

The neural basis of scene preferences

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What is the neural correlate of preference that governs our spontaneous selection of visual information? With a rapid, event-related functional magnetic resonance imaging design, we showed that the viewing of highly preferred compared to less preferred scenes (as assessed by participant ratings) was associated with greater blood-oxygen level dependent responses in the right parahippocampal cortex but not in the lateral occipital complex, ruling out feed forward and attentional effects. Highly preferred images also

produced greater activation in the ventral striatum, suggesting that perceptual preference might engage the conventional reward system. These results are consistent with the hypothesis that high activity in the parahippocampal cortex, an area with a high density of cortical μ -opioid receptors, may be experienced as cognitively pleasurable. *NeuroReport* 18:525–529 © 2007 Lippincott Williams & Wilkins.

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Introduction

It is self-evident that people prefer viewing some scenes over others, for example, a coastal vista rather than a parking lot. These preferences are manifested two or three times a second when making spontaneous eye movements as well as in the desirability of a 'room with a view.' What neural mechanism might control this spontaneous selection of scenes?

One possibility is suggested by the surprising discovery of a gradient of μ -opioid receptors [1] in the ventral visual pathway [2] subserving visual recognition. The receptors are sparse in the earliest stages (e.g. V1 and V2) and progressively increase in density reaching their maximum in association areas, such as the parahippocampal gyrus. Several candidate ligands for these receptors exist, one of which has been termed endomorphin [3]. A recent theoretical account [4] assumes that visual preferences – if not perceptual and cognitive preferences in general – are mediated by cortical μ -opioid activity so that high activity in areas rich in the ligands for such receptors produce strong preferences for the experiences that elicit those ligands. Experiences that produce high activation of associative connections would be those that are novel and richly interpretable (not just complex). Insofar as repetition would produce competitive learning that would reduce net activity, novelty, in general, would be a positive factor [4].

Images depicting a spatial layout activate a region of the parahippocampal cortex, termed the parahippocampal place area, more strongly than individual objects [5]. The same area shows greater activity to objects with strong contextual associations, such as beach chairs, than to objects with weak contextual associations, such as cherries [6,7].

These findings suggest that the parahippocampal cortex might be an association area, coding place-related information as well as mediating contextual associations to our environment. From the perspective of the μ -opioid hypothesis of perceptual pleasure, greater associative activity in the parahippocampal cortex – a region with a high density of opioid receptors – should be experienced as pleasurable. The current experiment was designed to test this hypothesis directly (although not the putative opioid substrate) by measuring activity in the parahippocampal cortex while participants rated their preference for scenes during functional magnetic resonance imaging (fMRI) scanning.

Repetition of an image reduces both the blood-oxygen level dependent (BOLD) response to it as well as its preference rating [4]. To assess differences in preferred vs. nonpreferred images, at their maximal values, each image was presented in the current experiment only once. This allowed us to present a larger set of images than has been employed in prior fMRI experiments.

One question raised by the hypothesis proposed by Biederman and Vessel [4] is whether spontaneous preference is driven by activation of the μ -opioid receptors independent of the conventional reward circuitry involving the ventral striatum, occurring in drug addiction [8] and highly emotional situations [9]. Although the proposed theory does not explicitly exclude the possibility that cognitive/perceptual pleasure could be subserved by the conventional reward system, it suggests that the perceptual pleasure system could function independently of the conventional, noncognitive, nonperceptual reward system. We investigated this possibility in this study.

Methods

Design

The main experiment used a rapid event-related design [10] with a total of 200 trials (scenes) run in four blocks of 50 scenes each. Each scene was presented only once for 1.5 s while the participant was being scanned, followed by a 2.5 s blank interval during which the participant rated his/her preference for the current scene by pressing one of eight keys on two button boxes, four with a box held with one hand and four with the other, designated 1 (don't prefer at all) to 8 (prefer greatly) from the offset of the scene (Fig. 1). Response keys were counterbalanced across participants (i.e. whether 1 was on the extreme right or left).

Stimuli

The scenes were selected from a commercial image CD (IMSI MasterClips and MasterPhotos Premium Image Collection, San Rafael, California, USA), and spanned a wide variety of settings (such as natural vistas, city streets, and rooms, etc.). None of the scenes depicted 'graphic' content that would be likely to elicit strong emotions such as fear, disgust, or sexual arousal. All scenes subtended a visual angle of 8° horizontally and 6° vertically. Scene luminance contrast was normalized so that all scenes had equal contrast.

The inclusion of scenes in the database (and our selection of scenes from that set) was designed so that the scenes would be readily recognizable. A rapid serial visual presentation experiment [11] showed high levels (~90%) of recognition accuracy for these images when the target was defined by its name, for example, 'Is there a market in the sequence?' In that rapid serial visual presentation experiment, the presentation durations (masked by the preceding and subsequent scene) were 100 ms. In the present experiment, the presentations were 15 × that duration with no masking and a full 4 s with which to make a judgment of preference. See Fig. 1a and [4] for some examples.

Further confirmation of the ease of recognizing these scenes derives from an experiment [4], where participants rated these scenes on six factors: (a) mystery (Likelihood that something new might appear or different information

will become available if you changed your vantage point), (b) vista (Can you see a wide expanse? How good is the view?), (c) nature (vs. urban or artifact), (d) refuge (Is there a position where you can see but not be seen?), (e) coherence (How rapidly and easily did you understand what the scene was about?), and (f) intelligibility (How easily would you be able to determine where you were in the scene and navigate through it?). The first four factors explained 62% of the variance of the ratings; the last two none of the variance, because all the scenes were rated high in coherence and intelligibility. The factors were suggested by evolutionary psychologists [12], who were considering the factors that might have induced our distant ancestors to make their encampments in one place rather than another.

Participants

Fourteen participants, graduate or undergraduate students at the University of Southern California, participated in the experiment for monetary compensation. Two participants were excluded from the data analysis because of excessive head movement, so the data are from the remaining 12 participants. The study was approved by the University of Southern California Internal Review Board. All participants gave signed, informed consent.

Instructions to participants

The participants were instructed to press one of eight keys to indicate how much they preferred the image presented on the screen. They were asked to distribute their ratings over the eight levels of preference as much as possible, and base their preference for an image on its content, rather than color, contrast, complexity, or any other low-level property of the image. They were explicitly told to rate an image after it disappeared from the screen, which give them ample time (1.5 s) to comprehend the image.

Imaging parameters

fMRI imaging was conducted in a 3T Siemens MAGNETOM Trio at the University of Southern California's Dana and David Dornsife Cognitive Neuroscience Imaging Center. Functional scanning used a gradient echo EPI PACE (prospective acquisition correction) sequence with 3D k-space motion correction (TR=2000 ms; TE=32 ms; flip angle=90°; 28 slices; 64 × 64 matrix size with resolution 3.5 × 3.5 × 4 mm³ voxels). The slices were positioned to be parallel to the Sylvian fissure, so that data were collected from most of the brain. The anatomical T1-weighted structural scan was done using an MPRAGE sequence (T1=1100; TR=2070 ms; TE=4.1 ms; flip angle=12°; 192 sagittal slices; 256 × 256 matrix size with resolution 1 × 1 × 1 mm voxels).

Region of interest

Four localizer runs were conducted, two in the beginning and the other two at the end of the rating blocks. Each localizer run included four conditions: pictures of places, strong context objects, weak context objects, and scrambled objects. Scrambled images were created by scrambling 8 × 8 patches of pixels from intact images of objects and translating the blocks so that no discernible structure was apparent. Each 20 s block of a localizer was composed of 10 images, each shown for 1000 ms. During the 1000 ms blank interval following each image, participants were

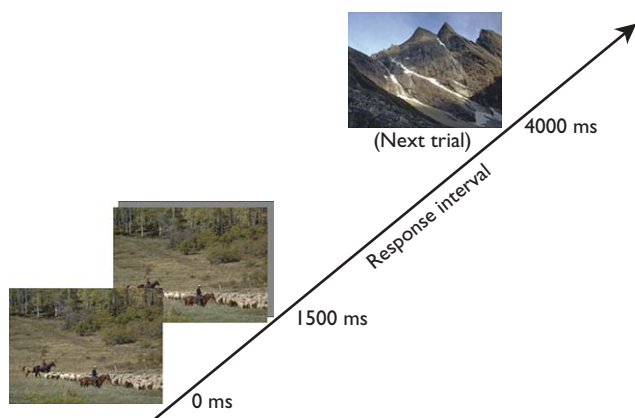


Fig. 1 Illustration of a single trial. A scene was shown for 1.5 s followed by a blank interval of 2.5 s during which the participant could produce the rating. All the scenes, including the two in the figure, had the same amount of contrast.

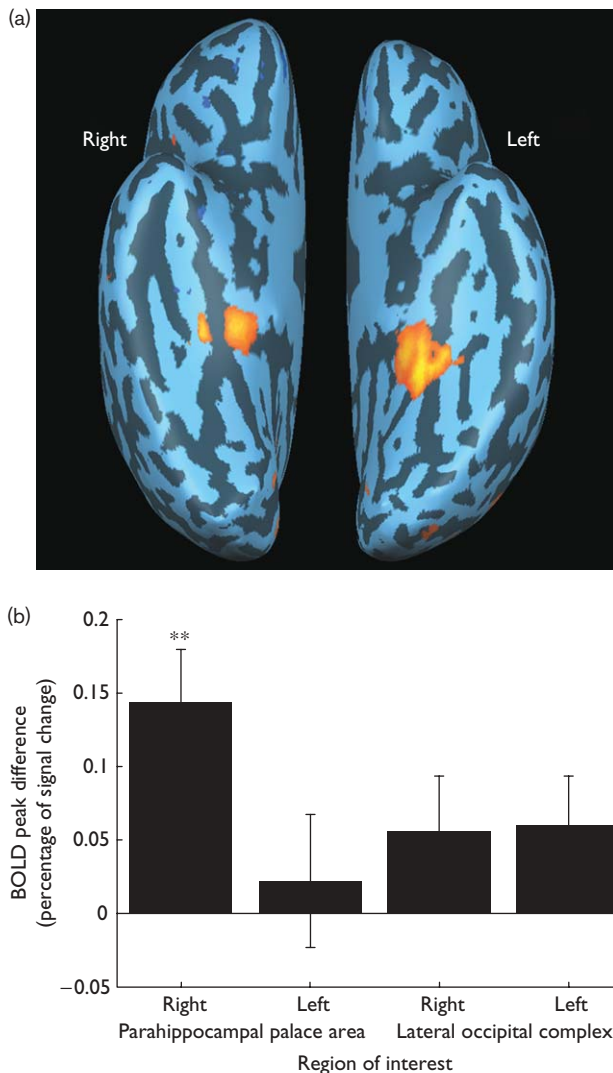


Fig. 2 Region of interest in the parahippocampal cortex and the peak hemodynamic responses as a function of high vs. low preferences for the right and left parahippocampal place areas (in the parahippocampal cortex) and lateral occipital complex. (a) Region of interest for the parahippocampal place area in the parahippocampal cortex defined by the contrast of place minus object images projected onto an inflated brain. (b) BOLD magnitude difference (high-low) at the hemodynamic peak value between scenes with high- and low-preference ratings. A scene was categorized as high if its rating was greater than the median of the ratings for that participant; otherwise, it was categorized as low. The statistical analysis was performed on the deconvolved hemodynamic responses for the two conditions. The peak (the percentage signal change at 6 s after stimulus onset) was computed for each condition for each participant. The statistical analyses were performed on the difference between these values. 0.01 level. Error bars are the SEM. BOLD, blood-oxygen level dependent response.

instructed to press any key to indicate if they could recognize the object(s) in the image, otherwise they were to maintain their alertness. As we did not find a consistent activation pattern across participants between strong and weak context objects, a region of interest (ROI) for parahippocampal cortex was defined by a contrast of places vs. objects (strong and weak context objects combined) at uncorrected $P < 10^{-4}$ (parahippocampal place area) (Fig. 2a). Lateral occipital complex was defined by a contrast of places,

strong and weak context objects vs. scrambled at uncorrected $P < 10^{-6}$ (Fig. 2a).

Functional MRI data analysis

The fMRI data were analyzed with BrainVoyager QX (Brain Innovation BV, Maastricht, The Netherlands). All data from a scan were preprocessed with 3D motion correction, slice timing correction, linear trend removal, and temporal smoothing with a high-pass filter set to three cycles over the run's length. No spatial smoothing was applied to the data. Each participant's motion-corrected functional images were coregistered with their same-session high-resolution anatomical scan. Then each participant's anatomical scan was transformed into Talairach coordinates. Finally, using the above transformation parameters, the functional scans were transformed into Talairach coordinates as well. All statistical tests reported were performed on this transformed data.

For the rapid event-related runs, a deconvolution analysis was performed on all voxels within each participant's localizer-defined ROIs to estimate the time course of the BOLD response. A scene was categorized as high if its rating was greater than the median of the ratings for that participant; otherwise it was categorized as low. Deconvolution was computed using the BrainVoyager QX software by having ten 1-s shifted versions of the indicator function for a participant's response to each stimulus as the regressor (high and low) in a general linear model.

To quantify the statistics between the deconvolved hemodynamic responses for the high and low conditions, the percentage signal change at the peak for each response was computed for each participant. Statistical analyses were performed on these values. The peak value occurred at 6 s and corresponded to the maximum value when fit with a double- γ function [13].

Whole brain analysis

For each participant, whole brain maps of percentage signal changes were computed for each condition using a deconvolution analysis similar to that described above. A group-level mixed effects analysis was then performed on these maps of percentage signal change for each voxel, with rating condition (low and high) modeled as fixed effects and participants modeled as a random effect. A voxel was reported as active if it fell beyond a statistical threshold of $P < 10^{-4}$, uncorrected. The percent signal change for active voxels was then exported into SPSS (SPSS Inc., Chicago, Illinois, USA) for an analysis of the difference (high minus low preference) in the peaks of the hemodynamic functions. For inclusion, active voxels had to be within a cluster (i.e. have nearest neighbors) that would constitute a volume of at least 50 mm³.

Results

Behavioral ratings

The pair-wise correlations of scene ratings across participants were all positive, with a mean of 0.4039 and a range of 0.1951–0.6145, indicating some consistency of preference between participants. The mean reaction times for high preference judgments were almost identical to the times for making low preference judgments, 919 ms (SD=248) and 922 ms (SD=239), respectively, $t(11) < 1$, suggesting that

irrespective of what produced lower preference ratings it was not greater difficulty in processing the scenes.

Parahippocampal cortex and lateral occipital complex

Figure 2b shows that the right parahippocampal cortex (Fig. 2a) had significantly larger BOLD responses to highly preferred scenes than scenes of low preference $t(11)=3.96$, $P<0.01$, but this differential BOLD activation was not present in the left parahippocampal cortex $t(11)<1.00$, ns. Only a minimal effect of preference was seen in either the left or the right lateral occipital complex [for right lateral occipital complex, $t(11)=1.50$, $P>0.10$; for left lateral occipital complex, $t(11)=1.78$, $P>0.10$], suggesting that the preference effect in the right parahippocampal cortex was not a feedforward or an attentional effect from earlier stages. This result was confirmed further by a multiple regression analysis of the right parahippocampal place area on three other areas (left parahippocampal cortex, right lateral occipital complex, and left lateral occipital complex) showing that the activity in the right parahippocampal cortex was independent of the activity in other areas, $F(3,8)<1.00$. In addition, randomly shuffling the trials resulted in a disappearance of differential BOLD activation in the right parahippocampal cortex [$t(11)=-0.73$, $P>0.10$], indicating that the greater response to more highly preferred scenes was not an artifact of the sequences but, instead, was produced by the participants' neural activity in response to the stimuli.

Ventral striatum

With the whole brain analysis, the right, but not the left, ventral striatum showed increased activity (Fig. 3) when compared to the rest condition, with 70 voxels centered on Talairach coordinates $(18.03 \pm 3.40, 2.02 \pm 6.19, 13.60 \pm 4.12)$. This region included the caudate body, putamen, lateral globus pallidus, and a small portion of the ventral anterior nucleus. A significantly greater peak BOLD response was present in this region for the high-preference responses than in the low-preference responses [$t(11)=2.80$, $P<0.02$]. The earliest cortical visual areas, V1 and V2, showed no differential response as a function of preference, as assessed by the whole brain analysis, $t(11)<1.00$. The whole brain analysis did not show above-threshold activation of the amygdala, indicating that the scene selection of the present experiment (by design) did not elicit the kinds of emotions, such as fear, generally associated with activation of that structure.



Fig. 3 Right ventral striatum (circled regions) with Talairach coordinates centered at $18.03 \pm 3.40, 2.02 \pm 6.19, 13.60 \pm 4.12$. The high-preference scenes evoked a significantly larger hemodynamic response at the peak value than did the low-preference scenes, $t(11)=2.80$, $P<0.02$.

Discussion

As the parahippocampal place area is defined as a region that yields a weaker BOLD response to faces and objects (without a depth background) than scenes [5], it might be the case that participants gave low ratings to those scenes with faces and objects, which would be alternative explanation to our differential BOLD responses to high and low preferences at the right parahippocampal place area. We examined the ratings for those scenes (23 of the 200), where a human, mammal, or artifact (a scarecrow) face was depicted sufficiently close that an expression could be discerned or where an entity was depicted without an apparent scene context (19 images). These images had ratings that were slightly above the median so a diminished BOLD response to those scenes could not be a source of the greater hemodynamic response to more highly preferred images.

The current results suggest that the system controlling real-time preferences for perceptual inputs might be concentrated in the parahippocampal cortex, a region with a high density of μ -opioid receptors. Higher activity in this region was associated with increased scene preference. This differential effect was not a consequence of feedforward activity from earlier visual areas, such as V1, V2, or lateral occipital complex. The differential effect in the ventral striatum (but not the amygdala), however, suggests that the activity in the right parahippocampal cortex mediating perceptual preference might project to the right ventral striatum, suggesting that perceptual preference is a function of the conventional reward system.

Why the differential activity witnessed in this experiment was confined to the right parahippocampal cortex and right ventral striatum in this study is unknown. Recent fMRI [14] and patient [15] research indicates that the right fusiform gyrus is more involved in visual recognition whereas the left fusiform gyrus is more involved in processing semantic categories. Further research will be required to determine whether this distinction also holds for the rewards that can be achieved through such processing.

Conclusion

These results are consistent with the hypothesis that high activity in the parahippocampal cortex may be experienced as pleasurable and activity in this area may subserve the spontaneous selection of visual experience.

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References

- Lewis ME, Mishkin M, Bragin E, Brown RM, Pert CB, Pert A. Opiate receptor gradients in monkey cerebral cortex: correspondence with sensory processing hierarchies. *Science* 1981; **211**:1166–1169.
- Ungerleider L, Haxby J. 'What' and 'where' in the human brain. *Curr Opin Neurobiol* 1994; **4**:157–165.
- Gutstein HB, Akil H. Opioid analgesics. In: Brunton L, Lazo J, Parker K, editors. *Goodman and Gilman's the pharmacological basis of therapeutics*. 11th ed. New York: McGraw-Hill; 2006.

4. Biederman I, Vessel EA. Perceptual pleasure and the brain. *Am Sci* 2006; **94**:249–255.
5. Epstein R, Kanwisher N. A cortical representation of the local visual environment. *Nature* 1998; **392**:598–601.
6. Bar M, Aminoff E. Cortical analysis of visual context. *Neuron* 2003; **38**:347–358.
7. Bar M. Visual objects in context. *Nat Rev Neurosci* 2004; **5**:617–629.
8. Everitt BJ, Robbins TW. Neural systems of reinforcement for drug addiction: from actions to habits to compulsion. *Nat Rev Neurosci* 2005; **8**:1481–1489.
9. Coricelli G, Critchley HD, Joffily M, O'Doherty JP, Sirigu A, Dolan RJ. Regret and its avoidance: a neuroimaging study of choice behavior. *Nat Neurosci* 2005; **8**:1255–1262.
10. Burock MA, Buckner RL, Woldorff MG, Rosen BR, Dale AM. Randomized event-related experimental designs allow for extremely rapid representation rates using functional MRI. *NeuroReport* 1998; **9**:3735–3739.
11. Vessel EA, Mangini MC, Biederman I. Experts vs. novices performing subordinate RSVP identification. Paper presented at the 7th annual workshop on object perception and memory. Los Angeles, 1999.
12. Kaplan S, Kaplan R. *Cognition and environment: Functioning in an uncertain world*. New York: Praeger; 1982.
13. Boynton GM, Finney EM. Orientation-specific adaptation in human visual cortex. *J Neurosci* 2003; **23**:8781–8787.
14. Simons JS, Koutstaal W, Prince S, Wagner AD, Schacter D. Neural mechanisms of visual object priming: evidence for perceptual and semantic distinctions in fusiform cortex. *Neuroimage* 2003; **19**:613–626.
15. Vandenberghe R, Peeters R, Flanders K, Vandenberghe R. Knowledge of visual attributes in the right hemisphere. *Nat Neurosci* 2006; **9**: 964–970.