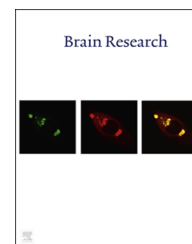


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Research Report

Value-driven attentional priority signals in human basal ganglia and visual cortex



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ABSTRACT

Goal-directed and stimulus-driven factors determine attentional priority through a well defined dorsal frontal-parietal and ventral temporal-parietal network of brain regions, respectively. Recent evidence demonstrates that reward-related stimuli also have high attentional priority, independent of their physical salience and goal-relevance. The neural mechanisms underlying such value-driven attentional control are unknown. Using human functional magnetic resonance imaging, we demonstrate that the tail of the caudate nucleus and extrastriate visual cortex respond preferentially to task-irrelevant but previously reward-associated objects, providing an attentional priority signal that is sensitive to reward history. The caudate tail has not been implicated in the control of goal-directed or stimulus-driven attention, but is well suited to mediate the value-driven control of attention. Our findings reveal the neural basis of value-based attentional priority.

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1. Introduction

Attention selects stimuli for cognitive processing, determining which stimuli become available to working memory, decision making, and action. Attention is limited in capacity, such that stimuli compete for selection (Desimone and Duncan, 1995). In order to determine which stimuli are selected via attention, the brain must represent the attentional priority of different stimuli.

Attentional priority has long been thought to arise from the interplay between goal-directed and stimulus-driven processes. Attention can be voluntarily deployed to goal-relevant stimuli (Wolfe et al., 1989) and locations (Posner, 1980; Yantis and Johnston, 1990), and involuntarily captured by physically salient stimuli (Theeuwes, 1992; Yantis and

Jonides, 1984). Stimulus-driven attentional priority can be modulated by the goals of the observer, such that selection is contingent on the goal-relevance of salient stimuli (Folk et al., 1992; Serences et al., 2005). Goal-directed attentional control is mediated by a dorsal frontal-parietal network of brain regions, and stimulus-driven attentional control by a ventral temporal-parietal network (Corbetta and Shulman, 2002; Serences et al., 2005; Yantis et al., 2002).

To promote survival and well-being, it is important that attentional priority be given to stimuli that provide information concerning reward availability. Indeed, reward-related stimuli have high attentional priority (e.g., Anderson et al., 2011a, 2012; Della Libera and Chelazzi, 2006, 2009; Hickey et al., 2010; Raymond and O'Brien, 2009). When attention to reward-related

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stimuli is promoted by task goals, it becomes difficult to assess whether the reward or the goals are modulating attention (Maunsell, 2004). Recent behavioral evidence demonstrates that stimuli previously associated with reward involuntarily capture attention even when they are nonsalient and task-irrelevant (Anderson et al., 2011b; Anderson and Yantis, 2012, 2013). These findings imply the existence of a distinctly value-driven computation of attentional priority.

Using human functional magnetic resonance imaging (fMRI), we investigated the representation of task-irrelevant distractors previously associated with reward in a well-developed experimental paradigm (see Anderson, 2013, for a review). Employing a whole-brain approach with targeted regions of interest (ROIs), we probed the nature of the priority signals underlying value-driven attention. Based on prior behavioral work and informed by recent findings using event-related potentials (Qi et al., 2013), we predicted that previously reward-associated distractors would evoke stronger signals in visual cortex indicative of preferential visual processing. As to the priority signals contributing to this bias in visual processing, several possibilities were considered and tested.

To the degree that value-driven attentional selection reflects perseverating or otherwise automatically activated goals that have been reinforced by means of reward feedback, previously reward-associated distractors should evoke increased activity in the frontal-parietal attention network known to subservise goal-directed selection (Corbetta and Shulman, 2002; Serences et al., 2005; Yantis et al., 2002). Another possibility is that value-driven attention reflects only a bias in visual processing, such that sensitivity to reward-associated features in early visual areas is enhanced in the absence of additional control signals. In essence, the representation of reward-associated features becomes potentiated, such that the same stimulus evokes a stronger, more salient signal in early vision with learning. Evidence for this possibility comes from studies showing that representations as early as V1 are sensitive to the expected value (Serences, 2008) and timing (Shuler and Bear, 2006) of a reward.

A third possibility that was considered concerns value-driven attentional priority signals arising from the basal ganglia, a subcortical network of brain structures implicated in both reward processing and habitual responding. The striatum of the basal ganglia, including the caudate nucleus and nucleus accumbens, plays an important role in the processing of reward outcomes and the anticipation of reward (e.g., Krebs et al., 2012; Mattfeld et al., 2011; O'Doherty, 2004). If a persisting representation of expected value plays a role in signaling value-based attentional priority, striatal contribution to value-driven attentional capture should be evident.

Different regions of the basal ganglia are also known to play an important role in motor control and habitual responding. In the case of visual selection, such habitual responding has been linked to the tail of the caudate nucleus. Neurons in the caudate tail represent both the identity and position of visual objects (Yamamoto et al., 2012), and these representations are strengthened by associative reward learning (Yamamoto et al., 2013). Stimulating neurons in the caudate tail can initiate a saccade (Yamamoto et al., 2012), and saccades are known to be guided by attentional priority signals (Hoffman and Subramaniam, 1995; Thompson

and Bichot, 2005). The role of the caudate tail in mediating involuntary attentional capture is not known, however, and whether the representation of stimuli in the caudate tail can be modulated by reward learning in humans has not been tested.

We independently identified regions of the frontal-parietal attention network and the basal ganglia, and looked for attentional priority signals evoked by previously reward-associated distractors in these regions. To anticipate, the distractors evoked stronger signals in the caudate tail and extrastriate visual cortex compared to other nontarget stimuli, indicating the neural correlates of value-driven attentional capture. Comparable signals were not observed for equally-familiar former targets that were never associated with reward in a control experiment.

2. Results

2.1. Experiment 1

2.1.1. Behavior

2.1.1.1. *Training phase.* One of two color targets was presented on each trial, and the color of the target provided information concerning the available reward following a correct response. One color was associated with a greater probability of a high reward and the other with a greater probability of a low reward (see Fig. 1A). By the end of training, during the last block of trials, participants identified the high-reward target faster than the low-reward target (Fig. 2A, $t=2.16$, $p=.045$), indicating that they had learned the contingencies. Accuracy was high and did not differ across conditions (high-reward: 90.9%, low-reward: 91.9%, $p=.30$).

2.1.1.2. *Test phase.* Participants searched for a shape-defined target; previously reward-associated color stimuli occasionally appeared as a distractor (see Fig. 1B). Consistent with our previous findings (Anderson et al., 2011b; Anderson and Yantis, 2012, 2013), target identification response time was slowed by the presence of a valuable distractor (Figs. 2B, $t=2.80$, $p=.012$), indicating that valuable distractors had high attentional priority. Also consistent with previous results (Anderson et al., 2012; Anderson and Yantis, 2012, 2013), the magnitude of this slowing did not differ between first and second half of the test phase ($p=.37$), indicating that value-based attentional priority was persistent. Accuracy was again high and did not differ across conditions (distractor absent: 91.9%, low-value distractor: 92.3%, high-value distractor: 92.0%, $p=.92$).

2.1.2. Neuroimaging

2.1.2.1. *Training phase.* The neuroimaging data from the training phase provided a basis for independently defining regions of interest (ROIs) that were used to address specific questions in the test phase.

2.1.2.1.1. *Extrastriate cortex ROI.* The magnitude of activity in extrastriate cortex is known to reflect the experienced salience of stimuli as a function of their attentional priority and has a contralateral retinotopic organization (Serences et al., 2005; Serences and Yantis, 2007; Yantis et al., 2002). We identified extrastriate cortex by contrasting cortical activity

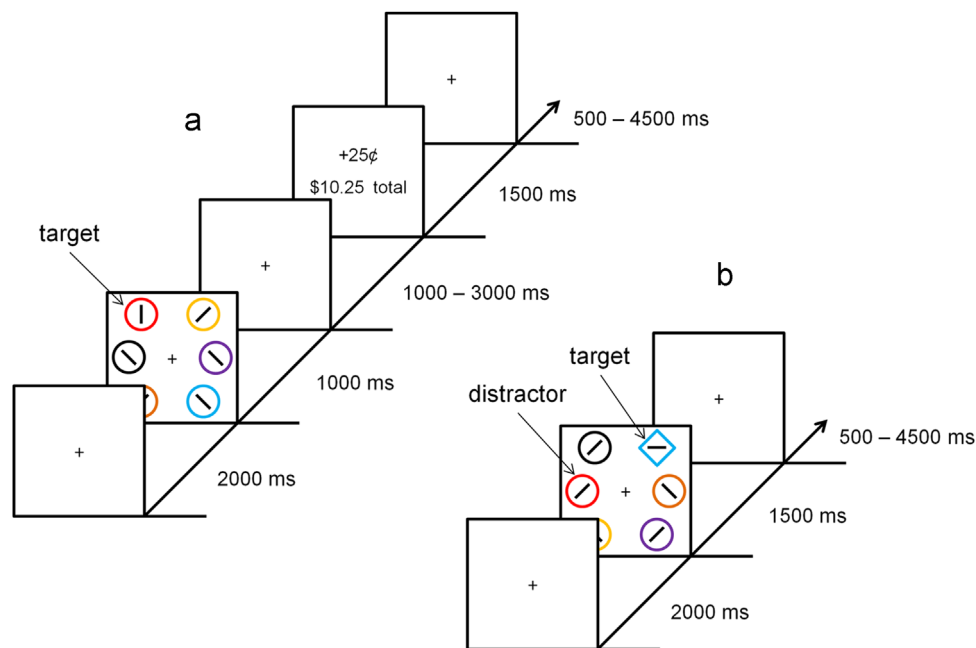


Fig. 1 – Behavioral task. (A) Training phase. Participants searched for a target that was unpredictably red or green, and reported the orientation of a bar contained within the target. Correct responses were followed by monetary reward feedback. **(B) Test phase.** Participants searched for a shape singleton target (circle among diamonds or diamond among circles, unpredictably) and were informed that color was irrelevant to the task. One of the nontarget shapes was occasionally rendered in the color of a formerly reward-predictive target. No trial-by-trial feedback concerning reward or performance was delivered.

evoked by the target when presented in the left versus the right visual hemifield (Table 1).

2.1.2.1.2. Frontal-parietal attention network ROIs. We identified regions that responded to the presentation of a target in order to define the frontal-parietal attention network mediating goal-directed target selection. This revealed significant bilateral activity in middle and inferior frontal gyrus, frontal eye field, and insula, consistent with previous work (Serences et al., 2005) (Table 1).

2.1.2.1.3. Striatum ROI. As the target was associated with reward outcome, activity associated with the presentation of a target also served to identify regions of the striatum representing both anticipated reward and the presence of a currently valued stimulus (Fig. 3).

2.1.2.2. Test phase. We compared trials on which a previously reward-associated stimulus was present or absent, collapsing across the high- and low-value distractor conditions. This was done to increase statistical power: behavioral evidence indicates that both high- and low-value stimuli have increased attentional priority compared to neutral, non-reward-related stimuli (Anderson et al., 2011b; Anderson and Yantis, 2012).

Several of our ROIs, including extrastriate visual cortex, frontal eye field, and the basal ganglia (in particular, the caudate tail of the basal ganglia), are known to respond preferentially to stimuli presented to the contralateral visual hemifield (Serences et al., 2005; Serences and Yantis, 2007; Yamamoto et al., 2012; Yantis et al., 2002). Therefore, we first compared trials on which a valuable distractor was present versus absent separately in the right and left visual hemifields. We excluded trials on which the distractor and target were presented in the same hemifield, to ensure that the

representation contralateral to the distractor reflected only the processing of task-irrelevant stimuli.

When the distractor was present in the right hemifield (compared to when it was absent; Fig. 4), left extrastriate cortex and intraparietal sulcus (IPS) were significantly more active by whole-brain analysis. The left caudate tail also showed increased activity in the presence of the distractor, but did not pass whole-brain cluster correction (Fig. 5). This is perhaps unsurprising, given its relatively small size. However, the increased activity in the caudate tail was robustly significant when using the left striatum ROI for small volume cluster correction ($p < .001$). No other significant activations were observed in this ROI or in any of the other ROIs corresponding to the frontal-parietal attention network.

When the distractor was presented in the left hemifield, a similar pattern emerged. Increased activity was present in both right extrastriate cortex (Fig. 4) and right caudate tail (Fig. 5), which was robustly significant using the right extrastriate and right striatum ROIs for small volume cluster correction ($p < .001$ and $p = .005$, respectively). As before, no other significant activations were observed in the striatal ROI or in any of the other ROIs. In each hemisphere, the location of the caudate tail activations identified in the present study closely matched those previously observed using a category learning task known to reliably recruit the caudate tail (Seeger et al., 2010) (see Supplemental Fig. 1).

Finally, we looked for brain regions in which activity was modulated by the presence of the distractor regardless of hemispheric projection, by contrasting trials on which a valuable distractor was present versus absent. The only region identified in this analysis that was not identified in prior analyses was left primary motor cortex, which was more

active when the distractor was absent (Talairach coordinates: $x=54.0, y=6.0, z=25.5$). The reason for this difference in activation is unclear; one possibility is that attentional capture by the distractors interfered with the process of selecting and executing the correct response to the target, which itself requires attention. Even at more liberal whole-brain thresholds and using each of the frontal-parietal attention network ROIs for small volume cluster correction, no additional significant modulations were observed.

2.2. Experiment 2

Previous research indicates that value-driven attentional capture depends critically on reward history and cannot be explained by

mere search history that is independent of reward (Anderson et al., 2011a, 2011b, 2012; Qi et al., 2013; Wang et al., 2013). However, it is unclear whether the same is true of the corresponding increases in neural representation identified in Experiment 1, which could reflect history-related changes that are independent of reward learning or value-based attention. To determine whether these changes in neural representation reflect value-driven attention rather than search history more generally, we investigated the representation of the exact same prior-target-color stimuli following an otherwise equivalent training procedure in which the reward feedback was omitted and thus subsequent attentional capture would not be expected (Anderson et al., 2011a, 2011b, 2012; Qi et al., 2013; Wang et al., 2013). Accuracy during the training phase was high (mean=94.2%), indicating compliance with the training procedure. During the test phase, RT ($t=.52, p=.609$) and accuracy ($t=.84, p=.418$) were unaffected by the presence of the prior-target-color distractors (mean absent: 748 ms, 96.1%; mean present: 752 ms, 95.2%), consistent with previous reports

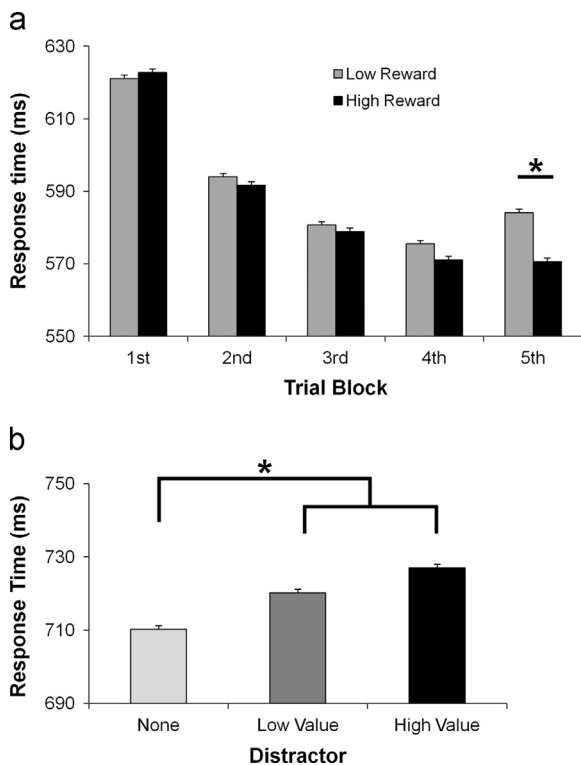


Fig. 2 – Behavioral results. (A) Response time to identify high- and low-reward targets across the five blocks of the training phase. Faster responses to high-reward targets indicate learning of the reward contingencies. (B) Response time in the test phase for the three distractor conditions. Slower responses in the presence of a valuable distractor indicate value-driven attentional capture. Error bars reflect with within-subjects SEM. * $p < .05$.

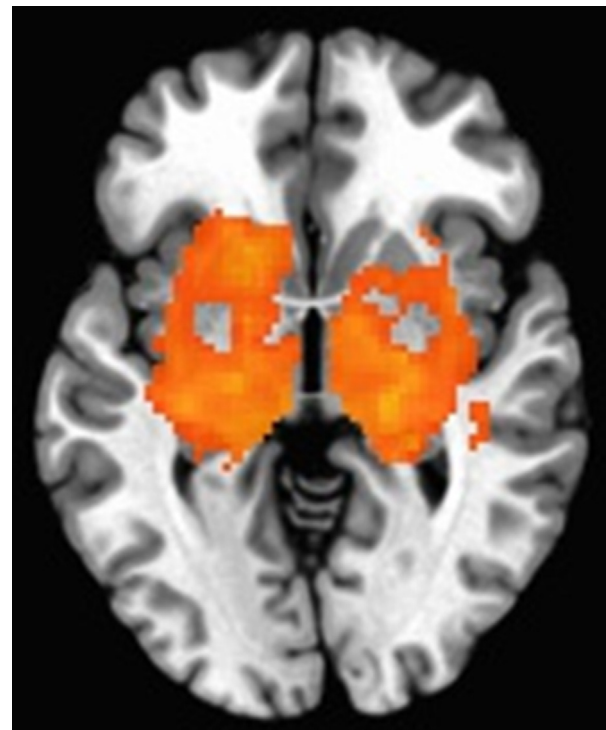


Fig. 3 – Region of activation elicited by the presentation of a reward-associated target during the training phase that was used to define the striatum ROI.

Table 1 – Brain areas identified as ROIs in the training phase. FEF=frontal eye field, IFG=inferior frontal gyrus, MFG=middle frontal gyrus. Coordinates reflect the center of mass.

	Left hemisphere				Right hemisphere			
	Talairach coordinates (x, y, z)			volume (ml)	Talairach coordinates (x, y, z)			volume (ml)
Extrastriate cortex	-37	-78	-2	19.472	38	-75	-2	3.092
Insula	-47	-6	10	4.532	49	11	4	9.198
FEF	-28	-16	55	2.746	30	-6	52	2.112
IFG	-52	3	29	4.397	44	6	28	3.917
MFG	-28	32	30	7.931	32	31	31	4.359

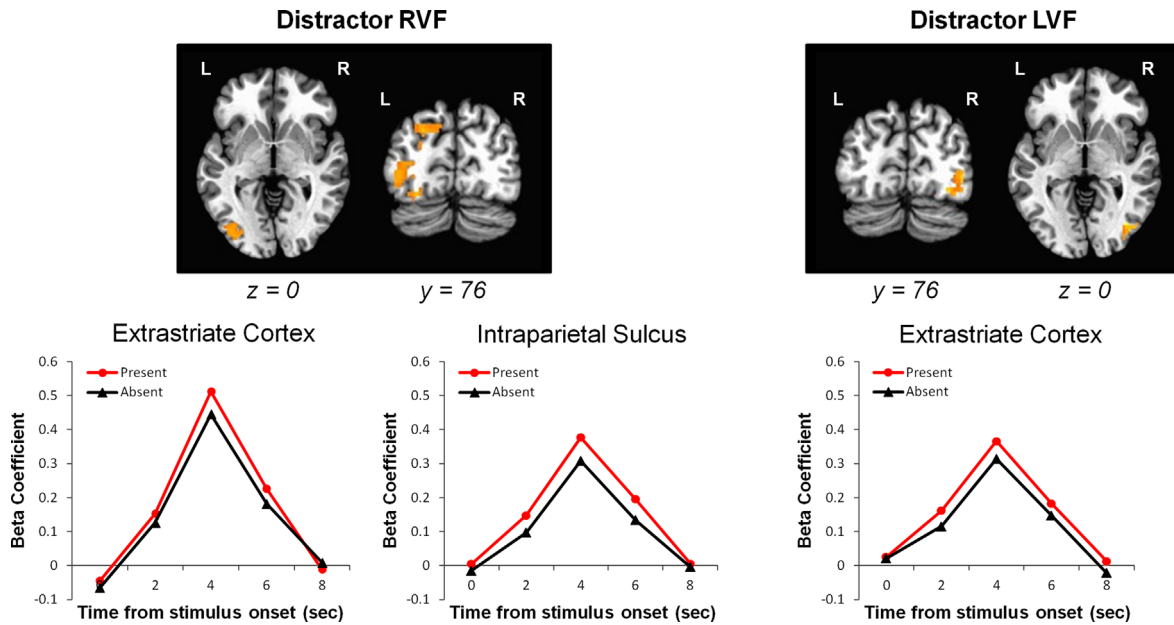


Fig. 4 – Cortical representation of value-based attentional priority. Regions showing increased activity when the previously reward-associated distractor was present versus absent in the contralateral visual hemifield (cluster size $p < .05$), along with corresponding beta coefficients. LVF=left visual field, RVF=right visual field.

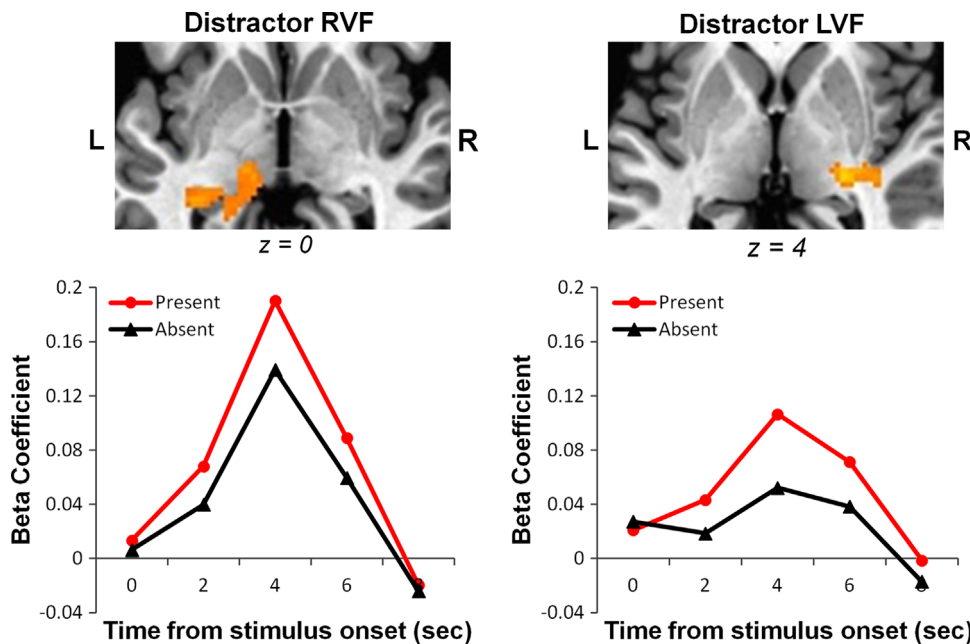


Fig. 5 – Subcortical representation of value-based attentional priority. Increased activity in the caudate tail when the previously reward-associated distractor was present versus absent in the contralateral visual hemifield (cluster size $p < .05$), along with corresponding beta coefficients. LVF=left visual field, RVF=right visual field.

(Anderson et al., 2011a, 2011b, 2012; Qi et al., 2013; Wang et al., 2013). Response time did not significantly differ in the distractor absent condition between experiments ($t=1.24, p=.229$). Next, we investigated the neural representation of former-target-color distractors using the regions of increased activation in the caudate tail, extrastriate visual cortex, and left IPS identified in Experiment 1 as ROIs. In contrast to Experiment 1, when the distractor was present versus absent in the contralateral hemifield, no difference was found in the caudate tail ($t's < .08$,

$p's > .24$), extrastriate cortex ($t's < .42, p's > .68$), or left IPS ($t = -.17, p = .87$).

3. Discussion

We investigated the neural basis of attentional priority for stimuli previously associated with reward. As in previous studies, we observed behavioral evidence of value-driven

attentional capture (Anderson et al., 2011b; Anderson and Yantis, 2012, 2013), and found corresponding attentional priority signals in the caudate tail and extrastriate visual cortex. Experiment 2 demonstrated that these observed modulations in brain activity do not occur in response to stimuli that are equally familiar as former targets but unassociated with reward outcome. Our findings highlight a distinctly value-driven network of attentional control.

The caudate tail is known to represent the identity and location of objects (Yamamoto et al., 2012), and the strength of these representations is modulated by an object's reward history (Yamamoto et al., 2013). These findings have led to the hypothesis that the caudate tail plays an important role in habitual visual selection (Hikosaka et al., 2013). Our results support the idea that such habitual selection underlies value-driven attention. We show that object representations in the caudate tail come to more strongly represent reward-predictive stimuli in humans. Importantly, this enhanced representation is evident even when the previously reward-associated stimulus is physically nonsalient and task-irrelevant; this reflects the attentional priority signal that could facilitate the automatic value-based selection observed in behavior. Stimuli previously associated with reward have been shown to capture both covert attention and overt attention (i.e., produce oculomotor capture) (Anderson and Yantis, 2012; Theeuwes and Belopolsky, 2012); the value-driven attentional priority signals observed in the present study may be related to either or both of these orienting mechanisms.

The observed activation in the caudate tail suggests that value-driven attention is not limited to a change in the sensitivity of early visual representations (e.g., Serences, 2008); although our findings are not inconsistent with the contribution of such a mechanism, we show that there is a subcortical component to value-driven attentional capture. We did not find evidence for value-based attentional priority signals in the frontal-parietal attention network or in other regions of the basal ganglia using targeted ROIs. Although we cannot rule out the influence of such mechanisms to value-driven attentional capture, as we may have had insufficient statistical power to detect them, our findings suggest that perseverating goals and expectations of current value do not play a prominent role in the automatic orienting of attention to previously reward-associated stimuli.

The caudate tail and extrastriate cortex share connections through the visual corticostriatal loop (Seger, 2013). Extrastriate cortex projects to the caudate tail, from which information flows either through an open loop to the superior colliculus or through a closed loop back to extrastriate cortex via the thalamus. Each of these pathways could contribute to the observed attentional capture. Input to the superior colliculus through the open loop is thought to underlie habitual eye movements directed toward valuable objects in primates (Hikosaka et al., 2013), and eye movements have been shown to be biased toward nonsalient but previously reward-associated distractors in humans (Anderson and Yantis, 2012; Theeuwes and Belopolsky, 2012). Through the closed loop, visual cortex activity remains elevated for the previously reward-associated stimulus, increasing its experienced salience and thus its ability to compete for representation.

We also found evidence that the biased representation of reward-associated stimuli is reflected in the IPS, a region of

parietal cortex implicated in the control of attention. The IPS has been shown to play a role in goal-contingent attentional capture (Serences et al., 2005; Serences and Yantis, 2007), and its primate homolog, the lateral intraparietal area, responds preferentially to stimuli that predict available reward (Peck et al., 2009). This region of the brain also responds preferentially to physically salient stimuli, and is thought to contain a priority map of the visual field that combines bottom-up and top-down signals (e.g., Balan and Gottlieb, 2006; Bisley and Goldberg, 2003). One possibility is that the observed IPS activation by the valuable distractors in the present study reflects competition from these stimuli in the priority map, such that the goals of the observer are not always effective in directing attention away from the distractor and to the target.

Mounting behavioral evidence suggests that the interaction between stimulus-driven and goal-driven factors cannot fully explain recently observed patterns of attention allocation. In particular, we have shown that previously reward-predictive stimuli capture attention even when nonsalient and task-irrelevant (Anderson et al., 2011b; Anderson and Yantis, 2012, 2013). These results suggest the need for a third mechanism of attentional selection that does not depend on goal-driven or stimulus-driven influences (Anderson, 2013; Awh et al., 2012). Our findings reveal a network for representing attentional priority that differs from the well defined stimulus-driven and goal-directed attention networks, highlighting distinct neural signatures linked to the influence of learned value on the control of attention.

Abnormal processing of non-drug rewards in the striatum has been well documented in drug-dependent patients (e.g., Hommer et al., 2011). Disordered patterns of attentional control have also been noted in addiction, such that drug-related stimuli become hypersalient (Field and Cox, 2008; Marissen et al., 2006). Here, we provide evidence that the striatum is involved in signaling value-driven attentional priority. This suggests that attentional biases for drug-related stimuli may be a consequence of changes in how the striatum responds to rewards and the stimuli associated with those rewards, consistent with recent behavioral evidence showing that value-driven attentional capture by stimuli associated with non-drug reward is also elevated in addiction (Anderson, Faulkner, Rilee, Yantis, and Marvel, 2013).

4. Experimental procedure

4.1. Experiment 1

4.1.1. Participants

Eighteen neurologically healthy adult volunteers (18–22 years of age, mean = 19.9, 8 females) with normal or corrected-to-normal visual acuity and color vision were recruited from the Johns Hopkins University community to participate. Written informed consent was obtained for each participant. All procedures were approved by the Johns Hopkins Medicine Institutional Review Board.

4.1.2. Behavioral task and procedure

Each participant was scanned during a single 1.5 h session. The participant completed 5 runs of the *training phase* consisting of 60

trials each (see Fig. 1A). Each trial began with a fixation display for 2000 ms, which was followed by a search array for 1000 ms and later by a reward feedback display for 1500 ms. Participants were instructed to search for a target circle that was unpredictably red or green and report the orientation of a bar within the target as either vertical or horizontal via a button press. Half of the trials in each run of the training phase contained a red target and half contained a green target; each target color appeared on each side of the screen (left or right) equally-often. The order of trials was randomized for each run.

Following a correct response that fell within a 1000 ms response deadline, a small amount of money was added to a running total in the reward feedback display. If participants responded incorrectly or too slowly (both were scored as errors), the reward feedback display indicated that 0¢ had been earned for that trial. One of the two target colors (counterbalanced) was followed by a high reward of 25¢ on 80% of the trials on which it was correctly reported, and by a low reward of 5¢ on the remaining 20% of correct trials (high-reward color); for the other (low-reward) color, these mappings were reversed. An interval during which only the fixation cross was visible was presented between the search array and the reward feedback display for either 1000 or 3000 ms (equally-often), and again immediately following the reward feedback display for 500, 2500, or 4500 ms (exponentially distributed); the fixation cross disappeared for the last 200 ms of the second interval to indicate to the participant that the next trial was about to begin.

Following the training phase, a high-resolution anatomical image of each participant was obtained, which was immediately followed by 4 runs of the test phase (see Fig. 1B). Each run of the test phase consisted of 80 trials, each of which contained a fixation display for 2000 ms, a search array for 1500 ms, and a second interval during which only the fixation cross was visible for 500, 2500, or 4500 ms (exponentially distributed). Once again, the fixation cross disappeared for 200 ms before the next trial began. Targets were defined as the unique shape, either a diamond among circles or a circle among diamonds (equally-often), and participants made the same identity judgment concerning the orientation of the bar contained within the target. The color of the shapes was now irrelevant to the task, and participants were instructed to ignore color and focus on identifying the unique shape. No trial-by-trial feedback about performance was provided during the task; participants were informed of their accuracy for each run of the test phase at the end of that run.

On 25% of the trials in the test phase, one of the nontarget shapes was rendered in the color of the formerly high-reward target (high-value distractor), and on another 25% of the trials, one of the nontarget shapes was rendered in the color of a formerly low-reward target (low-value distractor). On the remaining 50% of the trials, none of the shapes was rendered in the color of a formerly reward-predictive target (distractor-absent trials). The position of the target was determined randomly from among the 6 possible locations on each trial, as was the position of the distractor when it was presented.

In both the training phase and the test phase, each shape in the search array was $3.4^\circ \times 3.4^\circ$ visual angle in size. The middle of the three shapes on each side of the screen was presented 10° center-to-center from fixation, and the two outer shapes were presented 8° from the vertical meridian, 6°

above and below the horizontal meridian. Participants pressed a button held in the right hand for horizontal targets and a button held in the left hand for vertical targets.

The stimuli were displayed using an Epson PowerLite 7600p projector with a custom zoom lens onto a screen mounted at the end of the magnet bore behind the participant's head. Participants viewed the screen using a mirror mounted to the head coil. Stimulus displays were generated using Matlab software with Psychophysics Toolbox extensions (Brainard, 1997), and responses were recorded using two custom-built, fiber-optic push button boxes.

Each participant practiced both the training phase (without reward feedback) and the test phase prior to being scanned, and were trained to a performance criterion (accuracy: 85%, mean RT: 750 ms during training and 800 ms during test). Fixation on the central cross was emphasized at all times both during practice and during the experiment. Data from one run of the training phase was lost for one participant due to equipment failure (computer crash), and another participant voluntarily withdrew from the experiment before the final run of the test phase could be completed due to physical discomfort.

4.1.3. Analysis of behavioral data

Only correct trials were included in the RT analyses. RTs more than 2.5 standard deviations above and below the mean for a given condition for a given participant were trimmed.

4.1.4. MRI data acquisition

Images were acquired using a 3-Tesla Philips Gyroscan MRI scanner and a 32-channel transmit/receive sensitivity encoding (SENSE) head coil at the F. M. Kirby Research Center for Functional Brain Imaging located in the Kennedy Krieger Institute, Baltimore, MD. High-resolution whole-brain anatomical images were acquired using a T1-weighted magnetization-prepared rapid gradient echo pulse sequence [voxel size = 1 mm isotropic, repetition time (TR) = 8.1 ms, echo time (TE) = 3.7 ms, flip angle = 8° , acquisition matrix = 212×172 , 150 axial slices, 0 mm gap, SENSE factor = 2]. Whole-brain functional images were acquired using a T2*-weighted echoplanar imaging (EPI) pulse sequence (voxel size = 2.5 mm isotropic, TR = 2000 ms, TE = 30 ms, flip angle = 70° , acquisition matrix = 76×76 , 36 axial slices, .5 mm gap, SENSE factor = 2). Each EPI pulse sequence began with 4 dummy pulses that were not recorded in order allow magnetization to reach steady-state. Each of the 5 runs of the training phase lasted 8.2 min during which 242 volumes were acquired; each of the 4 runs of the test phase lasted 6.8 min during which 200 volumes were acquired.

4.1.5. MRI data analyses

4.1.5.1. Preprocessing. All preprocessing was conducted using the AFNI software package (Cox, 1996) except where otherwise noted. Each EPI run for each participant was slice-time corrected and then motion corrected using the last image prior to the anatomical scan as a reference. EPI images were then coregistered to the corresponding anatomical image for each participant. Using ANTs (Avants et al., 2011) nonlinear warping software, the images for each participant were warped to the Talairach brain (Talairach and Tournoux, 1988). Finally, the EPI images were converted to percent signal change normalized to

the mean of each run, and then spatially smoothed using a 5 mm full-width half-maximum Gaussian kernel.

4.1.5.2. Statistical analyses. All statistical analyses were performed using the AFNI software package. In both the training phase and the test phase, the data were modeled using deconvolution. Two general linear models (GLMs) were performed on each of the two phases of the experiment, which were analyzed separately.

For the training phase, the first GLM included the following regressors of interest: (1) high-reward target on the left, (2) high-reward target on the right, (3) low-reward target on the left, (4) low-reward target on the right, (5) high-reward feedback, (6) and low-reward feedback. For the second training phase GLM, regressors of interest included (1) the presentation of the stimulus array, (2) high-reward feedback, (3) and low-reward feedback.

For the test phase, the first GLM included the following regressors of interest: (1) target on left – no distractor, (2) target on right – no distractor, (3) target on left – distractor on same side, (4) target on left – distractor on opposite side, (5) target on right – distractor on same side, (6) and target on right – distractor on opposite side. For the second GLM, only distractor present and distractor absent trials were modeled, collapsing across side. In all four GLMs, each regressor of interest was modeled using five finite impulse response functions (e.g., Glover, 1999) beginning at the onset of the corresponding event, and drift in the scanner signal was modeled using nuisance regressors. The presentation of the stimulus array was not modeled for trials on which the participant failed to execute a motor response (2.2% of all trials).

The resulting beta-weight estimates were analyzed using one or more mixed-effects ANOVA contrasts or t-tests, with stimulus condition as a fixed effect and subject as a random effect. All ANOVAs and t-tests focused on the average beta-weight across time-points 3 and 4 (4–6 s post-stimulus), reflecting the peak of the hemodynamic response. The results of all analyses were assessed for statistical significance using the AFNI program AlphaSim, which determines the probability of the observed cluster sizes occurring in synthetic data randomly generated to match the smoothness and spatial extent of the actual data (n iterations=10,000; clusters defined using nearest neighbor method). For region of interest (ROI) analyses, we used small volume cluster correction to preserve information concerning the specific location of any observed modulations in activity. For the significant clusters identified by the test phase analyses, the average beta-weight estimate across participants was calculated in order to visualize the results.

4.2. Experiment 2

Fourteen neurologically healthy adult volunteers (18–28 years of age, mean=23.1, 9 females) with normal or corrected-to-normal visual acuity and color vision, none of whom had participated in Experiment 1, were recruited from the Johns Hopkins University community. The experiment again consisted of a training phase and a test phase. The behavioral task and procedure for the training phase were identical to Experiment 1 with the exception that the reward feedback display and preceding fixation interval were omitted, and the

length of the fixation interval at the end of each trial was lengthened by 500 ms. The test phase was exactly identical to Experiment 1. We performed the same contrasts on the test phase data as in Experiment 1 to determine if the regions showing increased activation in that experiment were similarly modulated by former-target-color distractors unassociated with prior reward. The regions of activation observed in the test phase of Experiment 1 served as ROIs for which the mean response on distractor present and distractor absent trials was compared across participants.

Contributions

B.A.A., P.A.L., and S.Y. conceived of the study and designed the experiments. B.A.A. collected the data. B.A.A. and P.A.L. analyzed the data. B.A.A., P.A.L., and S.Y. wrote and edited the manuscript.

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Appendix A. Supporting information

Supplementary data associated with this paper can be found in the online version at <http://dx.doi.org/10.1016/j.brainres.2014.08.062>.

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