

**Reward, Motivation and Emotion Systems Associated with Early-Stage Intense
Romantic Love**

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ABSTRACT

Early-stage romantic love can induce euphoria, is a cross-cultural phenomenon, and is possibly a developed form of a mammalian drive to pursue preferred mates. It has an important influence on social behaviors that have reproductive and genetic consequences. To determine which reward and motivation systems may be involved, we used functional magnetic resonance imaging and studied 10 women and 7 men who were intensely "in love" from 1-17 months. Participants alternately viewed a photograph of their beloved and a photograph of a familiar individual, interspersed with a distraction-attention task. Group activation specific to the beloved under the two control conditions occurred in dopamine-rich areas associated with mammalian reward and motivation, namely the right ventral midbrain and the right caudate nucleus. Activation in the left ventral midbrain was correlated with facial attractiveness scores. Activation in the right medial caudate was correlated with questionnaire scores that quantified intensity of romantic passion. In the left insula-putamen-globus pallidus, activation correlated with trait affect intensity. The results suggest that romantic love uses subcortical reward and motivation systems to focus on a specific individual, that limbic cortical regions process individual emotion factors, and that there is localization heterogeneity for reward functions in the human brain. **Keywords:** striatum, basal ganglia, ventral tegmental area, face, fMRI

INTRODUCTION

Intense romantic love is a cross-culturally universal phenomenon. In a survey of 166 contemporary societies, Jankowiak and Fischer (Jankowiak and Fischer 1992) found evidence of romantic love in 147 of them; they noted that the 19 remaining cases were examples of ethnographic oversight—the anthropologists failed to ask the appropriate questions; they found no negative evidence. They concluded that romantic love constitutes a “human universal...or near universal” (Jankowiak and Fischer 1992). Romantic love is also associated, particularly in early stages, with specific physiological, psychological and behavioral indices that have been described and quantified by psychologists and others (Fisher 1998; Gonzaga et al. 2001; Harris and Christenfeld 1996; Hatfield et al. 1988; Hatfield and Sprecher 1986; Shaver et al. 1987; Tennov 1979). These include emotional responses such as euphoria, intense focused attention on a preferred individual, obsessive thinking about him or her, emotional dependency on and craving for emotional union with this beloved, and increased energy. Tennov (1979) coined the term “limerance” for this special state, and Hatfield et al. (1986) developed a questionnaire scale to measure it. Worldwide, it plays a key role in courtship, suggesting that it evolved as a primary aspect of the human mating system (Fisher 1998). The universality, euphoria and focused attention of romantic love suggest that reward and motivation systems in the human brain could be involved (Fisher 1998; Liebowitz 1983).

In addition, cross-cultural descriptions of romantic love regularly include reward-related images and suggest strong motivation to win a specific mating partner. For example, the oldest love poem from Summeria, “Inanna and Dumuzi,” dating approximately 4,000 years ago and found on cuneiform tablets in the Uruk language is

translated, “My beloved, the delight of my eyes...” (Wolkstein and Kramer 1983). From the Song of Songs, the Hebrew 10th century poem comes, “...your love is more wonderful than wine ...the sound of your name is perfumeI sought the one my soul loves...” (Wolkstein and Kramer 1983). Furthermore, among the ethnographies canvassed in Jankowiak and Fischer’s review (1992) is one by Harris (1995) who cited evidence of the yearning for love and the motivation to win the beloved among the peoples of Mangaia, Cook Islands, Polynesia. These people have a word for “dying for love.” They translate it as, “You don’t want anything else; you die for love, but you don’t mind if you die; you don’t feel ashamed about loving that person to death. If you really love someone nothing will stop you.”

We used functional magnetic resonance imaging (fMRI) methods to test two predictions about the neural systems involved in romantic love. First, early stage romantic love would specifically involve subcortical regions that mediate reward, such as the ventral tegmental area (VTA) and ventral striatum/nucleus accumbens (Esposito et al. 1984; Hollerman et al. 2000; McBride et al. 1999; Porrino et al. 1984; Robbins and Everitt 1996; Schultz 2000; Wise and Hoffman 1992). Several of the behavioral aspects of romantic love suggest that it can be like cocaine-reward, producing exhilaration, excessive energy, sleeplessness and loss of appetite (Fisher 1998). Indeed, acute cocaine injection has been shown to activate the VTA in fMRI studies of humans (Breiter et al. 1997), consistent with animal studies of cocaine addiction (David et al. 2004; Kalivas and Duffy 1998; McBride et al. 1999; Wise and Hoffman 1992). In addition, fMRI studies have shown that secondary rewards like money activated the nucleus accumbens/subcallosal region and VTA (Breiter et al. 2001; Delgado et al. 2000; Elliott et al. 2000; Elliott et al. 2003; Elliott et al. 2004; Knutson et al. 2001).

Furthermore, chocolate, acting as a food reward, activated the VTA and subcallosal region (Small et al. 2001). More data implicating reward regions and dopamine as an important neurotransmitter for the feelings and behaviors of romantic love have been summarized previously (Fisher 1998).

In addition to basic reward functions, further evidence from studies of monogamous prairie voles suggests that the nucleus accumbens, striatum and dopamine could be involved in human romantic love. When a female prairie vole is mated with a male, she forms a distinct preference for this partner; however, when a dopamine agonist is infused into the nucleus accumbens, she begins to prefer a male present at the time of infusion, even if she has not mated with this male (Gingrich et al. 2000; Liu and Wang 2003). Further, a striatal output region through the ventral pallidum is strongly implicated as critical to male prairie vole mate preference behaviors (Lim et al. 2004). Also, electrochemical studies in male rats have shown increased dopamine release in the dorsal and ventral striatum in response to the presence of a receptive female rat, more so even than during copulation (Montague et al. 2004; Robinson et al. 2002). These data suggest that the nucleus accumbens and dopamine release are major factors underlying rodent mate preference. Thus, several lines of evidence from both human fMRI and animal studies support the prediction that multiple reward regions using dopamine could be activated during feelings of romantic love.

Our second prediction about the neural systems involved in early-stage romantic love was that it would be associated with other goal and reward systems, such as the caudate nucleus. The caudate plays a role in reward detection and expectation, the representation of goals, and the integration of sensory inputs to prepare for action (e.g. Lauwereyns et al. 2002; Martin-Soelch et al. 2001; O'Doherty et al. 2004; e.g. Schultz

2000). While some investigators view romantic love largely as a specific emotion (Gonzaga et al. 2001; Shaver et al. 1987; Shaver et al. 1996), others have proposed that romantic love is a goal-directed state that leads to varied emotions (Aron and Aron 1991). It tends to be hard to control, is not associated with any specific facial expression, and is focused on a specific reward. The caudate nucleus is a brain region that could represent rewards and goals in a complex behavioral state like romantic love because it has widespread afferents (Eblen and Graybiel 1995; Flaherty and Graybiel 1995; Kemp and Powell 1970; Saint-Cyr et al. 1990; Selemon and Goldman-Rakic 1985) and is organized to integrate diverse sensory, motor and limbic functions (Brown 1992; Brown et al. 1998; Eblen and Graybiel 1995; Haber 2003; Parent et al. 1995; Parent and Hazrati 1995; Parthasarathy et al. 1992).

One previous fMRI study (Bartels and Zeki 2000) used methods similar to ours, but investigated romantic love in a later stage. Participants in that study had been in love substantially longer than those in our study (28.8 months vs. 7.4 months $t[32] = 4.28, P < .001$). Also, participants in that study were less extremely in love, based on the same standard questionnaire (scores of 7.55 vs. 8.54, $t[31] = 3.91, P < .001$). Thus, this report is the first fMRI study of *early stage* romantic love. We also show novel effects in the human ventral midbrain that may be associated with different aspects of reward, novel time-dependent effects in the cingulate and insular cortex, and novel brain activation correlations with quantified self-reports of passion intensity and trait affect intensity.

METHODS

Participants: Ten women and seven men were recruited from the State University of New York at Stony Brook community, the Rutgers University community,

and the New York City area by word of mouth and with flyers seeking individuals who were currently intensely in love. All participants preferred their right hand (Edinburgh Handedness Inventory Oldfield 1971) and were not taking anti-depressant medications. The age range was 18-26 years ($M = 20.6$; median = 21). The reported duration of "being in love" was 1-17 months ($M = 7.4$; median = 7). All participants gave informed written consent and each received \$50 for his or her participation. The institutional review boards at Stony Brook and Rutgers approved all procedures.

Interviews and questionnaires: A few days in advance of the scanning session, one of us (HEF) orally interviewed each participant in a semi-structured format to establish the duration, intensity, and range of his or her feelings of romantic love. Just prior to the scanning session, each participant also completed two self-report questionnaires: (1) the Passionate Love Scale (PLS; Hatfield, 1986, example items: "I want ___ physically, emotionally and mentally"; "Sometimes I can't control my thoughts; they are obsessively on ___"; Cronbach's alpha for questionnaire reliability in the present study = .81; (Cronbach 1951) and (2) the Affect Intensity Measure (AIM Larsen et al. 1987, Cronbach's alpha in the present study = .85 example items: "I get overly enthusiastic" "Sad movies deeply touch me"), which assesses the general tendency to experience emotions intensely. After the scanning session, two of us (HEF and DJM) conducted exit interviews to determine whether the participants followed the instructions and what they thought about. Also, we tested whether any of the questionnaire data correlated significantly with sex, relationship length or the other questionnaire (or whether any of these variables correlated with each other); they did not. That is, there were no significant correlations among AIM scores, PLS scores, relationship length, and sex.

Stimuli: The stimuli and length of presentation we used were based on a preliminary investigation that identified a photograph of the beloved as better than other stimuli (e.g., touch, voice) for eliciting feelings of intense romantic love (Mashek et al. 2000). Also, Mashek et al. (2000) found that the intensity of feeling tended to diminish after about 30 sec of exposure to the photograph. Prior to the scanning session, each participant provided a photograph of the beloved (Positive stimulus) and a similar photograph of a familiar, emotionally neutral acquaintance of the same age and sex as the beloved (Neutral stimulus). Photographs were digitized and sized to show the head only. An angled mirror was mounted on the RF coil, enabling the participant to view each image, which was projected on a screen placed directly outside the MRI tube, subtending a visual angle of 17°. To be sure that the quality of the photos provided by participants was not a factor, we had a group of individuals rate picture quality. The quality of the Positive and Neutral photos did not differ significantly ($P = .88$). Also, picture quality did not correlate significantly with PLS, AIM, relationship length, sex, or separately rated attractiveness of the face (all P s > .14).

Because it is difficult to quell intense feelings of romantic love, we devised a protocol to decrease the carry-over effect after the participant viewed the Positive stimulus. We interspersed the Positive stimulus and Neutral stimulus with a distraction, serial Countback task. This task involved viewing a number such as 8,421 on the screen and mentally counting backwards in increments of seven beginning with this number. A randomly selected different starting number was presented each time the task was given. Pilot testing established that 40 sec of the Countback task effectively erased feelings associated with the previous Positive stimulus in most individuals. To provide a similar distraction after the Neutral stimulus (but reduce experiment duration),

participants did the Countback task for 20 sec. The different lengths of the Countback task preceding the Positive and Neutral stimulus presentations was a possible confound. However, the length of the stimulus presentation block was likely great enough to reduce any carryover effects from the countback task. Indeed, inspection of the data showed that the Positive and Neutral conditions began at the same response magnitude rather than different response magnitudes, which would be indicative of carryover effects from the previous block.

Instructions to participants and exit interviews. In preliminary studies, participants reported that in addition to a photo, thinking about specific events relating to their beloved was the best circumstance to elicit intense romantic love during a 30 second time period (Mashek et al. 2000). Thus, the instructions to the participants were to think about events that occurred with the beloved that were especially pleasurable, but not sexual, while they viewed the Positive picture. To control for event recall, instructions for the Neutral picture were to think about events with the person in that picture, also. During the interview before the experiment, the interviewer established pleasurable events that the participant might think about while looking at the beloved, and neutral events, like watching TV, while viewing the Neutral stimulus. These events were discussed also just before the fMRI session. During exit interviews, the participants reported that they had, indeed, thought about specific events when they looked at the stimuli. For example with regard to the Positive stimulus: "I thought about the time we both woke up at 3 AM and walked back from the 7/11 store, it was fun walking back and kissing..." With fewer sexual overtones one said, "I felt I could really rely on her, I could open up to her, I felt protected by her." One felt a rush of euphoria; one felt "happy" and "comfortable." These are descriptions of positive, rewarding

feelings, and almost all were without sexual overtones. Regarding the Neutral stimulus, participants reported that they thought about the specified events with the neutral person that were discussed before the experiment, and that by comparison, one felt “bored.” All reported that they did the Countback task, although we had no behavioral verification. Several reported that it was hard to do the Countback task after the Positive stimulus, but not after the Neutral stimulus, which is additional evidence that they carried out the task.

Experimental design and procedures: The protocol consisted of four tasks presented in an alternating block design. (1) For 30 sec the participant viewed the Positive stimulus; (2) for the following 40 sec the participant performed the Countback distraction task; (3) for the following 30 sec the participant viewed the Neutral stimulus; and (4) for the following 20 sec the participant performed the Countback task. The starting image was either the Neutral stimulus or Positive stimulus and was counter-balanced across participants. The four-part sequence was repeated 6 times; the total stimulus protocol was 720 sec (12 min).

Image acquisition and analysis: Data were acquired using a 1.5 T Marconi (Phillips) Edge MRI system. We measured the blood oxygen level-dependent (BOLD) response and took in-plane anatomical data for each participant. The images were: (1) anatomical, axial T1-weighted Spin-Echo Scans: 14 ms TE, 600 ms TR, 90 degree flip angle, 24 cm FOV, 4 mm slice thickness, 0 mm gap, 256 X 256 matrix size, 20 slices; (2) functional, T2-weighted Gradient-Echo EPI scans: 70 ms TE (not optimal), 5000 ms TR, 90 degree flip angle, 24 cm FOV, 4 mm slice thickness, 0 mm gap, 64 X 94 matrix size (zero filled into 128 X 128 before FFT and the resulting 128 X 128 images were

averaged into 64 X 64 before analysis), 20 slices. Voxel size for the functional images was 3.75 X 3.75 X 4.00 mm.

The fMRI data analyses were performed using Statistical Parametric Mapping software (SPM 99 Wellcome Department of Imaging Neuroscience, London, UK Friston et al. 1995) . Functional images were realigned, smoothed with a Gaussian kernel of 8 mm, and normalized to the SPM EPI template brain. (Nineteen participants were recruited, but two were dropped from the study because they moved more than 2 mm.) We treated each of the stimulus types (Positive, Neutral, Countback1, Countback2) as a separate regressor, modeled as a boxcar function convolved with the canonical hemodynamic response; we applied a high pass filter with a cutoff of 240 sec to remove low frequency signal components. We created contrast images for each comparison for each participant We then analyzed the contrast images across participants using a mixed-effects general linear model, treating participants as a random effect and conditions as a fixed effect. Interpretation of the group analyses was facilitated by inspection of individual results. Time course data are reported as “response,” a calculation by SPM99 based on raw data that uses the mean of all the conditions as the baseline.

For planned comparisons (hypothesis-driven analyses), we applied small volume corrections with a sphere as a region of interest ($P \leq .05$, corrected for multiple comparisons). The coordinates for the centers of the regions of interest were based on a review of fifteen fMRI articles that had studied reward or romantic love (Table 1). Rewards in the previous studies included acute cocaine injection, receipt of money and eating chocolate.

Using SPM99, we performed correlations between participant questionnaire scores and brain responses for the PLS and AIM. Also, because another study showed that there are specific BOLD responses in humans to faces rated as beautiful compared to faces rated as average (Aharon et al. 2001), we had five men and five women (non-participants) rate the images for overall “attractiveness.” We correlated the attractiveness score *difference* between Positive and Neutral for each participant with their neural response (for the Positive-minus-Neutral contrast). In addition, because we thought that differences between our data and the findings of the study of longer-term romantic love (Bartels and Zeki 2000) might be caused by the difference in relationship length, we correlated brain responses and months the participants reported having been in love.

We tested for differences between men and women; however, none met the criterion of $p < .001$ corrected for multiple comparisons.

Anatomical localization. To aid our identification of regions affected, we used the atlas of Duvernoy (1999) and the Talairach Daemon Client (Version 1.1, Research Imaging Center, University of Texas Health Science Center at San Antonio). Data were analyzed for individuals on their T1 images, on the mean T1 image for the group, and on the average 305 T1 MNI template in SPM99. To display some of the data, we chose the SPM99 Single Subject T1 (scanned multiple times) dataset because major landmarks are more visible than in the other renderings. The calculated error for SPM99 anatomic normalization within a group is up to 8 mm between sulci and there is 94% overlap among the same gray matter regions (Hellier et al. 2002; Hellier et al. 2001). Thus, the Talairach descriptions of the locations of cortical changes that include Brodmann’s areas are an approximation only; we include them in the report because

they are useful to compare to other studies. In addition, the data were smoothed with a Gaussian kernel of 8 mm so that any single localization point reported in the tables should be considered within an area of approximately 8 mm. Technical considerations limited us to twenty slices that did not cover the entire brain. Parts of the dorsal neocortex (~1-3 cm from the superior surface) were not sampled in some participants while the ventral temporal lobe was not included in others. Thus, we analyzed separately the amygdala and ventral hippocampus in the nine participants (6 women, 3 men) who had data in those regions.

Localization of activation to the medial caudate appeared to be partially in the ventricle in the normalized group images. To confirm that it was caudate activation, we examined unnormalized individual data. “Importantly, brain sections in the atlas of Duvernoy (1999) show caudate tissue lining the ventricle in the regions where we saw activation (Duvernoy, pages 365-393) and horizontal cadaver sections approx 3.5 mm thick show caudate tissue 3.0-4.0 mm wide protruding into the ventricular space (Brown, unpublished observation; also, see Discussion).” ***The following text will be added: “We calculated the distance (in mm) from the anterior commissure to the caudate peak activation in each individual and plotted it on a horizontal section from the Montreal Neurological Institute average brain template based on scans from 305 individuals (Fig. 1).

RESULTS

Positive-minus-Neutral stimulus contrast (activations) Predicted, small volume measurements showed significant differences in the right medial caudate (Fig. 1A, Table 2), in the right antero-dorsal caudate body (Fig. 1B, Table 2), in another region of

the right dorsal caudate body, and in the right BA30/retrosplenial cortex (Table 2). Significant bilateral caudate activations were in the antero-dorsal region (Table 2).

In the ventral midbrain, significant activation was localized in the region of the VTA/A10 dopamine cells (Fig. 2A, B; Also, plots of the time course of the BOLD response show that neural activation increased in response to the Positive image relative to the other conditions, while there was a decrease in the BOLD signal for each control task relative to the Positive stimulus (Fig. 2C). No caudate region showed a similar time course.

Positive-minus-Countback: We had included the Countback task to provide a distraction between Positive and Neutral stimuli. But also, we reasoned that it might serve as a supplementary control condition. That is, areas showing strong activation for the Positive-minus-Neutral subtraction that also showed activations for a Positive-minus-Countback subtraction may be additional evidence that these represent areas associated with intense romantic love. The Positive-minus-Countback subtraction yielded activations overlapping with the Positive-minus-Neutral subtraction for the right ventral midbrain and the right postero-dorsal caudate (Table 2), providing more evidence that activation in these regions is specific to the image of the beloved.

Self-report of degree of passionate love. Focusing again on the Positive-minus-Neutral contrast, we conducted a between-subject random effects analysis correlating degree of the BOLD response and participants' scores on the PLS. (Recall that there were no significant correlations among PLS scores, AIM scores, relationship length, and sex.) As shown in Fig. 3 and Table 2, PLS scores had high positive correlations with activation in two of the regions that were significant for the contrast by itself, the right antero-medial caudate body ($r = 0.60$; $P = .012$, Fig 3C) and the septum-

fornix region ($r = 0.54$; $P < .008$). That is, those who self-reported higher levels of romantic love than others also showed greater activation than others in this region of the caudate and septum when viewing their beloved. As noted by Kosslyn et al. (Kosslyn et al. 2002), the consistency of a between-subject correlation with a subtraction result provides particularly strong triangulating evidence for the link of a function with an activated area.

Attractiveness effects of the Positive and Neutral faces. The correlation between the BOLD response and independently rated attractiveness for the Positive image minus the attractiveness of the Neutral image was significant for voxels in the *left* VTA ($r = 0.74$, $P = .009$; Fig. 4). This is a different location from activation for the Positive-minus-Neutral contrast, which was in the *right* VTA (Fig. 2).

Neutral-minus-Positive stimulus (deactivations) The only predicted region of change to show a deactivation was the amygdala (coordinates: 20, -3, -15, $p < .002$)

Length of time in love. Because our participants were in love for a shorter amount of time than those in the study done by Bartels and Zeki (2000), we correlated degree of activation and participant's reported length of time in love. The correlation was done for the Positive-minus-Neutral contrast. As shown in Figure 5 and Table 3, several regions of special interest showed changes as the relationship lengthened: the right mid-insular cortex; the right anterior and posterior cingulate cortex; the right posterior cingulate/retrosplenial cortex. Scatter plots of the correlation in the anterior cingulate cortex and retrosplenial cortex suggest that participants in longer relationships (8-17 mos) were different from those engaged in relatively short relationships (1-7 mos; Fig. 5). Thus it appears that length of time in love is a major factor for neural activity in

the insula and cingulate/retrosplenial cortex when looking at an image of a romantic partner.

One brain region showed *greater* activation the *shorter* the length of time in love: the left posterior cingulate cortex/retrosplenial cortex region (Table 3).

Self-report of general tendency for emotional intensity. Once again using the Positive-minus-Neutral contrast, we correlated degree of activation and participant's scores on the AIM (the AIM was not significantly correlated with the PLS). The AIM is a self-assessment of general affect tendencies, and the correlation with the BOLD response tested for a potentially important trait difference among participants in a study that may involve emotion. The left mid-insular cortex (Talairach coordinates -42,-6,0) was correlated with AIM score ($r=0.58$; $p<.01$), a region similar to one where Bartels and Zeki (2000) reported activation in their study. Thus, a left insular cortical region was affected by the Positive stimulus, but the response varied depending on an individual's self-report of how strongly the person experiences affect in general.

DISCUSSION

Several results support our two predictions that (1) early stage, intense romantic love is associated with subcortical reward regions that are also dopamine-rich (e.g. Fisher 1998) and (2) romantic love engages a motivation system involving neural systems associated with motivation to acquire a reward rather than romantic love being a particular emotion in its own right (Aron and Aron 1991). Foremost, when our participants looked at a beloved, specific activation occurred in the right ventral midbrain around the VTA, and dorsal caudate body. These regions were significant compared

to two control conditions, providing strong evidence that they are associated with specific aspects of romantic love.

The VTA contains dopaminergic cells (A10) that send projections to several brain regions (Gerfen et al. 1987; Oades and Halliday 1987; Williams and Goldman-Rakic 1998), including the medial caudate where we found specific activations. In addition, both the VTA and caudate regions activated in this study receive visual afferents and respond to visual stimuli (Caan et al. 1984; Horvitz et al. 1997; Saint-Cyr et al. 1990). Although fMRI is limited to measurements of location and relatively long-term neural responses, and cannot determine neurotransmitters used, other electrophysiological, lesion, fMRI, voltammetry, drug infusion and self-stimulation studies have established that the VTA, dopamine and the caudate nucleus play major roles in reward and motivation in the mammalian brain (Delgado et al. 2003; Kawagoe et al. 1998; Martin-Soelch et al. 2001; Phillips et al. 2003; Salinas and White 1998; Schultz 2000; White and Hiroi 1998; Wise 1996). Most importantly, Zald et al. (2004) found that predictable monetary reward presentation caused dopamine release in the medial caudate body where we found activation. The combined findings implicate reward and motivation functions as likely aspects of early-stage romantic love, and dopamine as one of the candidate transmitters involved.

Cortical areas associated with emotion were involved, also, such as the insular and cingulate cortex. However, as expected for a goal-directed state with diverse outcomes, activation of emotion-associated areas varied among individuals depending on their general affect intensity, passion score and the length of the relationship. Two subcortical areas associated with emotion were affected, also: the amygdala and the septum. Amygdala activity was decreased relative to the Neutral stimulus while septal

activity was correlated with the PLS score. Deactivation there was seen in the amygdala by Bartels and Zeki, also (2000, 2004). They suggested that love reduces fearful responses (Bartels and Zeki 2004). However, amygdala activity plays a role in the recognition of faces in general, and it is not clear why it was specifically involved in studies of romantic love (Kosaka et al. 2003). The septum was one of the first regions found to be rewarding during electrical self-stimulation (Olds and Milner 1954). It is activated by VTA self-stimulation reward and medial forebrain bundle self-stimulation reward, and it is involved in several emotional responses in animals, including relief from aversive emotional states (Esposito et al. 1984; Porrino et al. 1984; Porrino et al. 1990; Yadin and Thomas 1996). Thus, it is consistent with a large body of data that the septum would be active during a reward state. Finally, the lateral septum has also been implicated in pair-bonding in prairie voles (Liu et al. 2001).

Regional heterogeneity of ventral midbrain area reward functions. To establish whether the ventral midbrain activation occurred because our participants were feeling romantic passion or were stimulated by an aesthetically pleasing face, we correlated facial attractiveness (as rated by others) with neural activation. This correlation showed that those with more aesthetically pleasing partners compared to the Neutral stimulus showed greater neural activity in the region of the *left* VTA than those with less attractive partners compared to the Neutral stimulus. Several fMRI studies indicate that the *right* VTA, where we found activation for our basic Positive-minus-Neutral contrast, is associated with rewards and/or working for rewards (Aharon et al. 2001; Breiter et al. 2001; Elliott et al. 2000; Elliott et al. 2004; Small et al. 2001), others show bilateral activation of the VTA (Breiter et al. 1997; O'Doherty et al. 2002). Importantly, Aharon et al. (2001) showed that the *left* VTA activation was specifically associated with a face

deemed aesthetically pleasing ('liking') while *right* VTA activation increased during presentation of a face that participants would work to see longer ('wanting'). Thus, several fMRI studies corroborate reward effects in the human VTA (Table 1), but this is the second fMRI study to show a localization effect within the VTA for two aspects of reward, 'wanting' and 'liking' (Berridge and Robinson 2003), and to show that this effect is lateralized. Caudate effects for the Positive-minus-Neutral contrast were on the right, also, providing more evidence that the lateralized VTA effect is not spurious.

The localization of the VTA activation appears to be quite specific in the figures, given the size of the original voxels, (3.75 x 3.75 x 4.0 mm) and the size of the smoothing filter (8 mm). The specificity appearance is enhanced by the normalized images (2 x 2 x 2 mm). The human VTA is approximately 8 mm across, from anterior to posterior, and 4mm dorsoventral, well within the area covered by several voxels. In addition, by smoothing the data, which tends to enhance effects in large regions of cortex, we probably diluted the observed effect in this small region. The VTA is a small region, however, and given the variability inherent in the brains of subjects and the normalization procedures, we cannot be sure that the activation does not include other surrounding areas.

Regional caudate effects implicate emotion and visual attention functions.

Participants who scored higher than others on the PLS showed greater activation in the right medial caudate body. This region is rich in limbic-associated membrane protein, calbindin, and medial cortical afferents, each of which is associated with higher-order cognitive and emotional functions (Parent et al. 1995). The specific region where activation correlated with the PLS in our study was activated during anticipation of a monetary reward (Knutson et al. 2001), reward-based stochastic learning (Haruno et al.

2004), attention (Zink et al. 2003), a spatial and temporal somatosensory discrimination task (Pastor et al. 2004) and simple passive visual processing (Bleicher et al. 2003). Recently, this same right-sided region showed increased dopamine release for a predictable money reward (Zald et al. 2004). In addition, our Countback task (when compared to the Neutral stimulus) activated this region. Thus, this area of the medial body of the caudate is most likely associated with rewarding, visual and perhaps attentional aspects of romantic love. Intense, focused attention on an individual is one of the cardinal behavioral signs of romantic love (Fisher 1998; Hatfield and Sprecher 1986). Visual attention, reward, motivation and motor planning are often related to caudate function (Dagher et al. 1999; Hikosaka et al. 2000; Lauwereyns et al. 2002; Zink et al. 2003). In addition, there is one report of electrical stimulation of the caudate through a chronically indwelling electrode in a human epilepsy patient (Delgado et al. 1973). The patient's words expressing love toward the investigator were stimulus-bound (Delgado, J. and Coons, E.E., personal communication) providing evidence that caudate activation could be causally related to feelings of romantic love.

Months in love: cortical and subcortical effects. One of the most interesting findings of this study is regional effects related to the number of months in love. Notably, several limbic cortical regions showed a correlation with the length of the relationship: anterior and posterior cingulate, mid insula and retrosplenial cortex; but also, parietal, inferior frontal and middle temporal cortex. One small region of the left ventral putamen and pallidum was associated with time in love, also. The ventral pallidum has been implicated in attachment in prairie voles (Lim et al. 2004; Lim and Young 2004). In their fMRI study of longer-term romantic love, Bartels and Zeki (2000) found activation in the anterior cingulate and mid-insula. Thus, we confirm the results of

Bartels and Zeki (2000) that these brain regions are involved, but in addition our results suggest that the activation is dependent on time factors. The time-related activations may be related to memory, familiarity, motivation and attention functions (Velanova et al. 2003; Yamasaki et al. 2002) or an emotional internal state factor such as heart rate (Critchley et al. 2003; Porro et al. 2003). The correlation in the anterior cingulate is notable because it is implicated in a cardinal trait of romantic love: obsessive thinking; it is also involved in cognition and emotion (Bush et al. 2000; Rauch et al. 2001; Ursu et al. 2003). The right retrosplenial cortex correlation with length of relationship is of special interest because metabolic activity there increased during satiation for chocolate (Small et al. 2001) and was correlated with level of thirst (Denton et al. 1999). In any case, these results highlight the importance of these cortical regions for processing stimulus/internal state change, and the importance of taking time factors into account in future studies of human relationships. At the same time, these results must be interpreted cautiously because they are cross-sectional, so that, for example, it is possible they represent differences in the kinds of people that remain intensely in love over a longer period rather than changes over time.

The evolution of romantic love and its distinction from the sex drive. Studies of prairie voles show that D2 dopamine and oxytocin receptor stimulation in the nucleus accumbens is associated with mate preference in females (Gingrich et al. 2000; Liu and Wang 2003) and recent studies of male voles focus on the ventral striatum/pallidum and the distribution of vasopressin and oxytocin receptors; however, oxytocin receptors are found throughout the striatum as well as in the accumbens in both males and females (Lim et al. 2004; Lim and Young 2004). A comparison with our findings leads us to speculate about the evolution of romantic love: with the development of the human

cerebral cortex, ancestral hominids employed the phylogenetically newer cortex and dorsal caudate to initiate partner preference. Romantic love may be a *developed* form of a general mammalian courtship system, which evolved to stimulate mate choice, thereby conserving courtship time and energy (Fisher 1998). Also, previous fMRI studies of human sexual arousal show regional activation largely different from the pattern we saw for our participants (Arnow et al. 2002; Redoute et al. 2000), consistent with romantic love being distinct from the sex drive (Aron and Aron 1991; Fisher 1998). Although sex is an important part of romantic love, the systems appear to be only partially overlapping.

Comparison with a study of longer-term romantic love. Bartels and Zeki (2000) reported findings of an fMRI study on the neural correlates of romantic love, and then reanalyzed their data in relation to another study they carried out on maternal love (Bartels and Zeki 2004). As previously stated, their participants were in love longer, and were not as intensely in love as in the present study (28.8 months vs. 7.3 months $t_{[32]} = 4.28, P < .001$; PLS scores of 7.55 vs. 8.54, $t_{[31]} = 3.91, P < .001$). Both studies used seventeen participants and a photograph of the beloved as the positive stimulus. In the present study, we used a familiar acquaintance as a control while Bartels and Zeki used photographs of friends. Also, we used a distraction task that served as a second control condition, the Countback task. Many of the basic results are remarkably similar. The ventral midbrain region/VTA and dorsal caudate nucleus were activated by romantic love in both studies (Bartels and Zeki 2000, 2004); the amygdaloid region was deactivated in both studies; the mid insula, anterior and posterior cingulate were affected in both studies, but in the present study activation in the cortex was found to be correlated with relationship length. The fact that all of the above regions were affected

in both studies strongly suggests that they are involved in romantic love in important ways and that reward and motivation systems are critical.

In addition, there were differences between the two studies for the Positive-minus-Neutral contrast. Among them, the present study showed effects in several regions of the caudate, in the septum, and the retrosplenial cortex, and no effect in the dorsal hippocampus or putamen, as was seen by Bartels and Zeki (2000). These differences may be caused by the difference between early-stage and longer-term romantic love that could not be assessed with the limited time range in our study, but could also be caused by individual characteristic responses that differed between the two samples or by the differences in experimental methods.

Technical considerations and assumptions. The BOLD responses that we measured were relatively sustained during the presentation of the stimuli and also limited by the hemodynamic response function model that we used. If we had employed other models of response, we might have detected other areas that could be involved. For example, Moritz et al. (2000) reported that caudate-putamen BOLD responses to finger-tapping had a short duration, quite different from the cortex. Also, we base our interpretation of the data on the assumption that a BOLD response largely reflects axon terminal activity and field potentials rather than cell body activity, although the two can be correlated (Arthurs et al. 2004; Logothetis et al. 2001; Mata et al. 1980; Sokoloff 1999, 1993). In an animal study using metabolic mapping of natural somatosensory corticostriate activity, increased metabolism was associated with corticostriate axon terminal fields (Brown et al. 2002). Thus, we interpret the measured activation in the caudate to be largely the result of afferent activity from the cortex, VTA,

and intrinsic caudate cell axon collaterals. Likewise, the BOLD response in the VTA may reflect afferent activity from the caudate or accumbens or other region, not necessarily activity of local cells.

The 30 sec trial period to look at faces was relatively unconstrained, although instructions were given. Also, differences between the Positive and Neutral conditions may have been caused by different eye movements or different habituation effects. If number of eye movements had been a major factor, we expect that the frontal eye fields would have shown an effect. It is possible that a difference in habituation is an inextricable factor.

Conclusions. The results lead us to suggest that early stage, intense romantic love is associated with reward and goal representation regions, and that rather than being a specific emotion, romantic love is better characterized as a motivation or goal-oriented state that *leads to* various specific emotions such as euphoria or anxiety. With this new view of romantic love as a motivation state, it becomes clearer why the lover expresses an imperative to be with a preferred individual (the beloved) and to protect the relationship. Moreover, our results suggest to us that romantic love does not use a functionally specialized brain system. Romantic love may be produced, instead, by a constellation of neural systems that converge onto widespread regions of the caudate where there is a flexible combinatorial map representing motivating stimuli and memories dependent on the individual and the context (Brown 1992; Brown et al. 1998; Lidsky and Brown 1999). As such, it would be an example of how a complex human behavioral state that includes emotions is processed. Taken together, our results and those of Bartels and Zeki with longer-term in love participants (2000; 2004) show similar cortical, VTA and caudate localization, suggesting that these regions are consistently

and critically involved in this aspect of human reproduction and social behavior, romantic love. Further experiments will be needed to determine whether a circumscribed caudate region and specific afferents are necessary to the experience and behaviors of romantic love. Importantly, we found potential regional heterogeneity for different aspects of reward in the VTA, and identified some cortical regions whose neural activation was different for individuals who had been in love over a time scale of months, or who showed affect trait differences.

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FIGURE LEGENDS

Fig. 1. Caudate nucleus, Positive-minus-Neutral contrast. **A.** Activity in the right medial caudate (Table 2) increased in response to the Positive stimulus compared to the Neutral stimulus. The black dots indicate the location of peak activity for all subjects in this region, placed on the Montreal Neurological Institute template created from 305 subjects. **B.** A sagittal section from an individual participant shows an example of the posterior dorsal caudate activation. Images in this and all following figures are presented in radiologic convention (participants' right on the left side of the image). C, caudate. L, left side.

Fig. 2. Group mean data and an individual subject show the ventral midbrain/VTA region effect. **A.** Group mean activity on a template single-subject brain from SPM99. Positive-minus-Neutral contrast. **B.** Positive-minus-Countback contrast. Activity in the right VTA region (arrows) specifically increased in response to the Positive image compared to Neutral and Countback conditions. **C.** The time course of the BOLD response (mean \pm SEM, 0 = mean of all conditions) for a voxel in the right ventral midbrain shows that the signal increased to the Positive image (solid line) relative to the others; the signal during control stimuli presentations decreased relative to the Positive image, especially for the Countback task (small-dash line; 40 sec Countback task shown). Solid line, Positive stimulus. **D.** In a single subject, a sagittal view shows the anteroposterior extent of the right VTA region activation (arrow). **E.** In the same subject, a coronal view of the right VTA region activation (arrow) shows how it is limited to the medial midbrain. Locations of responses shown in the graph are given in Talairach coordinates. L, left side. VTA, ventral tegmental area.

Fig. 3. Activation in the medial caudate body was correlated with the Passionate Love Scale (PLS) scores of the participants. **A.** The caudate location for the correlation (arrow) is similar to that shown for individuals in Fig. 1, close to the ventricle. **B.** The graph illustrates the correlation of activity in the caudate with PLS scores. Location of responses shown in the graph are given in Talairach coordinates. C, caudate. L, left side.

Fig. 4. Activity in the ventral midbrain/VTA region for the Positive-minus-Neutral contrast was correlated with the independently rated attractiveness of the Positive minus the attractiveness of the Neutral faces. **A.** The activation is on the left and on the midline (arrow), and different from the localization of activation in Fig. 2A,B. **B.** The graph of the correlation shows that the neural activity in response to Positive images was greater when the Positive face was more attractive than the Neutral face.

Fig. 5. Length of time in love correlated with activation in specific regions. Regions are indicated on axial (A) and sagittal (C) sections. **A.** The cluster location for the retrosplenial cortex correlation (arrow) is similar to a region correlated with satiation while eating chocolate (Small et al., 2001). **B.** The graph shows the correlation for the peak voxel in the cluster labeled R, in A. **C.** The location of voxel clusters correlated with relationship length in the AC and PC (arrows). **D.** Graph of the correlation between the BOLD response and months in love for the AC. AC, anterior cingulate cortex. PC, posterior cingulate cortex. R, posterior cingulate/BA30 retrosplenial cortex.

Table 1. Predicted regions of change

Region	Talairach			Reference papers ^a
	coordinates			
	x	y	z	
VTA/SN	0	-10	-10	1,3,5,6,9,10,11,14,15
Caudate head/body	10	10	12	2,5,7,12,13
Putamen	10	0	0	2,5,13,15
Accumbens/subcallosal cortex/ventral striatum	0	10	0	4,5,6,7,9,13,15
Amygdala	20	- 2	-14	2,5,6,10
Posterior hippocampus	35	-30	-5	2,5
Anterior cingulate	5	25	24	2,5,13
Posterior cingulate	1	-25	28	2,5,12,13
Mid insula	34	10	2	2,4,5
Retrosplenial cortex	26	-54	12	8,15
Medial orbitofrontal cortex	0	55	0	10,11

Lateral orbitofrontal cortex	50	30	-9	11
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The table shows the Talairach and Tournoux (1988) coordinates (x,y,z) used for the center of the small volume search sphere. Sphere diameter was 4 mm. Both left and right sides were searched.

^a Selected fMRI reference papers that studied reward, beautiful faces or romantic love and on which the small volume search coordinates were based:

¹Aharon et al. 2001; ²Bartels and Zeki 2000; ³Bartels and Zeki 2004(VTA coordinates: personal communication) ⁴Berns et al. 2001; ⁵Breiter et al. 1997; ⁶Breiter et al. 2001; ⁷Delgado et al. 2000; ⁸Denton et al. 1999; ⁹Elliott et al. 2000; ¹⁰Elliott et al. 2003; ¹¹Elliott et al. 2004; ¹²Garavan et al. 2000; ¹³Knutson et al. 2001; ¹⁴O'Doherty et al. 2002; ¹⁵Small et al. 2001.

Table 2. Regional activations specific to the picture of the beloved compared to a picture of a familiar, neutral acquaintance

Left									
	x	y	z	P		x	y	z	P
Positive-minus-Neutral									
Contrast									
Caudate body, medial†						12	11	14	.005
Caudate body, postero-dorsal*†						18	-18	22	.005
Caudate body, antero-dorsal†	-16	1	22	.014	2.85	14	-4	22	.014
Posterior cingulate/BA30/ Retrosplenial cortex†						30	-52	4	.014
Ventral tegmental region*†						2	-15	-9	.025
Passionate Love Scale									
Correlation									
Caudate Body, antero-medial*						8	6	14	.012
Septum/Fornix						0	-1	17	.008

The table shows the Talairach and Tournoux (1988) coordinates (x,y,z) for the highest intensity voxel in a cluster. BA=Brodmann's area.

* indicates that the cluster for Positive-minus-Neutral contrast overlapped with the cluster in the same region for the Positive-minus-Countback contrast.

† indicates regions predicted to change, small volume, corrected for multiple comparisons.

All regions not predicted to change, which do not meet the unplanned comparison criterion of $p < .001$ corrected, were deleted from the table. The countback task data were deleted, also.

Table 3. Regional changes in brain activity that were correlated with the length of the relationship**The longer the relationship the greater the difference between the Positive and Neutral stimuli**

	Left				Right			
	x	y	z	P	x	y	z	P
Mid Insula BA 13					42	-2	2	.013
Anterior Cingulate					4	36	28	.002
Posterior cingulate*					9	-50	15	.001
Posterior cingulate/ Retrosplenial cortex					18	-65	18	.001
Parietal/Precuneus					12	-70	40	.004
Inf. Frontal Gyrus	-40	52	1	.001				
Middle Temporal gyrus	-51	-60	3	.002				
Ventral Putamen/Pallidum	-28	-2	-7	.013				

The shorter the relationship the greater the difference between Positive and Neutral stimuli

	Left				Right			
	x	y	z	P	x	y	z	P
Posterior cingulate/BA30/ Retrosplenial cortex	-22	-38	9	.005				

The table shows the Talairach and Tournoux (1988) coordinates (x,y,z) for the voxel with the highest correlation.

* indicates that the cluster for Positive-minus-Neutral contrast overlapped at least partially with the cluster in the same region for the Positive-minus-Countback contrast.

Figure 1

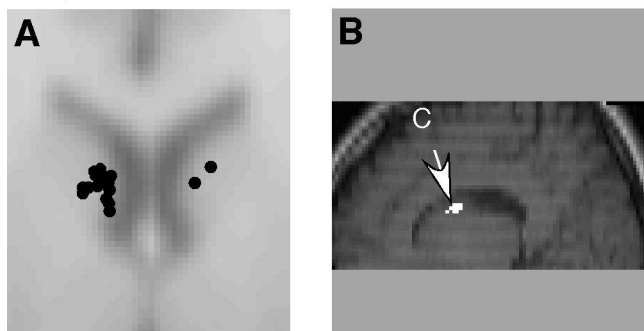


Figure 2

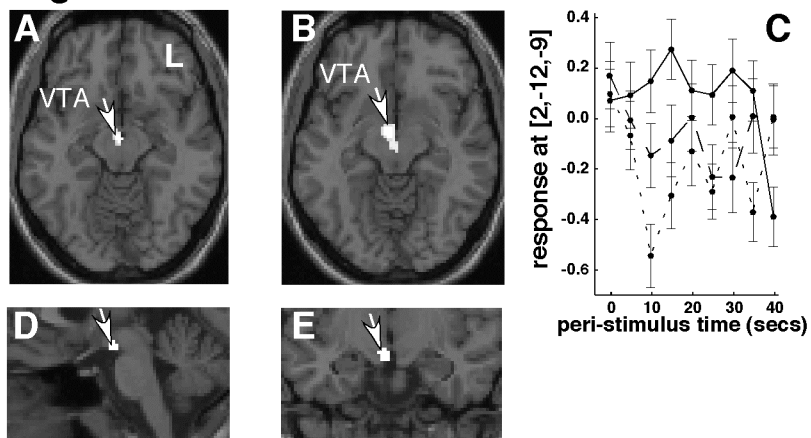


Figure 3

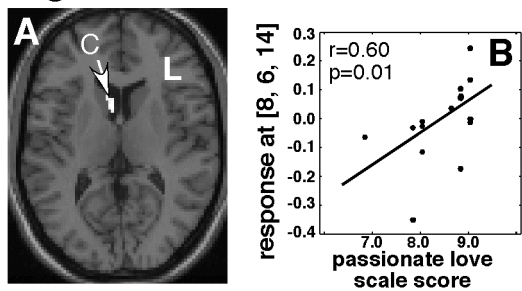


Figure 4

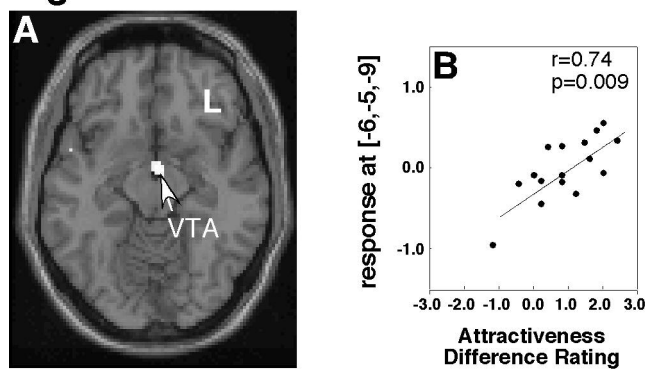
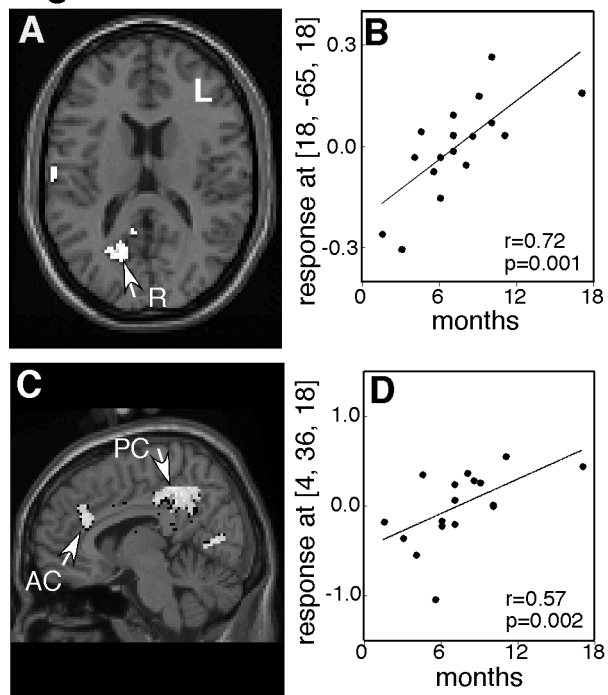


Figure 5



REFERENCES

- Aharon I, Etcoff N, Ariely D, Chabris CF, O'Connor E, and Breiter HC.** Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron* 32: 537-551, 2001.
- Arnow BA, Desmond JE, Banner LL, Glover GH, Solomon A, Polan ML, Lue TF, and Atlas SW.** Brain activation and sexual arousal in healthy, heterosexual males. *Brain* 125: 1014-1023, 2002.
- Aron A and Aron EN.** Love and sexuality. In: *Sexuality in close relationships*, edited by McKinney K, Sprecher, S., 1991, p. 25-48.
- Arthurs OJ, Stephenson CM, Rice K, Lupson VC, Spiegelhalter DJ, Boniface SJ, and Bullmore ET.** Dopaminergic effects on electrophysiological and functional MRI measures of human cortical stimulus-response power laws. *Neuroimage* 21: 540-546, 2004.
- Bartels A and Zeki S.** The neural basis of romantic love. *Neuroreport* 11: 3829-3834, 2000.
- Bartels A and Zeki S.** The neural correlates of maternal and romantic love. *Neuroimage* 21: 1155-1166, 2004.
- Berridge KC and Robinson TE.** Parsing reward. *Trends Neurosci* 26: 507-513, 2003.
- Bleicher AG, Lipton M, Popper A, and Brown LL.** Activation of basal ganglia circuits with a neutral visual stimulus. In: *Program No. 600.13. 2003 Abstract Viewer/Itinerary Planner*. Washington, D.C., Society for Neuroscience, 2003, Online, 2003.
- Breiter HC, Aharon I, Kahneman D, Dale A, and Shizgal P.** Functional imaging of neural responses to expectancy and experience of monetary gains and losses. *Neuron* 30: 619-639, 2001.
- Breiter HC, Gollub RL, Weisskoff RM, Kennedy DN, Makris N, Berke JD, Goodman JM, Kantor HL, Gastfriend DR, Riorden JP, Mathew RT, Rosen BR, and Hyman SE.** Acute effects of cocaine on human brain activity and emotion. *Neuron* 19: 591-611, 1997.
- Brown LL.** Somatotopic organization in rat striatum: evidence for a combinational map. *Proc Natl Acad Sci U S A* 89: 7403-7407, 1992.
- Brown LL, Feldman SM, Smith DM, Cavanaugh JR, Ackermann RF, and Graybiel AM.** Differential metabolic activity in the striosome and matrix compartments of the rat striatum during natural behaviors. *J Neurosci* 22: 305-314, 2002.

- Brown LL, Smith DM, and Goldbloom LM.** Organizing principles of cortical integration in the rat neostriatum: corticostriate map of the body surface is an ordered lattice of curved laminae and radial points. *J Comp Neurol* 392: 468-488, 1998.
- Bush G, Luu P, and Posner MI.** Cognitive and emotional influences in anterior cingulate cortex. *Trends Cogn Sci* 4: 215-222, 2000.
- Caan W, Perrett DI, and Rolls ET.** Responses of striatal neurons in the behaving monkey. 2. Visual processing in the caudal neostriatum. *Brain Res* 290: 53-65, 1984.
- Critchley HD, Mathias CJ, Josephs O, O'Doherty J, Zanini S, Dewar BK, Cipolotti L, Shallice T, and Dolan RJ.** Human cingulate cortex and autonomic control: converging neuroimaging and clinical evidence. *Brain*, 2003.
- Cronbach LJ.** Coefficient Alpha and the internal structure of tests. *Psychometrika* 16: 297-334, 1951.
- Dagher A, Owen AM, Boecker H, and Brooks DJ.** Mapping the network for planning: a correlational PET activation study with the Tower of London task. *Brain* 122 (Pt 10): 1973-1987, 1999.
- David V, Segu L, Buhot MC, Ichaye M, and Cazala P.** Rewarding effects elicited by cocaine microinjections into the ventral tegmental area of C57BL/6 mice: involvement of dopamine D(1) and serotonin(1B) receptors. *Psychopharmacology (Berl)*, 2004.
- Delgado JMR, Obrador S, and Martin-Rodriguez JG.** Two-way radio communication with the brain in psychosurgical patients. In: *Surgical Approaches in Psychiatry*, edited by Laitinen LV and Livingston KE. Lancaster, England: Medical and Technical Publishing, 1973, p. 215-223.
- Delgado MR, Locke HM, Stenger VA, and Fiez JA.** Dorsal striatum responses to reward and punishment: effects of valence and magnitude manipulations. *Cogn Affect Behav Neurosci* 3: 27-38, 2003.
- Delgado MR, Nystrom LE, Fissell C, Noll DC, and Fiez JA.** Tracking the hemodynamic responses to reward and punishment in the striatum. *J Neurophysiol* 84: 3072-3077, 2000.
- Denton D, Shade R, Zamarippa F, Egan G, Blair-West J, McKinley M, Lancaster J, and Fox P.** Neuroimaging of genesis and satiation of thirst and an interoceptor-driven theory of origins of primary consciousness. *Proc Natl Acad Sci U S A* 96: 5304-5309, 1999.
- Duvernoy HM.** *The Human Brain: Surface, Three-Dimensional Sectional Anatomy with MRI, and Blood Supply.* New York: Springer-Verlag Wien, 1999.

- Eblen F and Graybiel AM.** Highly restricted origin of prefrontal cortical inputs to striosomes in the macaque monkey. *J Neurosci* 15: 5999-6013, 1995.
- Elliott R, Friston KJ, and Dolan RJ.** Dissociable neural responses in human reward systems. *J Neurosci* 20: 6159-6165, 2000.
- Elliott R, Newman JL, Longe OA, and Deakin JF.** Differential response patterns in the striatum and orbitofrontal cortex to financial reward in humans: a parametric functional magnetic resonance imaging study. *J Neurosci* 23: 303-307, 2003.
- Elliott R, Newman JL, Longe OA, and William Deakin JF.** Instrumental responding for rewards is associated with enhanced neuronal response in subcortical reward systems. *Neuroimage* 21: 984-990, 2004.
- Esposito RU, Porrino LJ, Seeger TF, Crane AM, Everist HD, and Pert A.** Changes in local cerebral glucose utilization during rewarding brain stimulation. *Proc Natl Acad Sci U S A* 81: 635-639, 1984.
- Fisher HE.** Lust, attraction, and attachment in mammalian reproduction. *Human Nature* 9: 23-52, 1998.
- Flaherty AW and Graybiel AM.** Motor and somatosensory corticostriatal projection magnifications in the squirrel monkey. *J Neurophysiol* 74: 2638-2648, 1995.
- Friston KJ, Frith CD, Frackowiak RS, and Turner R.** Characterizing dynamic brain responses with fMRI: a multivariate approach. *Neuroimage* 2: 166-172, 1995.
- Gerfen CR, Herkenham M, and Thibault J.** The neostriatal mosaic: II. Patch- and matrix-directed mesostriatal dopaminergic and non-dopaminergic systems. *J Neurosci* 7: 3915-3934, 1987.
- Gingrich B, Liu Y, Cascio C, Wang Z, and Insel TR.** Dopamine D2 receptors in the nucleus accumbens are important for social attachment in female prairie voles (*Microtus ochrogaster*). *Behav Neurosci* 114: 173-183, 2000.
- Gonzaga GC, Keltner D, Londahl EA, and Smith MD.** Love and the commitment problem in romantic relations and friendship. *J Pers Soc Psychol* 81: 247-262, 2001.
- Haber SN.** The primate basal ganglia: parallel and integrative networks. *J Chem Neuroanat* 26: 317-330, 2003.
- Harris CR and Christenfeld N.** Gender, jealousy, and reason. *Psychological Science* 7: 364-366, 1996.

- Harris H.** Rethinking Heterosexual Relationships in Polynesia: A Case Study of Mangaia, Cook Island. In: *Romantic Passion: A Universal Experience?* edited by Jankowiak W. New York: Columbia University Press, 1995.
- Haruno M, Kuroda T, Doya K, Toyama K, Kimura M, Samejima K, Imamizu H, and Kawato M.** A neural correlate of reward-based behavioral learning in caudate nucleus: a functional magnetic resonance imaging study of a stochastic decision task. *J Neurosci* 24: 1660-1665, 2004.
- Hatfield E, Schmitz E, Cornelius J, and Rapson RL.** Passionate love: How early does it begin? *Journal of Psychology & Human Sexuality* 1: 35-51, 1988.
- Hatfield E and Sprecher S.** Measuring passionate love in intimate relationships. *J Adolesc* 9: 383-410, 1986.
- Hellier P, Ashburner J, Corouge I, Barillot C, and Friston KJ.** Intersubject registration of functional and anatomical data using SPM. *Lecture Notes in Computer Science* 2489: 590-597, 2002.
- Hellier P, Barillot C, Corouge I, Gibaud B, Le Goualher G, and Collins L.** Retrospective evaluation of inter-subject brain registration. *Lecture Notes in Computer Science* 2208: 258-265, 2001.
- Hikosaka O, Takikawa Y, and Kawagoe R.** Role of the basal ganglia in the control of purposive saccadic eye movements. *Physiol Rev* 80: 953-978, 2000.
- Hollerman JR, Tremblay L, and Schultz W.** Involvement of basal ganglia and orbitofrontal cortex in goal-directed behavior. *Prog Brain Res* 126: 193-215, 2000.
- Horvitz JC, Stewart T, and Jacobs BL.** Burst activity of ventral tegmental dopamine neurons is elicited by sensory stimuli in the awake cat. *Brain Res* 759: 251-258, 1997.
- Jankowiak WR and Fischer EF.** A Cross-Cultural Perspective on Romantic love. *Ethnology* 31: 149-155, 1992.
- Kalivas PW and Duffy P.** Repeated cocaine administration alters extracellular glutamate in the ventral tegmental area. *J Neurochem* 70: 1497-1502, 1998.
- Kawagoe R, Takikawa Y, and Hikosaka O.** Expectation of reward modulates cognitive signals in the basal ganglia. *Nat Neurosci* 1: 411-416, 1998.
- Kemp JM and Powell TP.** The cortico-striate projection in the monkey. *Brain* 93: 525-546, 1970.
- Knutson B, Adams CM, Fong GW, and Hommer D.** Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *J Neurosci* 21: RC159, 2001.

- Konishi S, Wheeler ME, Donaldson DI, and Buckner RL.** Neural correlates of episodic retrieval success. *Neuroimage* 12: 276-286, 2000.
- Kosaka H, Omori M, Iidaka T, Murata T, Shimoyama T, Okada T, Sadato N, Yonekura Y, and Wada Y.** Neural substrates participating in acquisition of facial familiarity: an fMRI study. *Neuroimage* 20: 1734-1742, 2003.
- Koski L, Iacoboni M, Dubeau MC, Woods RP, and Mazziotta JC.** Modulation of cortical activity during different imitative behaviors. *J Neurophysiol* 89: 460-471, 2003.
- Kosslyn SM, Cacioppo JT, Davidson RJ, Hugdahl K, Lovallo WR, Spiegel D, and Rose R.** Bridging psychology and biology. The analysis of individuals in groups. *Am Psychol* 57: 341-351, 2002.
- Larsen RJ, Diener E, and Cropanzano RS.** Cognitive operations associated with individual differences in affect intensity. *J Pers Soc Psychol* 53: 767-774, 1987.
- Lauwereyns J, Takikawa Y, Kawagoe R, Kobayashi S, Koizumi M, Coe B, Sakagami M, and Hikosaka O.** Feature-based anticipation of cues that predict reward in monkey caudate nucleus. *Neuron* 33: 463-473, 2002.
- Lidsky TI and Brown LL.** Behavioural context and a distributed system: metabolic mapping studies of the basal ganglia. *Can J Exp Psychol* 53: 35-44, 1999.
- Liebowitz M.** *The Chemistry of Love*. Boston: Little Brown and Co., 1983.
- Lim MM, Murphy AZ, and Young LJ.** Ventral striatopallidal oxytocin and vasopressin V1a receptors in the monogamous prairie vole (*Microtus ochrogaster*). *J Comp Neurol* 468: 555-570, 2004.
- Lim MM, Wang Z, Olazabal DE, Ren X, Terwilliger EF, and Young LJ.** Enhanced partner preference in a promiscuous species by manipulating the expression of a single gene. *Nature* 429: 754-757, 2004.
- Lim MM and Young LJ.** Vasopressin-dependent neural circuits underlying pair bond formation in the monogamous prairie vole. *Neuroscience* 125: 35-45, 2004.
- Liu Y, Curtis JT, and Wang Z.** Vasopressin in the lateral septum regulates pair bond formation in male prairie voles (*Microtus ochrogaster*). *Behav Neurosci* 115: 910-919, 2001.
- Liu Y and Wang ZX.** Nucleus accumbens oxytocin and dopamine interact to regulate pair bond formation in female prairie voles. *Neuroscience* 121: 537-544, 2003.
- Logothetis NK, Pauls J, Augath M, Trinath T, and Oeltermann A.** Neurophysiological investigation of the basis of the fMRI signal. *Nature* 412: 150-157, 2001.

- Martin-Soelch C, Leenders KL, Chevalley AF, Missimer J, Kunig G, Magyar S, Mino A, and Schultz W.** Reward mechanisms in the brain and their role in dependence: evidence from neurophysiological and neuroimaging studies. *Brain Res Brain Res Rev* 36: 139-149, 2001.
- Mashek D, Aron A, and Fisher HE.** Identifying, evoking, and measuring intense feelings of romantic love. *Representative Research in Social Psychology* 24: 48-55., 2000.
- Mata M, Fink DJ, Gainer H, Smith CB, Davidsen L, Savaki H, Schwartz WJ, and Sokoloff L.** Activity-dependent energy metabolism in rat posterior pituitary primarily reflects sodium pump activity. *J Neurochem* 34: 213-215, 1980.
- McBride WJ, Murphy JM, and Ikemoto S.** Localization of brain reinforcement mechanisms: intracranial self-administration and intracranial place-conditioning studies. *Behav Brain Res* 101: 129-152, 1999.
- Montague PR, McClure SM, Baldwin PR, Phillips PE, Budygin EA, Stuber GD, Kilpatrick MR, and Wightman RM.** Dynamic gain control of dopamine delivery in freely moving animals. *J Neurosci* 24: 1754-1759, 2004.
- Moritz CH, Meyerand ME, Cordes D, and Haughton VM.** Functional MR imaging activation after finger tapping has a shorter duration in the basal ganglia than in the sensorimotor cortex. *AJNR Am J Neuroradiol* 21: 1228-1234, 2000.
- O'Doherty J, Dayan P, Schultz J, Deichmann R, Friston K, and Dolan RJ.** Dissociable roles of ventral and dorsal striatum in instrumental conditioning. *Science* 304: 452-454, 2004.
- O'Doherty JP, Deichmann R, Critchley HD, and Dolan RJ.** Neural responses during anticipation of a primary taste reward. *Neuron* 33: 815-826, 2002.
- Oades RD and Halliday GM.** Ventral tegmental (A10) system: neurobiology. 1. Anatomy and connectivity. *Brain Res* 434: 117-165, 1987.
- Oldfield RC.** The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9: 97-113, 1971.
- Olds J and Milner P.** Positive reinforcement produced by electrical stimulation of septal area and other regions of rat brain. *J Comp Physiol Psychol* 47: 419-427, 1954.
- Parent A, Cote PY, and Lavoie B.** Chemical anatomy of primate basal ganglia. *Prog Neurobiol* 46: 131-197, 1995.

- Parent A and Hazrati LN.** Functional anatomy of the basal ganglia. I. The cortico-basal ganglia-thalamo-cortical loop. *Brain Res Brain Res Rev* 20: 91-127, 1995.
- Parthasarathy HB, Schall JD, and Graybiel AM.** Distributed but convergent ordering of corticostriatal projections: analysis of the frontal eye field and the supplementary eye field in the macaque monkey. *J Neurosci* 12: 4468-4488, 1992.
- Pastor MA, Day BL, Macaluso E, Friston KJ, and Frackowiak RS.** The functional neuroanatomy of temporal discrimination. *J Neurosci* 24: 2585-2591, 2004.
- Phillips PE, Stuber GD, Heien ML, Wightman RM, and Carelli RM.** Subsecond dopamine release promotes cocaine seeking. *Nature* 422: 614-618, 2003.
- Porrino LJ, Esposito RU, Seeger TF, Crane AM, Pert A, and Sokoloff L.** Metabolic mapping of the brain during rewarding self-stimulation. *Science* 224: 306-309, 1984.
- Porrino LJ, Huston-Lyons D, Bain G, Sokoloff L, and Kornetsky C.** The distribution of changes in local cerebral energy metabolism associated with brain stimulation reward to the medial forebrain bundle of the rat. *Brain Res* 511: 1-6, 1990.
- Porro CA, Cettolo V, Francescato MP, and Baraldi P.** Functional activity mapping of the mesial hemispheric wall during anticipation of pain. *Neuroimage* 19: 1738-1747, 2003.
- Rauch SL, Dougherty DD, Cosgrove GR, Cassem EH, Alpert NM, Price BH, Nierenberg AA, Mayberg HS, Baer L, Jenike MA, and Fischman AJ.** Cerebral metabolic correlates as potential predictors of response to anterior cingulotomy for obsessive compulsive disorder. *Biol Psychiatry* 50: 659-667, 2001.
- Redoute J, Stoleru S, Gregoire MC, Costes N, Cinotti L, Lavenne F, Le Bars D, Forest MG, and Pujol JF.** Brain processing of visual sexual stimuli in human males. *Hum Brain Mapp* 11: 162-177, 2000.
- Robbins TW and Everitt BJ.** Neurobehavioural mechanisms of reward and motivation. *Curr Opin Neurobiol* 6: 228-236, 1996.
- Robinson DL, Heien ML, and Wightman RM.** Frequency of dopamine concentration transients increases in dorsal and ventral striatum of male rats during introduction of conspecifics. *J Neurosci* 22: 10477-10486, 2002.
- Saint-Cyr JA, Ungerleider LG, and Desimone R.** Organization of visual cortical inputs to the striatum and subsequent outputs to the pallido-nigral complex in the monkey. *J Comp Neurol* 298: 129-156, 1990.

- Salinas JA and White NM.** Contributions of the hippocampus, amygdala, and dorsal striatum to the response elicited by reward reduction. *Behav Neurosci* 112: 812-826, 1998.
- Schultz W.** Multiple reward signals in the brain. *Nat Rev Neurosci* 1: 199-207, 2000.
- Selemon LD and Goldman-Rakic PS.** Longitudinal topography and interdigitation of corticostriatal projections in the rhesus monkey. *J Neurosci* 5: 776-794, 1985.
- Shaver P, Schwartz J, Kirson D, and O'Connor C.** Emotion knowledge: further exploration of a prototype approach. *J Pers Soc Psychol* 52: 1061-1086, 1987.
- Shaver PR, Morgan HJ, and Wu S.** Is love a "basic" emotion. *Personal Relationships* 3: 81-96, 1996.
- Small DM, Zatorre RJ, Dagher A, Evans AC, and Jones-Gotman M.** Changes in brain activity related to eating chocolate: from pleasure to aversion. *Brain* 124: 1720-1733, 2001.
- Sokoloff L.** Energetics of functional activation in neural tissues. *Neurochem Res* 24: 321-329, 1999.
- Sokoloff L.** Sites and mechanisms of function-related changes in energy metabolism in the nervous system. *Dev Neurosci* 15: 194-206, 1993.
- Talairach J and Tournoux P.** *Co-Planar Stereotaxic Atlas of the Human Brain*. New York: Thieme Medical Publishers, 1988.
- Tennov D.** *Love and limerance: the experience of being in love in New York*. New York: Stein and Day, 1979.
- Ursu S, Stenger VA, Shear MK, Jones MR, and Carter CS.** Overactive action monitoring in obsessive-compulsive disorder: evidence from functional magnetic resonance imaging. *Psychol Sci* 14: 347-353, 2003.
- Velanova K, Jacoby LL, Wheeler ME, McAvoy MP, Petersen SE, and Buckner RL.** Functional-anatomic correlates of sustained and transient processing components engaged during controlled retrieval. *J Neurosci* 23: 8460-8470, 2003.
- Wheeler ME and Buckner RL.** Functional Dissociation among Components of Remembering: Control, Perceived Oldness, and Content. *J Neurosci* 23: 3869-3880, 2003.
- White NM and Hiroi N.** Preferential localization of self-stimulation sites in striosomes/patches in the rat striatum. *Proc Natl Acad Sci U S A* 95: 6486-6491, 1998.
- Williams SM and Goldman-Rakic PS.** Widespread origin of the primate mesofrontal dopamine system. *Cereb Cortex* 8: 321-345, 1998.

Wise RA. Neurobiology of addiction. *Curr Opin Neurobiol* 6: 243-251, 1996.

Wise RA and Hoffman DC. Localization of drug reward mechanisms by intracranial injections. *Synapse* 10: 247-263, 1992.

Wolkstein D and Kramer SN. *Inanna, Queen of Heaven and Earth, Her Stories and Hymns from Sumer.* New York: Harper and Row, 1983.

Yadin E and Thomas E. Stimulation of the lateral septum attenuates immobilization-induced stress ulcers. *Physiol Behav* 59: 883-886, 1996.

Yamasaki H, LaBar KS, and McCarthy G. Dissociable prefrontal brain systems for attention and emotion. *Proc Natl Acad Sci U S A* 99: 11447-11451, 2002.

Zald DH, Boileau I, El-Dearedy W, Gunn R, McGlone F, Dichter GS, and Dagher A. Dopamine Transmission in the Human Striatum during Monetary Reward Tasks. *J Neurosci* 24: 4105-4112, 2004.

Zink CF, Pagnoni G, Martin ME, Dhamala M, and Berns GS. Human striatal response to salient nonrewarding stimuli. *J Neurosci* 23: 8092-8097, 2003.