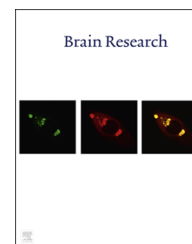


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Research Report

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



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ARTICLE INFO

Article history:

Accepted 19 August 2014

Available online 27 August 2014

Keywords:

Selective attention

Attentional capture

Reward learning

fMRI

Basal ganglia

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

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