Lee and Shomstein, 2013) and value-biased competition observed in a similar task without the go/no-go manipulation (Anderson et al., 2012). All together, these findings suggest that reward learning produces a general approach bias which influences not only the attentional system but also selection-for-action (Anderson,

2017).

Typically, response execution and inhibition are achieved via the direct and indirect pathways in the basal ganglia (Aron and Poldrack, 2006; Nambu et al., 2002). Dopamine exerts an excitatory effect in the direct pathway, facilitating response execution. On the other hand, dopamine exerts an inhibitory effect in the indirect pathway, facilitating response inhibition (Eagle et al., 2011; Nandam et al., 2013). Given the established relationship between value-driven attention and striatal dopamine (Anderson et al., 2016c, 2017), one interesting possibility is that distractor-evoked dopamine not only biases perceptual processing but also processing in the motor system, such that value-driven attentional orienting and biases in selection-for-action are intricately linked. Future studies might seek to directly relate the magnitude of reward's effect on behaviour in this task to task-dependent dopamine release using positron emission tomography, as well as investigate possible value-dependent modulations of flanker-evoked responses in specific subregions of the direct and indirect pathway using high-resolution fMRI.

In the present study, we employed a task designed to isolate responses evoked by task-irrelevant stimuli in the motor system with and without the conflicting goal of withholding responses to such stimuli based on colour information. Although the present study clearly indicates that stimulus-evoked responses in the motor system are subject to automatic value-dependent modulation, linking the principle of value-driven attention to selection-for-action (Anderson, 2017), a limitation of the present study is that the specific nature of the interaction observed in brain and behaviour is unclear. One interpretation, consistent with the presence of a reverse-compatibility effect for the uncued low-value flankers, is that low-value stimuli evoked some measure of response inhibition in a response-irrelevant context, which was less effectively applied to the high-value flankers due to their more robust stimulus-evoked response. Another possibility is that the low-value flankers were more effectively ignored or disengaged from in a response-irrelevant context, which made it more difficult to subsequently reengage the same response selection process when the target shared the flanker identity, thereby producing the observed pattern of behaviour. Yet another possibility, not mutually exclusive, is that suppression of the high-value flankers (and associated response) required greater attentional effort (Sarter et al., 2006), which was reflected in stronger engagement of the motor system. Errors of commission are very infrequent in our task, such that the motor plan activated by the flankers was generally insufficient to trigger overt behaviour, suggesting that any influence of the cueing manipulation on inhibitory control would likely be operating at the level of inhibiting flanker interference rather than a motor plan. Importantly, whether or not explicitly inhibitory processes were engaged by our task, our findings clearly demonstrate a role for value associations in the automatic processing of response-related information in the motor system. Future research is necessary to determine whether such value-dependent modulation has a more direct influence on mechanisms of inhibitory control per se.

Another limitation of the present study concerns the somewhat low number of observations per condition in the critical contrasts involving flanker-only trials, which was twenty-four. Setting up the colour-response contingencies, assessing the effects of these contingencies on behaviour as a function of flanker value, and isolating the neural response to task-irrelevant stimuli on flanker-only trials requires a large number of trial types, limiting trials-per-cell in the design. Examination of internal reliability suggested that this was sufficient to produce reliable estimates of flanker-evoked brain activation in the ROI analyses, which were central to the conclusions of the present study. However, this internal reliability might not extend to other brain areas in the whole-brain analysis, potentially limiting the power of this analysis, which is especially pertinent given the small size of certain structures in the direct and indirect pathway of the basal ganglia that might have also been subject to value-dependent modulations (e.g., putamen). As such, the absence of significant value-dependent modulations in such regions in the present study should be interpreted with caution.

In conclusion, the present study provided neural evidence that the principle of value-driven attention extends to automatic stimulus-evoked responses in the motor system. Responses generated by stimuli associated with high-value were less subject to goal-contingent suppression in contexts where responses should be withheld, with evoked motor activity being largely impervious to the influence of task goals. This stands in contrast to the significantly reduced responses for low-value stimuli in the same context. A similar pattern was evident in the right inferior parietal lobule as well, consistent with prior studies of value-driven attention in the visual system (Anderson et al., 2014; Barbaro et al., 2017; Lee and Shomstein, 2013). These results demonstrate that repeatedly associating stimuli with value grants them priority, facilitating approach behaviour, which is particularly evident when such behaviour conflicts with task goals. In this way, our findings offer a potential mechanism by which reward-associated stimuli involuntarily bias selection-for-action, potentiating behaviours that may conflict with current goals (Anderson, 2017).

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Declarations of interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2018.12.050.

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