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Neural Mechanisms of Incentive Salience in Naturalistic Human Vision

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SUMMARY

What role does reward play in real-world human vision? Reward coding in the midbrain is thought to cause the rapid prioritization of reward-associated visual stimuli. However, existing evidence for this incentive salience hypothesis in vision is equivocal, particularly in naturalistic circumstances, and little is known about underlying neural systems. Here we use human fMRI to test whether reward primes perceptual encoding of naturalistic visual stimuli and to identify the neural mechanisms underlying this function. Participants detected a cued object category in briefly presented images of city- and landscapes. Using multivoxel pattern analysis in visual cortex, we found that the encoding of reward-associated targets was enhanced, whereas encoding of reward-associated distractors was suppressed, with the strength of this effect predicted by activity in the dopaminergic midbrain and a connected cortical network. These results identify a novel interaction between neural systems responsible for reward processing and visual perception in the human brain.

INTRODUCTION

Dopaminergic cells in the midbrain respond to cues that predict reward (e.g., Schultz et al., 1997). While there is debate regarding the precise computational nature of this signal (e.g., Flagel et al., 2011), there is consensus about its purpose: it recruits the cognitive systems necessary to pursue the reward (Ikemoto and Panksepp, 1999; Berridge and Robinson, 1998). Theories of approach behavior suggest that this is achieved in part through an effect on perception and attention. By this, reward-elicited activity in the dopaminergic midbrain initiates a sequence of events that ultimately causes reward-predictive stimuli to become salient and attention drawing (Berridge and Robinson, 1998; Roelfsema et al., 2010). This could benefit evolutionary behaviors like the search for food.

Though this incentive salience hypothesis has been the subject of substantial research, there is little evidence for its basis in vision. Work with animals demonstrates involvement of the dopamine (DA) system in overt approach behavior, but it is not clear that this reflects discrete changes in perceptual encoding rather than motor control or other cognitive stages. Human work suffers the opposite problem: a handful of studies have documented reward-related changes in perception and attention (e.g., Anderson et al., 2011; Hickey et al., 2010), but there is little linking these effects to the midbrain or DA system.

Existing work on reward's role in vision has moreover employed stimuli presented in artificial arrays and distinguished by low-level visual features (see Chelazzi et al., 2013 for review). Outside the laboratory, however, the features that characterize reward-associated objects naturally vary as a function of factors like perspective, lighting, distance, and occlusion, and reward is commonly linked to a category of objects where individual examples share few basic characteristics. Stimuli in the real world moreover appear in complicated scenes, providing a powerful context that constrains both the position and visual properties of objects and improves search in ways not predicted by traditional models (Wolfe et al., 2011; Peelen and Kastner, 2014). It is unclear that a mechanism acting to prime low-level visual features of reward-associated objects would provide substantive evolutionary utility under these circumstances.

Here we use human fMRI to test the idea that reward might guide naturalistic human vision and to identify the neural mechanisms underlying this function. We had 20 participants view pictures of real-world scenes while in the scanner, reporting the presence or absence of examples of a cued target category in each image (Figure 1A; Figure S1). The target category—cars, trees, or people—was indicated at the beginning of each block of trials and correct responses were rewarded with points that had cash value. For each participant, one of the three object categories was special: when this category was cued, correct target detection earned 100 points, with all other types of correct response earning only a single point. Importantly, when one of the reward-neutral categories was cued, scenes could contain task-irrelevant examples of the reward-associated category as distractors.

This design provided three key strengths. First, it created a situation in which the reward-associated category was commonly task irrelevant, allowing us to dissociate reward's impact on perceptual salience from its impact on strategic preparation. Specifically, we could determine how examples of the reward-associated category were represented not only when they were the strategic target of search, but also when participants were searching for examples of some other category. Our expectation was that a reward-associated distractor would be

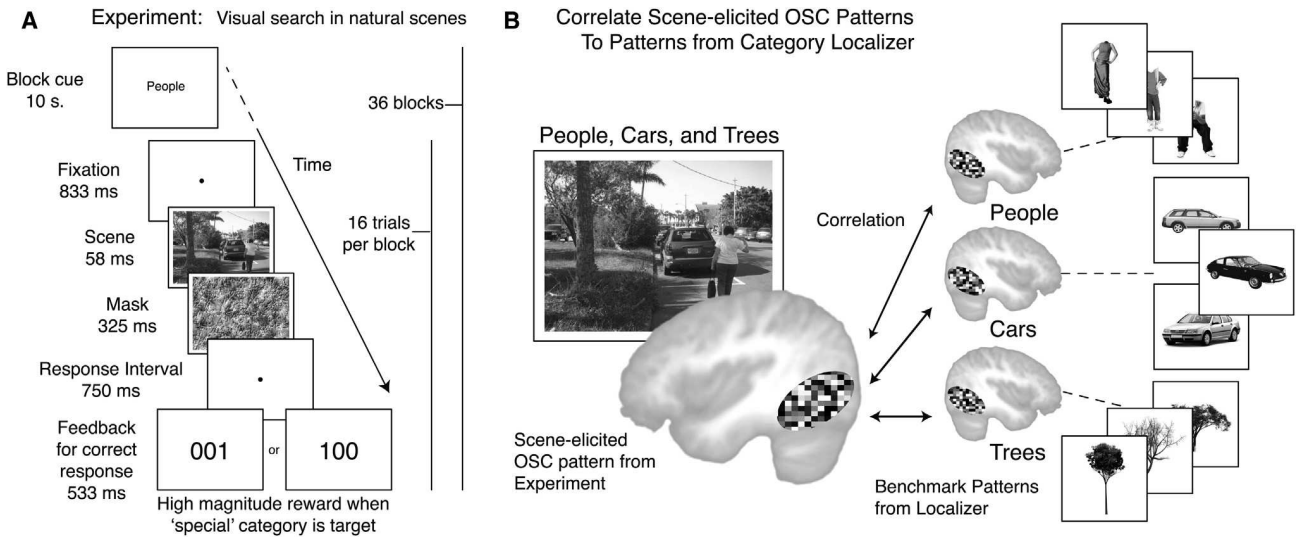

Figure 1. Visual Search through Natural Scenes

(A) Experimental paradigm. One target category was "special"; when cued, correct detection of these objects garnered 100 points. The identity of this category was counterbalanced across subjects. (B) Analytic approach. Scene-evoked activity patterns in OSC were cross-correlated with benchmark patterns identified in a separate localizer experiment. Strong correlations indicate increased category information in visual cortex during scene perception.

of greater salience than a reward-neutral distractor, creating the need for strong attentional suppression.

Second, the design provided conditions in which correct detection of a target did in fact lead to reward, allowing us to identify neural structures in the midbrain that are sensitive to cues that validly predict reward. These structures could be subsequently examined for reactivity to reward-associated stimuli when eliciting stimuli were not the target of search and reward was not available. This allowed us to test the idea that reactivity to naturalistic reward cues might predict the quality of representation for these objects in visual cortex.

Finally, by employing meaningful real-world scenes as stimuli, the design allowed us to investigate reward's impact on categories of visually heterogeneous objects embedded in cluttered but meaningful scene context. For example, in our design an image of a person could be located at a wide range of positions, could be partially occluded by other objects, could be viewed from any angle or distance, and could be of any sex, race, age, or size. If the association of reward has the ecologically important role in vision that is ascribed to it by theory, it must be able to guide vision under these naturalistic circumstances.

RESULTS

Our first aim was to determine whether the prior association of reward would impact the salience of category examples present in real-world scenes as targets and distractors. To do this, we measured category information in object-selective visual cortex (OSC) by comparing scene-evoked OSC activity patterns to benchmark patterns identified in a separate localizer experiment (Figure 1B; Figure S1). The degree to which the scene-evoked pattern matched each of the individual category benchmarks provided a measure of the strength with which each of these categories was represented in OSC (Peelen et al., 2009). Prior work using this method has shown that targets are better represented than distractors and that distractor information decreases when distractor salience is increased through prior task relevance (Seidl et al., 2012). This is consistent with the idea that irrelevant, attention-drawing stimuli require attentional suppression, and we accordingly expected a decrease of information for reward-associated distractors in the current study.

Results confirmed this prediction. As illustrated in Figure 2, OSC carried more information about reward-associated targets and less about reward-associated distractors when these objects were presented alongside a reward-neutral counterpart. In a repeated-measures ANOVA (RANOVA), this expressed as a significant interaction between object status and reward factors ($F(1, 19) = 7.643$, $p = 0.010$; main effect of object status: $F(1,19) = 11.25$, $p = 0.003$; main effect of reward: $F(1,19) = 1.30$, $p = 0.269$). Fifteen of 20 participants showed an increase in OSC information for reward-related targets relative to reward-neutral targets (exact binomial $p = 0.041$) and 16 of 20 showed a decrease in information for reward-related distractors relative to reward-neutral distractors (exact binomial $p = 0.012$). We replicated the reduction of reward-associated distractor category information in a separate analysis of activity patterns evoked by three-category scenes. These contained a reward-neutral target, a reward-associated distractor, and a reward-neutral distractor, and here 17 of 20 participants showed a relative reduction in OSC information content for the reward-associated distractor relative to the reward-neutral distractor (exact binomial $p = 0.003$). Analysis of behavior revealed that participant reaction times (RTs) to a reward-neutral target were significantly slower and nominally less accurate when presented alongside a reward-associated distractor (520 ms versus 506 ms, $t(19) = 2.61$, $p = 0.017$; 84.5% versus 86.2%, $t(19) = 1.05$,

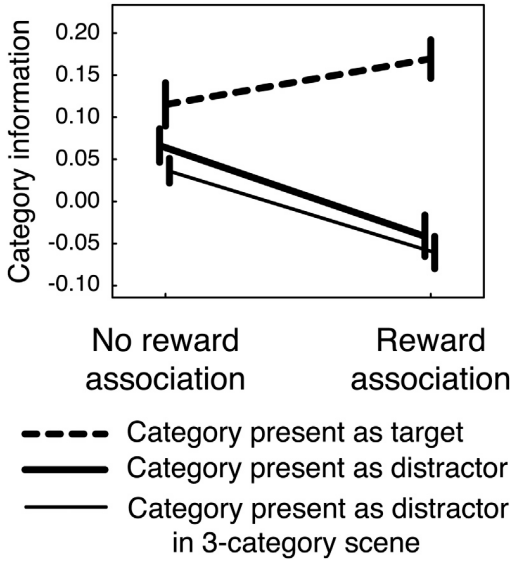

Figure 2. Mean Category Information in OSC for Reward-Associated and Reward-Neutral Targets and Distractors

In the case of two-category scenes, category information was calculated as the correlation between scene-elicited pattern and target or distractor benchmark minus the correlation between scene-elicited pattern and benchmark for the category absent from the scene. In the case of three-category scenes, no such subtraction was made and information content for all three categories was based on the same set of trials. Error bars reflect within-subject SE (Cousineau, 2005).

p = 0.307) and there was a relationship across participants between this RT cost and the difference in OSC representation of a reward-associated versus reward-neutral distractor (r = 0.39, 95% CI: 0.005 to 0.731). The reward-related distractor thus slowed performance in those individuals who did not suppress the visual representation of this stimulus.

Our second aim was to determine whether the reward-related modulation of OSC information described above was mediated by activity in the dopaminergic midbrain. To test this, we correlated univariate activity in a reward-sensitive midbrain region of interest (ROI) with our multivariate measure of OSC distractor information observed across participants. The midbrain ROI was functionally defined by contrasting activity elicited in trials containing a reward-associated target against activity elicited when the target was reward neutral (Figure 3A, blue trace). We subsequently calculated the difference in activity elicited in this ROI by two-category scenes containing a reward-neutral target and reward-neutral distractor versus those containing a reward-neutral target and reward-associated distractor. Our measure of midbrain sensitivity to the reward-associated distractor reliably predicted the strength with which information about this object was suppressed in that participant's OSC (Figure 3C, blue markers; r = −0.538, 95% CI: −0.281 to −0.711).

We conducted two subsequent analyses to confirm and further investigate this relationship. In the first, we functionally defined the midbrain ROI at a more stringent inclusion threshold (Figure 3A; red trace). This identified a small cluster of reward-sensitive voxels in the ventral tegmental area (VTA) and substantia nigra pars compacta (SNc). In the second analysis, we used a brain atlas to define an anatomical ROI describing the bilateral substantia nigra (SN; Figure 3B). Results for these analyses were much the same: the midbrain response to a reward-associated distractor predicted the reduction in distractor information in OSC (conservative functional ROI: Figure 3C, r = −0.493, 95% CI: −0.246 to −0.678; SN anatomical ROI: Figure 3D, r = −0.431, 95% CI: −0.175 to −0.638). Independent examination of target-absent trials also identified this relationship, with activity elicited by the reward-associated distractor in the conservative VTA/SNc cluster reliably predicted the suppression of information about this object in OSC (r = −0.658, 95% CI: −0.345 to −0.849; Figure S2).

Whole-brain analyses revealed a number of additional clusters outside the midbrain where a relationship between hemodynamic response and OSC information suppression could be identified across participants (Figure 4; Table S1). These notably include the left orbitofrontal cortex (OFC), bilateral dorsolateral prefrontal cortex (DLPFC), and anterior cingulate (ACC), all areas with strong connectivity to dopaminergic midbrain nuclei in primates (e.g., Haber et al., 2000; Williams and Goldman-Rakic, 1993). Other clusters were located bilaterally across the inferior and superior parietal lobules, areas associated with selection in vision (e.g., Behrmann et al., 2004), and bilaterally in the inferior frontal gyri, areas linked to inhibition and attentional control (e.g., Aron et al., 2004).

Finally, we examined the relationship between the measures of OSC information content and midbrain activity described above with an inventory measure of trait reward sensitivity. Before entering the scanner, participants completed a Dutch translation (Franken et al., 2005) of the BIS/BAS questionnaire (Carver and White, 1994). We calculated scores on a subscale of this measure that indexes trait sensitivity to reward feedback—BAS reward responsiveness (BAS_{rr})—and found a significant correlation both with univariate reactivity to reward-associated distractors in the conservative VTA/SNc ROI (Figure 3E; r = 0.467, 95% CI: 0.064 to 0.709) and with our multivariate measure of reward-associated distractor information in OSC (Figure 3F; r = −0.447, 95% CI: −0.090 to −0.662). Participants who showed trait reward sensitivity in the personality assessment thus showed strong effects of reward association on both midbrain activity and OSC information suppression. This links individual variability in these measures to reward sensitivity rather than other factors that may vary across individuals, thereby supporting our interpretation of the cross-participant correlations between midbrain activity and OSC suppression (Figures 3C and 3D).

DISCUSSION

Our study addresses an important unresolved question: whether the bias to approach reward-associated objects in the environment partly reflects change in perceptual encoding. Consistent with prior results, we found enhanced perceptual representation of objects when their selection and processing would lead to rewarding outcome (e.g., Serences, 2008). However, it is unclear whether this reflects a direct impact of reward on representation or one mediated by the strategic allocation of attention

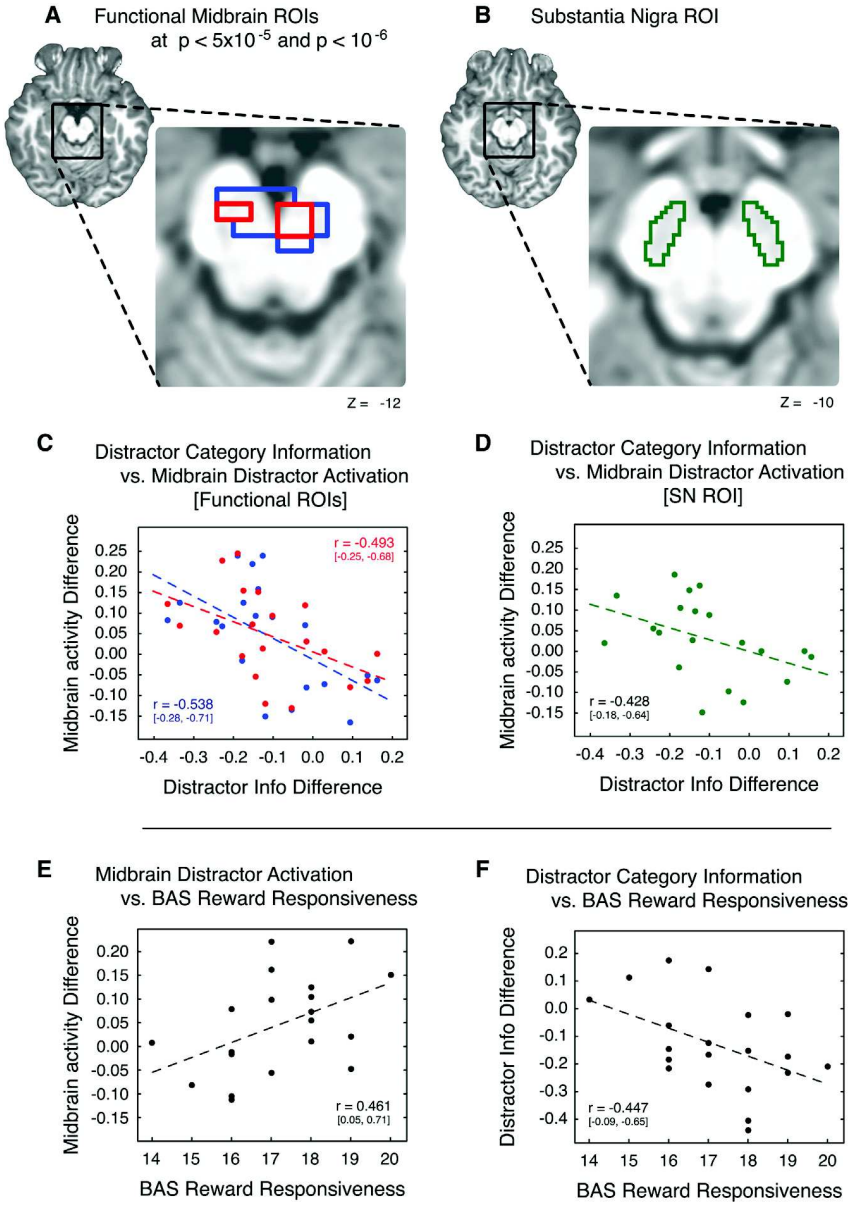

Figure 3. Analysis of Results from Midbrain ROI

(A) Functionally defined reward-sensitive ROIs with threshold of $p < 5 \times 10^{-5}$ (blue trace) and $p < 10^{-6}$ (red trace). (B) Anatomical substantia nigra ROI. (C and D) Correlation between mean OSC distractor information difference and midbrain activity caused by the presence of a reward-associated distractor. (E) Correlation between midbrain activity increase caused by reward-associated distractor and BAS_{rr}. (F) Correlation between OSC distractor information and BAS_{rr}. Values provided in square brackets reflect correlation 95% confidence intervals.

(Maunsell, 2004). We decoupled these potential influences by examining the representation of reward-associated and reward-neutral objects when they acted as task-irrelevant distractors. Results showed that information about reward-associated distractors was strongly suppressed in OSC, that participants were generally slower to respond to reward-neutral targets when scenes contained such a distractor, and that this behavioral cost was reduced in participants whose imaging results showed stronger distractor suppression. Reward thus appears to have a direct and non-strategic impact on the salience of real-world object categories, causing reward-associated distractors to disrupt search and require attentional suppression.

Our results demonstrate an impact of reward on salience in spite of marked visual heterogeneity between individual category examples. This may reflect the priming of highly overlearned intermediate-level shape features that together are diagnostic of a semantic category, such as those characterizing a person's arm or a car's tire (Evans and Treisman, 2005; Ullman et al., 2002; Reeder and Peelen, 2013). Alternatively, reward may have the ability to impact representations at the level of conceptual category (Wachsmuth et al., 1994; Messinger et al., 2001). This would allow for reward following selection of one category example to prime processing of another even when these individual instances share no visual characteristics.

The quality with which a reward-associated distractor is represented in OSC is predicted in our data by activity in a network of areas including the OFC, DLPFC, ACC, parietal lobe, and, notably, dopaminergic midbrain. Midbrain signaling probably plays two roles in this context. On the one hand, a broadband dopaminergic response to a reward cue indicating the potential for reward in the environment could serve an online function, recruiting frontal structures that support cognitive operations necessary for pursuit of the reward (Berridge and Robinson, 1998; Noudoost and Moore, 2011a). In the current data, an attentional response triggered in this way could be reflected in activation of the DLPFC, a brain area that has been associated with the implementation and maintenance of attentional set in other contexts (MacDonald et al., 2000; Miller and Cohen, 2001). On the other hand, the DA reward signal may initiate a sequence of events leading to long-term plasticity in visual cortex. This would be consistent with a recent theory of perceptual learning suggesting that reward signals in visual cortex—perhaps locally instantiated in acetylcholine—cause the reinforcement of visual representations when eliciting objects are selectively attended at the time that the reward signals are received (Roelfsema et al., 2010; Noudoost and Moore, 2011b). These mechanisms could act synergistically: an existing

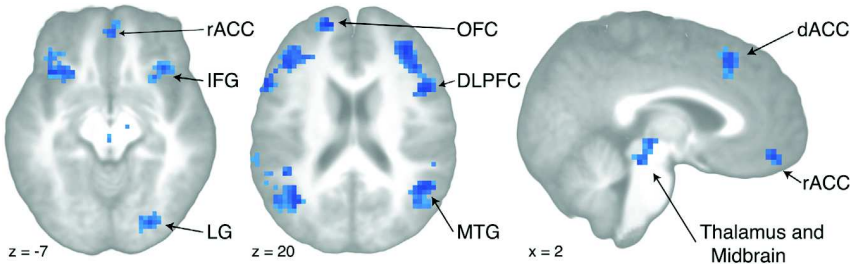

Figure 4. Results from Whole-Brain Correlation Analysis

In highlighted voxels activation in response to a reward-related distractor predicted reduced distractor category information in OSC across participants ($p < 0.05$ FDR corrected, minimum cluster size of 30 voxels). rACC, rostral anterior cingulate; IFG, inferior frontal gyrus; LG, lingual gyrus; OFC, orbitofrontal cortex; DLPFC, dorsolateral prefrontal cortex; MTG, middle temporal gyrus; dACC, dorsal anterior cingulate.

perceptual benefit for reward-associated stimuli would ensure that these objects are rapidly detected in the environment, optimizing the online attentive response. However, neither of these accounts is intended to suggest a direct impact of DA on visual cortex. Indeed, DA's impact on vision must be mediated by brain structures like the ACC, DLPFC, and frontal eye fields that have DA receptor sites (Haber et al., 2000; Williams and Goldman-Rakic, 1993; Noudoost and Moore, 2011b).

Existing results show a pattern of greater activation followed by suppression in the visual response to reward-associated distractors (Hickey et al., 2010; Hickey and van Zoest, 2012) that is similar in nature to that observed in response to physically salient distractors (e.g., Reynolds and Desimone, 2003; Fellrath et al., 2014). Importantly, however, this pattern will not be evident in BOLD fMRI. The limited temporal resolution of this technique means that when brief activation is followed by sustained suppression, suppression will dominate the observed signal. We thus approached analysis in the current experiment with the idea that an increase in the salience of distractors would express as a reduction in OSC information content (Seidl et al., 2012).

The suppression of reward-associated distractors we identify, however, is important above and beyond this role as proxy index of salience. Our study was premised on the idea that reward-associated stimuli become salient and attention drawing in order to gain preferential access to subsequent cognitive processes. This kind of mechanism would be beneficial in exploratory behavior where prioritized investigation of reward-associated objects would provide benefit. However, task-irrelevant reward-associated stimuli must ultimately be ignored in order that strategic behavior can continue, and failure of this system could have unexpectedly dire consequences. For example, drug stimulation of the DA system is thought to impact the incentive salience of environmental stimuli present during drug use (Robinson and Berridge, 1993). These "drug triggers" become salient and attention drawing and induce craving once noticed, making this a potentially important determinant of addictive behavior. Individual variability in the capacity to ignore such stimuli could underlie the puzzlingly large variability in propensity to addiction.

In this context the neural system responsible for the suppression of incentive salience becomes an important research topic in its own right. Previous work has identified the ACC as a region that is both strongly connected to the dopaminergic midbrain and centrally involved in the evaluation of strategic control (MacDonald et al., 2000). The dorsal ACC has been implicated in the modulation of distractor salience by reward outcome (Hickey et al., 2010; Buschschulte et al., 2014) and ACC activity is observed in addicts completing tasks requiring that drug-related stimuli be ignored (Goldstein et al., 2007; Luijten et al., 2011). In line with these prior results, ACC activity in the current results was correlated with the strength of distractor suppression in visual cortex (see Figure 4).

In summary, we show that reward impacts the salience of real-world objects in cluttered daily-life environments, causing reward-associated distractors to disrupt search and require attentional suppression. We identify a role for dopaminergic midbrain structures in mediating reward's impact on visual representation and characterize a cortical network involved in the suppression of reward-associated distractors when this is necessary for goal-directed behavior. Together, these results identify a novel interaction between neural systems responsible for reward processing and visual perception in the human brain.

EXPERIMENTAL PROCEDURES

All procedures were approved by the ethics committee of the University of Amsterdam Department of Psychology.

Participants

Twenty healthy volunteers with normal or corrected vision gave informed consent before beginning the experiment (7 male, mean 24 years ± 3.2 SD). Sixteen participants were right handed.

Experimental Stimuli

Black and white pictures of natural scenes (n = 384) were selected from an online database (Russel et al., 2008; Figure S1). Scenes were organized into eight groups of 48 based on whether they contained cars, trees, or people: three groups were of single-category scenes, containing one or more examples of cars, trees, or people but never any combination thereof; three groups were of two-category scenes, containing a combination of two categories but no example from the third; one was of three category scenes, containing examples of all three categories; and one was of control scenes, containing no example of any of the three categories.

Experimental Design

The experiment consisted of 6 scanner runs of 330 s duration, each composed of 6 blocks of 16 trials. All runs began and ended with a 15 s fixation interval. Within each, an experimental block began with the 10 s presentation of a word cue identifying the target category for the coming 16 trials. Each of the three categories acted as target an equal number of times, and order of target types within a run was counterbalanced across runs. A trial began with a fixation interval (833 ms), followed by brief presentation of a scene (58 ms; 3° × 4° visual angle), a mask (325 ms), the reappearance of fixation (750 ms), and reward feedback (533 ms; see Figure 1A). Participants reported the presence of an example of the target category with the left index finger response and its absence with the right. Each block contained 8 trials where the target was present: twice alongside examples of both distractor categories, four times with examples of a single distractor category, and twice on its own. In the other 8

trials, the target was absent from the scene: twice the scene contained examples of both distractor categories, four times an example of one distractor category, and twice no example of any relevant category. Order of trials was randomized within a block and throughout the course of the experiment participants saw each scene at least once and none more than twice. Scenes were masked with one of 48 images created by generating white noise at different spatial frequencies and superimposing a naturalistic texture. Errors garnered no reward. Participants were paid based on the number of points accumulated throughout the experiment, but because of consistent performance in the sample there was little variability in earnings (€40–45).

OSC Localizer

Two localizer experiments preceded the primary task. The first was designed to identify OSC and comprised 2 scanner runs of 315 s duration, each containing 16 blocks of 20 trials and 3 fixation blocks. A trial began with fixation (350 ms) followed by either a central image of an isolated everyday object on a white background or a pixel-scattered version of such an image (400 ms; 3° × 3° visual angle; see Figure S1). Participants monitored for image repetition, which occurred twice in each block. All trials in a block contained either whole or scattered images, block order was counterbalanced across runs, and every fifth block was a 15 s fixation block with no stimuli.

An OSC ROI was defined for each subject in native space by contrasting activity evoked by intact and scrambled objects. ROIs were generated for each subject by identifying occipital and temporal voxels in the ventral visual stream where this contrast garnered uncorrected p values less than 0.05. Mean OSC size was ~72 cm^3 (2,667 voxels) ±38 cm^3 SD (1,421 voxels).

Category Pattern Localizer

The second localizer was designed to identify voxel-wise patterns of activation in OSC for the three stimuli categories. It comprised 2 runs of 375 s duration, each containing 19 blocks of 20 trials and 4 fixation blocks. Again, a trial consisted of a fixation period (350 ms) followed by a central image (400 ms; 3° × 3° visual angle), but here images were isolated examples of cars, trees, or headless human bodies on a white background (see Figure 1C). Participants monitored for trial-to-trial image repetition, all trials in a block contained images taken from the same category, and every fourth block was a fixation block. Block order was counterbalanced across runs such that mean serial position of each condition was equal. Participants were provided with task instructions for the main experiment, including identification of the reward-associated category, only after having completed the localizers. Body images in the localizer procedure were headless because faces in the experimental scene stimuli were commonly too small to visually resolve. We did not want the localizer pattern to reflect the encoding of face information if face processing was not possible in the experiment itself.

Data Acquisition and Preprocessing

Whole-brain scanning was performed with a 3T Philips Achieva XT MRI scanner using a 32 channel head-coil (functional data: echo planar imaging, 37 slices, 3 × 3 × 3 mm voxel size with 0.3 mm gap, repetition time [TR] = 2.0 s., echo time [TE] = 27.68 ms, flip angle [FA] = 76.1°; structural data: T1-weighted MPRAGE, 220 slices, 1 × 1 x 1 mm voxel size, 240 × 240 matrix, TR = 8.2 ms, TE = 4.38 ms, FA = 8°). Functional data were slice time and motion corrected, low-frequency drift was removed with a 0.006 Hz high-pass filter, and results were spatially smoothed with a Gaussian kernel (6-mm full-width, half-maximum). To allow for whole-brain group analysis, we transformed structural and functional data to Talairach space. Data were analyzed using the AFNI software package (Cox, 1996) and custom MATLAB scripts (MathWorks).

Statistical Analysis

Analysis of experiment and localizer results began with the creation of general linear models for each participant with predictors for each condition. These were convolved with a standard model of the hemodynamic response function. Additional regressors were included to account for changes in mean signal across scanning runs and for head motion. This garnered a t value for each voxel for each condition. In line with existing work (Haxby et al., 2001), these were normalized by subtracting for each value the mean t calculated for that voxel across all conditions of the experiment. This eliminates voxel-wise conditional shifts in hemodynamic response unrelated to experimental manipulations while retaining conditional variance.

Normalized t values observed in the OSC ROI were extracted for all category localizer and experiment conditions, and results from the category localizer were correlated with conditional results from the main experiment. Each condition of the main experiment thus had three associated correlation values describing the degree to which the scene-elicited pattern was similar to the cars, trees, or people benchmark pattern from the localizer. These values were Fisher transformed and organized in terms of whether the category acted as target, distractor, or was absent from the scene, and whether it was associated with reward. Tests of conditional differences in information content relied on standard repeated-measures ANOVA and exact binomial tests. Confidence intervals associated with cross-participant correlation values reflect bootstrap estimates (10,000 samples with replacement).

Correlations between Activity and Information

An index of reward's impact on distractor information was calculated by subtracting category information observed when two-category scenes contained a reward-neutral distractor and a reward-neutral target from that observed when the distractor came from the reward-associated category. These values were correlated with mean parameter estimates of the corresponding univariate contrast in three midbrain ROIs (Figure 3). The first of these ROIs was functionally defined by selecting reward-sensitive voxels that reliably differentiated between trials in which the target was taken from the high-reward versus normal category ($p < 5 \times 10^{-5}$, uncorrected). This ROI is illustrated in Figure 3A in blue trace and had a total volume of 3.59 cm^3 (133 voxels). The second ROI employed a more stringent inclusion parameter ($p < 10^{-6}$, uncorrected; red trace in Figure 3A; 162 mm^3, 6 voxels). The third ROI was anatomically defined using a Talairach atlas implemented in AFNI ("TT_Daemon"; green trace in Figure 3B; 648 mm^3, 24 voxels).

Method for Whole-Brain Correlation Analysis

Using Talairach transformed data, we contrasted activity evoked by two-category scenes containing a reward-neutral target and reward-associated distractor with activity evoked by two-category scenes containing a reward-neutral target and reward-neutral distractor, yielding a contrast value for each voxel for each participant. We subsequently calculated the Spearman's rank correlation between each voxel's contrast values and the OSC distractor information difference for two-category scenes (see Figure 2A). The threshold for this exploratory correlation map was set to r = 0.604, reflecting the critical value associated with a false discovery rate (FDR) of 0.05 based on the results across all 68,303 voxels with nonzero value in the group-average anatomical brain space.

SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures and one table and can be found with this article online at http://dx.doi.org/10.1016/j.neuron.2014.12.049.

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