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Research report

A direct comparison of appetitive and aversive anticipation: Overlapping and distinct neural activation☆

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HIGHLIGHTS

- Neural substrates of pleasant and unpleasant anticipation are directly compared.
- Pleasant anticipation uniquely activates ventral mPFC and striatal reward regions.
- Activation in other regions (e.g., dorsal mPFC) is enhanced during pleasant or unpleasant anticipation.

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ABSTRACT

fMRI studies of reward find increased neural activity in ventral striatum and medial prefrontal cortex (mPFC), whereas other regions, including the dorsolateral prefrontal cortex (dlPFC), anterior cingulate cortex (ACC), and anterior insula, are activated when anticipating aversive exposure. Although these data suggest differential activation during anticipation of pleasant or of unpleasant exposure, they also arise in the context of different paradigms (e.g., preparation for reward vs. threat of shock) and participants. To determine overlapping and unique regions active during emotional anticipation, we compared neural activity during anticipation of pleasant or unpleasant exposure in the same participants. Cues signalled the upcoming presentation of erotic/romantic, violent, or everyday pictures while BOLD activity during the 9-s anticipatory period was measured using fMRI. Ventral striatum and a ventral mPFC subregion were activated when anticipating pleasant, but not unpleasant or neutral, pictures, whereas activation in other regions was enhanced when anticipating appetitive or aversive scenes.

1. Introduction

Anticipation of emotional events is central to many personality and clinical disorders, with dysregulated appetitive anticipation critical in reward-seeking, gambling, and substance use (or abuse) behavior [1], while anticipatory apprehension and distress is characteristic of human anxiety disorders [2,3]. Addressing the neural mechanisms of emotional anticipation, numerous fMRI studies have found that, when individuals anticipate receiving a reward, the ventral striatum (which includes the nucleus accumbens) and ventral medial prefrontal cortex (mPFC) are activated [4–11]. Conversely, anticipating exposure to an aversive stimulus (such as electric shock) activates other brain regions, including the dorsolateral prefrontal cortex (dlPFC), anterior cingulate cortex (ACC), and the anterior insula, but does not reliably activate ventral striatum or mPFC [12–15]. Although these findings suggest that different regions might be involved when anticipating pleasant or unpleasant events, the data result from comparisons across different paradigms, classes of stimuli, and participants. Thus, to more directly compare neural activity in appetive and aversive anticipation, this study measures BOLD activity while participants anticipate arousing natural scenes containing pleasant (erotica/romance) or unpleasant (violence) content, as well as pictures depicting neutral, everyday scenes.

Studies of reward anticipation often assess neural activity when preparing to make a rewarded motor response and/or winning money. In the typical paradigm, participants are shown a cue that predicts a subsequent imperative "go" signal, and a rapid button

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press to the go signal is rewarded by a monetary gain. Using this paradigm, ventral striatum and ventral mPFC activation is reliably enhanced during the preparatory interval leading up to a rewarded button press, relative to an unrewarded reaction time condition [e.g.,4–6]. Later studies reported similar results using alterations to the typical paradigm, such that receipt of reward was not so closely contingent upon behavioral performance; however, these studies nonetheless invariably involve a motor component and also a monetary reinforcer, as well as some degree of uncertainty or "chance" during the anticipatory interval [e.g.,10,11].

Studies of aversive anticipation, meanwhile, typically involve a passive conditioning paradigm, in which a conditioned signal reliably predicts the subsequent presentation of a noxious reinforcer, typically an electric shock [e.g., [12]; for a review, see [14]]. Thus, although the extant research as a whole suggests possible distinctions in the neural networks that mediate reward or aversive anticipation, different activation patterns could also be the function of other paradigmatic differences, including differences in the active vs. passive nature of the paradigm or the use of secondary (money) vs. primary (shock) reinforcers. In addition, given the lack of a within-subjects comparison of pleasant and unpleasant anticipation, it could be that different patterns across studies at least partially result from individual differences across samples.

To directly compare activation during pleasant and unpleasant anticipation in the same participants, colored cues specified whether an upcoming scene would depict erotica/romance, violence, or everyday events. Emotional scenes reliably elicit measurable cardiovascular, sympathetic (e.g. pupil, electrodermal), and motor (facial EMG) activity [16], and these images also prompt heightened neural activity in both subcortical (e.g. amygdala) [17] and cortical (e.g., fusiform) [18] regions. By measuring regional changes in BOLD activity during the anticipatory period preceding the presentation of highly arousing scenes of romance or violence, this design allows a direct comparison of functional brain activity in the context of appetitive or aversive anticipation, to determine whether distinct or overlapping regions are engaged in these different anticipatory contexts. These data could help to elucidate whether the anticipatory processes involved in putatively distinct emotional phenomena (e.g., drug-seeking behavior or experience of anxiety) are distinct, or similar, processes.

2. Materials and methods

2.1. Participants

Twenty-seven undergraduate students participated for course credit. Data for 3 students were excluded due to excessive movement (n = 1) or equipment failure (n = 2), leaving a sample of 24 participants (15 female, 23 right-handed; M_{age} = 19.0 yrs) with complete data.

2.2. Design and materials

Forty-two grayscale pictures were selected from the International Affective Picture System [19] to comprise three hedonic contents: "romance" (erotica and romantic scenes), "violence" (mutilated bodies and attack scenes), and "everyday events" (people at work or engaged in mundane activities).[1] Based on normative ratings [19], picture sets were constructed such that: 1) compared to everyday events, pictures of violence were rated as significantly more unpleasant and pictures of romance were rated as significantly more pleasant, and; 2) pictures of violence and pictures of romance were each rated as significantly more arousing than everyday events, and did not differ from each other.

Cues were red, blue, or green rectangles presented full-screen (1024 × 768 pixels), with the color signalling the content of the upcoming picture (e.g., blue = romance, red = violence, green = everyday event) that would be presented following the anticipatory interval. Colors were counterbalanced such that, across participants, each content was cued by each color. Cues were presented for 9 s and were followed by a 3-s scene presentation, and then a variable-length inter-trial interval (15 or 18 s). For each content, there were 7 anticipatory trials; another 7 trials were un-cued and are not presented here.

The order of cues was counterbalanced such that no more than two cues signalling erotica, violence, or everyday events occurred in a row. Different presentation orders were generated such that each block of 6 trials contained one cued and one un-cued picture from each hedonic content (i.e., romance, violence, everyday events). Presentation orders were constructed such that, across orders: 1) each trial type occurred equally often as the first trial of the experiment, 2) each trial type occurred equally often in each block position (1st, 2nd, 3rd, 4th, 5th, or 6th trial), and; 2) each IAPS image was presented equally often in the beginning, middle, and end of the experiment. Finally, one foil trial occurred in each half of the experiment.

2.3. Procedure

Prior to the study, participants were informed that different colors would signal the hedonic content of the upcoming picture, such that one color would be followed by presentation of a romance scene, another color would be followed by presentation of a violent scene, and a third color would be followed by an everyday event. Correct report of the color cuing each category was required of the participant prior to starting the experiment. To encourage maintenance of the hedonic cue throughout the anticipatory interval, the participant was instructed to press a button if a cue was *not* followed by the anticipated content; this occurred on 2 foil trials which were not included in the data analysis.

After removal from the scanner, the participant rated the pleasantness of anticipating each content on a Likert scale that ranged from 1 (very unpleasant) to 7 (very pleasant) (4 = neutral). Anticipating violent scenes was rated as more unpleasant than anticipating everyday events ($t(24) = 5.41$, $p < 0.001$), whereas anticipating romantic scenes was rated as more pleasant than everyday events ($t(23) = 4.65$, $p < 0.05$).

2.4. fMRI data collection

Data were collected in a 3-T Philips scanner with a 32-channel head coil. The scanning sequence began with acquisition of a 160-slice sagittal scout set using a standard T1-weighted fast-field echo sequence. Functional images comprised 53 coronal slices (3 mm width, 0.5 mm gap; voxel size = 2.5 × 2.5 mm) covering the whole brain. Functional images were acquired using a T2*-weighted echo planar sequence (180 × 180 × 185 mm FOV, 90° flip angle, TE 30 ms, TR 3000 ms).

2.5. Data preprocessing and analysis

Raw functional time series data for each participant were aligned with the (skull-stripped) structural volume for that participant, slice-time corrected, and spatially filtered with a 2-voxel (5.0 mm) full-width-at-half-maximum kernel using AFNI software [20]. Outliers were calculated using an AFNI procedure that identi-

[1] IAPS numbers: *Romance*, 4003, 4008, 4085, 4290, 4470, 4505, 4530, 4575, 4647, 4658, 4660, 4668, 4695, 4698; *Violence*, 3010, 3017, 3051, 3060, 3068, 3191, 3225, 3261, 3530, 6350, 6520, 6561, 9420, 9900; *Everyday*, 2038, 2102, 2104, 2190, 2220, 2222, 2305, 2312, 2377, 2397, 2515, 2579, 2595, 2850.

fies, by algorithm, data points deviating excessively from the time series trend; TRs in which greater than 5% of the whole-brain data were statistical outliers were not included in the analysis (<1% of all data). Functional time series data for each voxel were transformed into percent signal change relative to the average signal across the entire time series for each voxel. These percent change data and the structural volume were then converted into standardized coordinate space [21]. Impulse response functions were estimated directly from the data (i.e., no canonical model was fitted to the data) for each trial, using a cubic spline interpolation and parameters that modeled hedonic content (romance, violence, everyday event) and motion in the x, y, and z planes across five 3 s TRs (beginning at cue onset). Resulting impulse response functions were averaged separately when anticipating romance, violence, and everyday events for each student.

Whole brain analysis was conducted using an analysis of variance (ANOVA) of the peak BOLD response (6 s after cue onset) with anticipated hedonic content as a repeated-measures factor. Voxels showing a main effect of content were determined using a threshold F statistic of 3.44 (uncorrected $p < 0.05$) and a cluster size of 55 voxels (~1013 ml^3). To avoid inflation of type II error when findings are restricted to large clusters based on statistical criteria, the cluster threshold was selected based on cluster sizes reported in previous anticipation studies [e.g.,13], allowing for smaller activation clusters that presumably arise in the absence of sensory or motor processing [22]. Significant voxels across the whole brain were aggregated into functional clusters based on spatial contiguity, similarity of activation across voxels, and alignment with standard anatomical regions identified using the Eickhoff-Zilles macro labels in Talairach space [21]. Effects of anticipated hedonic content within each functional cluster were then determined by averaging across all significant voxels within that cluster and conducting pairwise tests of hedonic content.

3. Results

Functional clusters showing a main effect of hedonic content during anticipation are listed in Table 1, and included frontal, temporal, and occipital brain areas. Frontal regions showing a significant hedonic content effect included portions of the medial prefrontal cortex (separated into distinct dorsal and ventral clusters), the dorsolateral prefrontal cortex, and the anterior and middle cingulate gyri, along with the inferior frontal gyrus. Temporal regions included ventral striatum, along with medial temporal activation in hippocampal and parahippocampal gyri and the posterior thalamus. Finally, hedonic effects were also apparent bilaterally in primary visual cortex and in both the ventral and dorsal visual streams (Table 2) presents pairwise comparisons of each content within regions showing an overall content effect.

As illustrated in Fig. 1, the ventral striatum and a ventral region of the mPFC showed selective enhancement of BOLD activity when anticipating pleasant stimuli. In the striatum, functional activation was reliably enhanced when anticipating pictures of romance compared to anticipating violent scenes, $t(23) = 3.98$, $p < 0.001$, or everyday events, $t(23) = 4.08$, $p < 0.001$, and striatal activation did not differ when anticipating violence or everyday events, $t(23) = 0.06$, $p = 0.95$. A similar pattern arose in ventral mPFC – activation was greater when anticipating romance than when anticipating violence, $t(23) = 2.24$, $p < 0.01$, or everyday events, $t[23] = 2.64$, $p < 0.05$, which in turn did not differ $t(23) = -0.72$, $p = 0.48$ (Fig. 1).

Unlike in the ventral mPFC, activity in the dorsal mPFC was enhanced when anticipating any emotional stimulus, relative to anticipating everyday scenes. Thus, activation in dorsal mPFC was enhanced when anticipating romance, $t[23] = 4.06$, $p < 0.001$, or violence, $t(23) = 2.22$, $p < 0.05$, compared to when anticipating everyday events, and dorsal mPFC activation did not differ when anticipating romance or violence, $t(23) = 1.69$, $p = 0.11$. This pattern was similar to patterns of activation in other frontal cortical areas, including the dlPFC and cingulate cortex (Fig. 2), in which functional activity was heightened when anticipating pictures depicting romance (dlPFC, $t[23] = 2.79$, $p < 0.05$; ACC, $t(23) = 4.62$, $p < 0.001$; MCC, $t(23) = 2.37$, $p < 0.05$) or violence (dlPFC, $t(23) = 2.16$, $p < 0.05$; ACC, $t(23) = 2.36$, $p < 0.05$; MCC, $t(23) = 3.87$, $p < 0.01$) compared to anticipating everyday events. Also similarly to the dmPFC, anticipating scenes of romance or violence did not elicit differential activity in the dlPFC ($t(23) = 0.96$, $p = 0.35$) or cingulate (ACC, $t(23) = 0.79$, $p = 0.49$; MCC, $t(23) = 0.44$, $p = 0.67$).

Activation in temporal and occipital areas mirrored patterns in the dorsal frontal cortex. Thus, activation in both the lateral and medial (i.e., hippocampus/parahippocampus) temporal cortices was enhanced both when anticipating scenes of romance (lateral $t(23) = 2.51$, $p < 0.05$; medial $t(23) = 3.83$, $p < 0.001$) or violence (lateral $t(23) = 2.67$, $p < 0.05$; medial $t(23) = 3.14$, $p < 0.01$), compared to anticipating the presentation of everyday scenes.

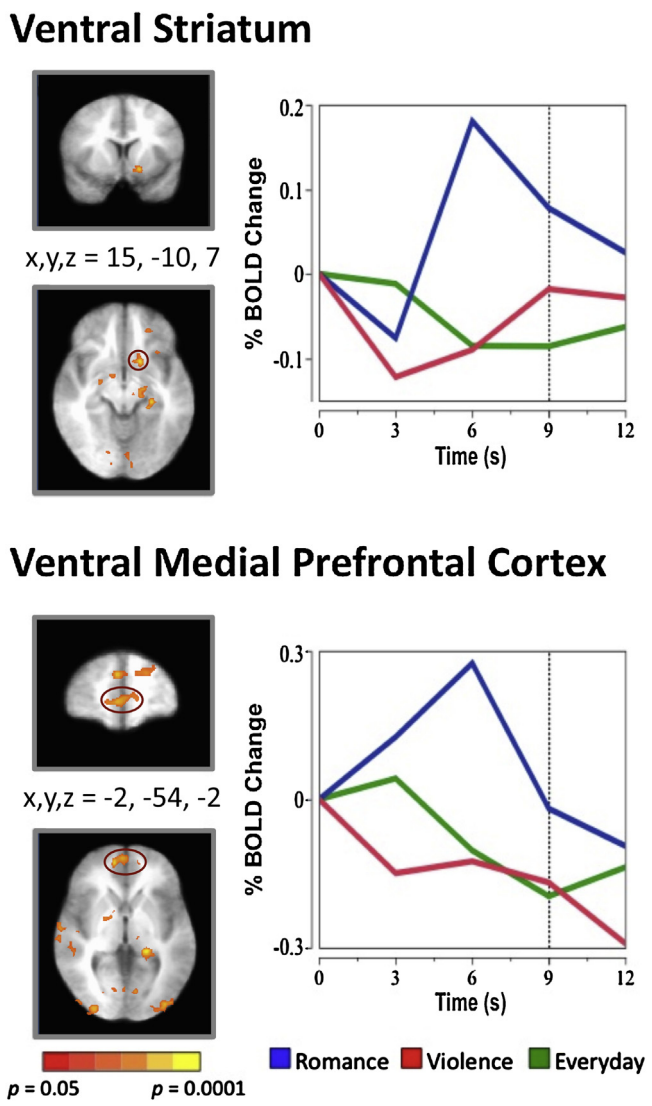

Fig. 1. BOLD activation in the ventral reward circuit (striatum and medial prefrontal cortex) when anticipating romance, violence, and everyday events. Brain images depict voxels showing a main effect of anticipated hedonic content. Dotted line in waveform plots indicates picture onset.

Table 1
Peak percent BOLD signal change for regions showing a main effect of anticipated hedonic content. Coordinates locate the peak effect within each region, and the *F*-value is taken from that voxel.

	Cluster Size	*x, y, z* +L, +P, +I	% Δ, Romance	% Δ, Violence	% Δ, Everyday	Content *F*
Frontal						
Medial Prefrontal						
Dorsal	122	−4, −54, −21	0.02	−0.08	−0.28	8.9
Ventral	101	−2, −54, −2	0.21	−0.09	−0.07	10.5
Dorsolateral Prefrontal	68	16, −54, −24	0.13	0.09	−0.09	5.3
Inferior Frontal Gyrus	161	−40,−31, −21	0.11	0.08	0.22	6.6
Cingulate Gyrus						
Anterior	89	9, −29, −20	0.13	0.16	−0.04	9.1
Middle	108	1, 24, −31	0.31	0.20	0.03	9.8
Medial/Temporal						
Ventral Striatum	146	15, −10, 7 −21, 1, 11	0.14	−0.07	−0.04	9.6
Temporal Gyrus						
Lateral	111	±54, 24, −9	0.10	0.12	−0.02	9.1
Medial	153	±19, 19, 4	0.05	0.01	−0.08	6.2
Posterior Thalamus	54	±24, 24, −4	0.16	0.05	−0.00	7.3
Cerebellar Vermis	141	1, 51, 26	0.16	−0.03	−0.04	6.6
Occipital						
Posterior Parietal Cortex	525	±44, 36, −34	0.05	0.11	−0.05	7.3
Dorsal Visual Stream	475	±4, 71, 4	0.06	0.08	−0.03	6.0
Ventral Visual Stream	219	±31, 86, −1	0.18	0.09	−0.04	8.0
Primary Visual Cortex	87	±4, 71, 4	0.15	0.13	0.01	6.5
Cuneus/Precuneus	273	1, 69, −29	0.34	0.22	0.11	9.5

Note: All *F*s significant at $p < 0.01$.

Table 2
T-test comparisons for regions showing a main effect of anticipated hedonic content. Coordinates locate the peak effect within each region, and the *F*-value is taken from that voxel.

	Cluster Size	*x, y, z* +L, +P, +I	Romance v. Evry	Violence v. Evry	Rom v. Vio	Content *F*
Frontal						
Medial Prefrontal						
Dorsal	122	−4, −54, −21	4.44	2.27	1.87	8.9
Ventral	101	−2, −54, −2	2.96	−0.30	2.82	10.5
Dorsolateral Prefrontal	68	16, −54, −24	3.27	2.24	1.43	5.3
Inferior Frontal Gyrus	161	−40,−31, −21	−2.61	−3.17	0.34	6.6
Cingulate Gyrus						
Anterior	89	9, −29, −20	2.70	2.54	0.33	9.1
Middle	108	1, 24, −31	3.02	2.82	−0.06	9.8
Medial/Temporal						
Ventral Striatum	146	15, −10, 7 −21, 1, 11	4.27	0.00	3.79	9.6
Temporal Gyrus						
Lateral	111	±54, 24, −9	−2.71	−3.61	1.90	9.1
Medial	153	±19, 19, 4	3.71	3.33	−0.33	6.2
Posterior Thalamus	54	±24, 24, −4	3.55	1.00	3.16	7.3
Cerebellar Vermis	141	1, 51, 26	3.93	1.81	1.70	6.6
Occipital						
Posterior Parietal Cortex	525	±44, 36, −34	−2.47	−3.54	1.28	7.3
Dorsal Visual Stream	475	±28, 88, −2	3.72	2.76	−0.06	6.0
Ventral Visual Stream	219	±31, 86, −1	2.38	3.59	−0.68	8.0
Primary Visual Cortex	87	±4, 71, 4	3.04	3.40	−0.93	6.5
Cuneus/Precuneus	273	1, 69, −29	2.67	4.64	−1.61	9.5

Note: All *F*s significant at $p < 0.01$.

Moreover, activation was enhanced for emotional, compared to neutral, anticipation throughout posterior parietal and occipital areas as well (see Table 1).

Whereas previous studies have reported significant activation in anterior insula during emotional anticipation (e.g., threat of shock), in this study the main effect of hedonic content was not reliable in the anterior insula. On the other hand, exploratory analyses in bilateral anterior insula indicated a significant increase in BOLD activity during the cuing interval, relative to a pre-cue baseline, when anticipating the upcoming presentation of any scene (left, 31, −14, −11, $t[23] = 4.46$, $p < 0.001$; right, −31, −16, −9, $t[23] = 4.84$, $p < 0.001$). As indicated by the non-significant hedonic content effect, this activation was similar when anticipating romance, violence, or everyday scenes (see Fig. 3).

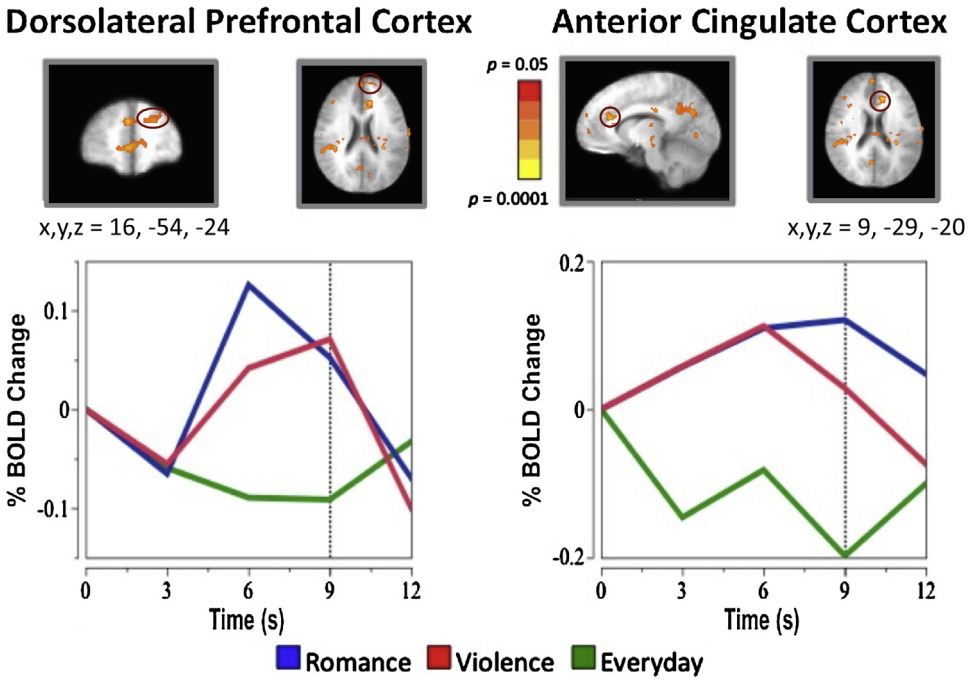

Fig. 2. BOLD activation in dorsal regions showing a main effect of emotional content during anticipation (lateral prefrontal cortex and anterior cingulate cortex) when anticipating romance, violence, and everyday events. Brain images depict voxels showing a main effect of anticipated hedonic content. Dotted line in waveform plots indicates picture onset.

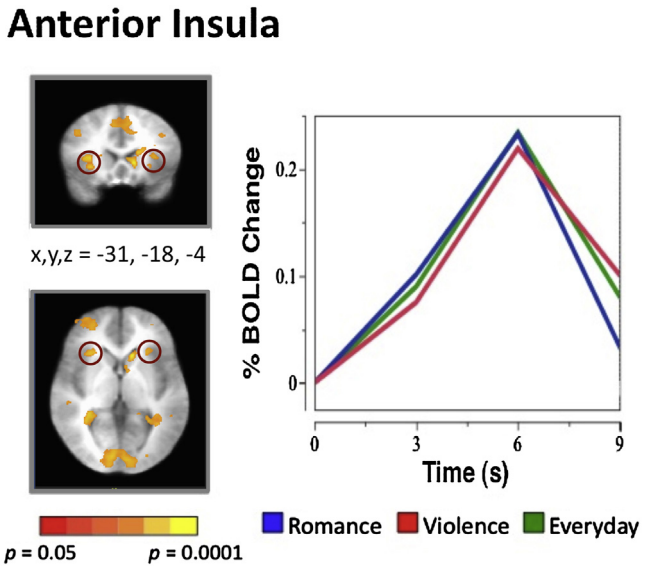

Fig. 3. BOLD activation in anterior insula when anticipating romance, violence, and everyday events. Brain images depict voxels showing a Cue > baseline effect.

4. Discussion

Anticipating pleasant scenes was associated with selective enhancement of BOLD activity (relative to neutral or unpleasant anticipation) in the ventral striatum and in a ventral region of the medial prefrontal cortex. In contrast, functional activity in other regions of the brain that prompted a significant main effect of anticipated content, including the dorsal mPFC, dorsolateral prefrontal cortex and the cingulate cortex, was enhanced when anticipating any emotional scene, pleasant or unpleasant, compared to neutral anticipation. These data support a hypothesis that ventral striatum and ventral mPFC are uniquely involved in appetitive processing, even in the absence of motor activity or monetary reward. On the other hand, functional activity in other regions is involved when anticipating either pleasant or unpleasant, compared to neutral, events. This pattern of modulation is similar to findings in both emotional picture viewing [23] and emotional imagery [24] contexts, in which pleasant stimuli uniquely prompt enhanced activation in ventral striatum and ventral mPFC, whereas activity in other, task-specific regions is enhanced during both pleasant and unpleasant processing.

Animal research has identified reciprocal projections from the nucleus accumbens and surrounding ventral striatum to the mPFC [25] that suggests that direct modulation of nucleus accumbens activity by the mPFC is important in mediating reward-seeking behavior [26,27]. Human findings are consistent with the animal work, as the data implicate a role for both the ventral striatum and mPFC in tasks in which individuals prepare to make a rewarded motor response. In fact, human studies have found that activation of the nucleus accumbens/striatum tracks the magnitude of an anticipated reward [8,10,11], and a recent investigation that independently manipulated reward magnitude and motor response difficulty found that the strength of striatal activation was related to expected reward value but not to the effort required to obtain the reward [28]. The present data extend these findings, implicating a role for ventral striatum and mPFC in anticipating pleasant outcomes even when no overt effort is required.

Whereas ventral mPFC activity was selectively enhanced when anticipating pleasant, compared to neutral or unpleasant, scenes, dorsal mPFC activity was enhanced when anticipating either pleasant or unpleasant highly arousing scenes relative to neutral anticipation. These data are consistent with research finding neural activity in a ventral region of the mPFC showing valence-specific activation (relative activation for pleasant contents and *deactivation* for unpleasant contents) and a more dorsal aspect of the

mPFC showing enhanced activation for all emotionally arousing stimuli [e.g.,29,30]. Moreover, prior work has shown strong functional connectivity between the ventral mPFC and striatum/nucleus accumbens specifically when processing pleasant stimuli, whereas the dorsal mPFC shows significant functional connectivity with the amygdala during either pleasant or unpleasant processing [30]. These findings suggest that ventral and dorsal subregions of the mPFC participate in distinct motive circuits, with the former specifically involved in mediating appetitive behavior and the latter mediating motivated behavior more generally [31].

As with dorsal mPFC, activation in dlPFC and cingulate cortex (previously found when anticipating shock) [e.g.,12], as well as in temporal and occipital cortical regions, was enhanced when anticipating any emotional stimulus, compared to anticipating neutral scenes. Thus, results suggest that these brain regions play roles that are not specific to anticipating pleasant stimuli or unpleasant, but rather are augmented when anticipating any emotionally salient stimulus. Moreover, whereas threat-of-shock studies hypothesize that anterior insula activation is specifically involved in anticipating unpleasant stimuli [32], the present data found significant activation of the bilateral insula in the context of all anticipatory cues, including those predicting neutral stimuli. In threat-of-shock studies, insula activation when anticipating shock is usually compared to a "safe" condition, which involves no anticipatory processing [e.g.,14], which confounds the basic process of anticipating a stimulus with the aversive content of that stimulus. The current data suggest that anticipating any stimulus may involve significant activation of the insula; future investigations comparing insula activity during threat-of-shock to anticipation of non-aversive tactile stimulation would be helpful in addressing this issue.

The pattern of arousal-based, rather than valence-specific, enhancement of BOLD activation outside of the ventral striatum and mPFC parallels fMRI findings in picture viewing [23] and imagery [24] studies. From a motivational perspective, these data are consistent with the interpretation that highly arousing pleasant or unpleasant processing each engage selective attention and heightened sympathetic arousal in preparation for action [33,34]. Further, the engagement of regions of the pre-frontal cortex specific to pleasurable stimuli suggests additional elaborative processing that may reflect later development. Because the appetitive cues presented here were social scenes of erotica and romance, processes additionally implicated in social cognition and awareness, in which medial prefrontal activity figure strongly [35] may be engaged. Future studies exploring anticipatory activity with more basic appetitive cues (e.g., food/water following deprivation) could assess this hypothesis.

5. Conclusion

Taken together, a direct comparison of appetitive and aversive anticipation in the same participants provides data consistent with the characterization of a ventral striatum – ventral mPFC circuit that is activated when processing pleasant or rewarding stimuli even if no overt approach-related action is required. Anticipating pleasant scenes also recruits a broader network of brain regions, including the dlPFC and ACC, that is also active when anticipating unpleasant stimuli. These findings contribute to the database that suggests that strength of activation in the ventral striatum and the ventral mPFC specifically reflects appetitive motivation, whereas regional brain activation outside of those areas reflects motivational engagement rather than specific approach or avoidance processing [29]. These data also highlight the utility of including both pleasant and unpleasant contexts in studies of emotional processing, particularly when seeking to determine whether a particular brain region is a uniquely active during appetitive or aversive processing.

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