

# The neural basis of romantic love

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The neural correlates of many emotional states have been studied, most recently through the technique of fMRI. However, nothing is known about the neural substrates involved in evoking one of the most overwhelming of all affective states, that of romantic love, about which we report here. The activity in the brains of 17 subjects who were deeply in love was scanned using fMRI, while they viewed pictures of their partners, and compared with the activity produced by viewing pictures of three friends of similar age, sex and duration of friendship as their partners. The activity was restricted to foci in the medial insula and the anterior cingulate cortex and,

subcortically, in the caudate nucleus and the putamen, all bilaterally. Deactivations were observed in the posterior cingulate gyrus and in the amygdala and were right-lateralized in the prefrontal, parietal and middle temporal cortices. The combination of these sites differs from those in previous studies of emotion, suggesting that a unique network of areas is responsible for evoking this affective state. This leads us to postulate that the principle of functional specialization in the cortex applies to affective states as well. *NeuroReport* 11:3829–3834 © 2000 Lippincott Williams & Wilkins.

**Key words:** Anterior cingulate; Attachment; Emotion; fMRI; Friendship; Galvanic skin response; Insula; Love; Striatum

## INTRODUCTION

Romantic love, celebrated throughout the ages as one of the most overwhelming of all affective states, has been the inspiration for some of the loftiest achievements of mankind. Characteristically directed towards a single person, it is a complex sentiment involving erotic, cognitive, emotional and behavioural components [1–3], which are difficult if not impossible to disentangle. Hence any study of 'romantic love' is a study of a sentiment with several components, some of which, like the erotic one, can also act independently of the others; the converse is not true, in that all the above components constitute essential ingredients of romantic love. Visual input plays a leading role in arousing and sustaining romantic love and yet nothing is known of the neural mechanisms underlying this complex sentiment. This, together with the high position that romantic love assumes in the lives of most, even if transiently, prompted this imaging study. Given its uniqueness, we hypothesised that there may be special systems or pathways for romantic love.

Past neuro-imaging studies of emotions have charted brain areas responsible for producing an emotional state, or those responsible for recognising one; here we concentrate on the former. Negative affective states such as fear, anger, anxiety and sadness [4–10] have been studied more extensively than positive ones such as happiness [5,6], sexual arousal [11,12] or 'pleasant' states provoked by visual stimulation [8,9,13]; here we concentrate on the latter. We wanted to chart the neural correlates of this affective state when it is generated by a visual input which

is emotionally neutral to an external observer. An abstract of our results has been published [14].

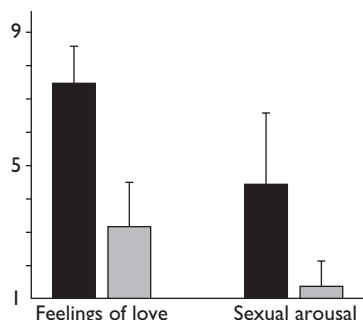
## MATERIALS AND METHODS

**Subjects and stimuli:** Volunteers who professed to be 'truly, deeply and madly in love' were recruited by posters and via the Internet. Out of ~70 who had replied (75% of whom were female), 17 normal subjects were selected by means of short written statements describing how much they were in love and by an interview (11 female; all right handed except for one male subject; ages 21–37, median 23, mean 24.5 years). Eleven countries and several ethnic groups were represented. All gave informed written consent. Prior or after the scan the galvanic skin response was measured in response to the pictures (see later). After the scan, subjects filled in the short version of the 'passionate love scale' (PLS) [15], thought to be a reliable means of quantifying this complex sentiment. The PLS asks subjects to rate the truth of statements such as: 'For me, XXX is the perfect romantic partner' by means of ratings from 1 to 9, with 9 being the maximum. In a slight modification of the PLS, we asked our subjects to give ratings corresponding to the time when we scanned them. Their high mean scores of  $7.55 \pm 0.97$  were higher than the highest scores reported in the original version (7.36 for women at the 'exclusive dating' stage of their relationship [15]). During the scan each subject viewed coloured pictures of the faces of four people on a neutral background: their boy- or girlfriend and three friends of same sex as their loved partner. All four were of similar age, and the duration of friendships

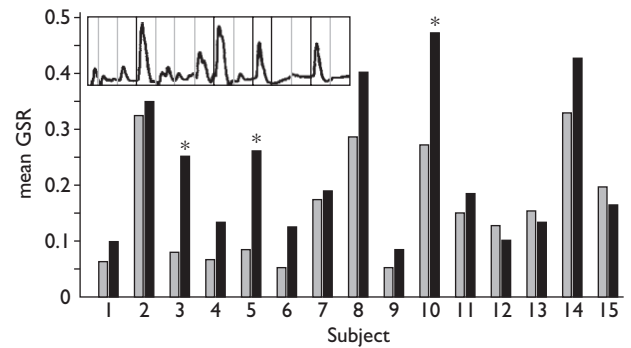
( $4.3 \pm 5.2$  years, median 3 years) was not shorter than the one of the loving relationships ( $2.4 \pm 1.7$  years, median 2.3 years). Ten subjects provided one picture per person, seven provided two. Pictures were shown for 17.36 s (4 TRs) each, in nine random permutations of the four people. Sequences were counterbalanced across subjects and lasted 10 min 25 s. Subjects were instructed to view the pictures, to think of the viewed person and to relax. After the scan, they were asked to report their emotional experience while viewing the different pictures, and each confirmed having felt being in love when seeing the partner (see below). A decay of emotional response was reported for the last few repeats of the nine four-people cycles. We therefore analyzed the fMRI data not only for all nine repeats, but also for the first six (first 6 min 57 s). The results were the same for both and all data shown here are for the first six repeats for all 17 subjects.

After the scan, subjects were asked to rate feelings of love and sexual arousal on a scale from 1 to 9, with 9 being the maximum, when viewing the loved partner and when viewing friends. As expected, sexual arousal was one of the components of the feelings when viewing the loved partner, but the feelings of love were clearly dominant, scoring nearly twice as much as sexual arousal for lovers compared to friends (Fig. 1): feelings of love: loved partner  $7.46 \pm 1.1$ , friends  $3.2 \pm 1.3$ ; sexual arousal: loved partner  $4.4 \pm 2.2$ , friends  $1.4 \pm 0.7$ . They were also asked to report any other associations or imagery during the scan, to either friends or loved partner. No common imagery or associations emerged.

**Electro-galvanic skin response (GSR):** On a separate day before or after the scan the GSR to the pictures was measured ( $n = 15$ ) (Fig. 2). Pictures were presented in a pseudorandom sequence, for 10 s with no gap between pictures; GSRs to the first two were discarded to minimize novelty/adaptation effects, leaving 15 pictures of the loved partner and 17 pictures of friends. The normalized GSR response to a picture was given by the peak GSR 1–4 s after the picture presentation (the GSR in response to the picture), from which the baseline (minimum GSR within the 2 s following a picture presentation) was subtracted.



**Fig. 1.** Subjects' ratings of their feelings of love and sexual arousal when viewing pictures of the loved partner (black bars) and pictures of friends (gray bars) on a scale from 1 to 9, with 1 = none, 4 = moderate and 9 = very much. The scores show that the contribution of brain activity stemming from feelings of love dominate over those of sexual arousal, but that both form components of the experience of romantic love recorded in terms of brain activity.



**Fig. 2.** Galvanic skin responses (GSRs) induced when 15 subjects viewed pictures of their loved partner (in black) and those of their friends (in gray). Over the whole group, the GSR to loved partners is significantly larger than the one to friends ( $t$ -test,  $p < 0.0025$ ). For GSRs collected in single subjects over 32 pictures only the ones indicated with a star reached a statistically significant difference. Black bars: mean GSR to the loved partner, gray bars: mean GSR to friends. Inset: A sample trace from subject no. 5. Gray lines: picture onset showing a friend, black: picture onset showing the loved partner. Pictures were presented every 10 s.

This was then normalized by dividing it by the maximum peak-baseline difference in the whole sequence.

This paradigm could have been optimized, e.g. by using a similar sequence as in the scanner, where each person was shown with equal probability, while here each category (friends/loved partner) occurred with equal probability. This would almost certainly have led to even higher GSRs to pictures of the loved partner. Moreover, GSR is extremely unspecific, and any emotion or even association, whether positive or negative, may lead to an enhanced GSR. Applying GSR to pictures of people known to the subjects, each of which elicits specific associations, seems therefore a rather risky approach to detecting a very specific emotion. In spite of these factors, all working against a positive result, we found that, for the group of subjects as a whole, the GSR to pictures of the loved partner was significantly higher than that to pictures of friends ( $t$ -test,  $p < 0.0025$ ), confirming objectively a differential emotional response to the partner compared to the friends.

**Image acquisition and analysis:** Data for all 17 subjects were acquired in a 2T Siemens Vision MRI scanner and analysed using SPM99 ([www.fil.ion.ucl.ac.uk](http://www.fil.ion.ucl.ac.uk)) [16], as described elsewhere [17]. Activity in the whole head was measured using an echo-planar imaging sequence (EPI) that acquired 48 transverse slices (2.5 mm thickness, 0.5 mm gap), each subtending  $64 \times 64$  voxels of  $3 \times 3$  mm. Repetition time (TR) of each whole-brain acquisition was 4.341 s, echo time (TE) 40 ms. Data were smoothed with a Gaussian kernel of 10 mm full width at half maximum. All four viewed people were modelled using a multiple regression analysis and contrast images for the comparisons lover *vs* friends and friends *vs* lover were calculated. In a second level (random effects) analysis a  $t$ -test was applied to the 17 contrast images of all subjects to obtain those areas that were commonly activated across the whole group, making the results presented here valid for the

population that the subjects are representative of. This type of analysis reveals the regions that are commonly activated in all subjects, and therefore the common denominator of regions involved in love. The ICA analysis [18,19] was performed as reported elsewhere [17], with voxel sizes of  $4 \times 4 \times 4$  mm to reduce the computational load.

## RESULTS

No visual area in the occipital lobe or in the fusiform gyrus, which is involved in various aspects of visual face recognition, including attention to faces [20], was activated or deactivated. Instead, the blood oxygen level dependent signal (BOLD) specific to viewing pictures of the loved partner revealed activity focally restricted to two main cortical areas remote from the visual brain, the middle insula, mainly on the left, and the anterior cingulate cortex bilaterally ( $p < 0.001$ , uncorrected, random effects analysis); with a lowered threshold ( $p < 0.005$ ), bilateral activation in the posterior hippocampus became apparent. There were also prominent activations in two subcortical parts of the cerebrum, the head of the caudate nucleus and the putamen, both stronger on the left, and in sites in the cerebellum ( $p < 0.001$ , uncorrected, random effects analysis) (Table 1; Fig. 3a,b). The regions apparent in the reverse contrast (friends *vs.* partner) were interpreted as deactivations specific to viewing the loved partners (Table 1; Fig. 4). Cortically, these were concentrated in the right

prefrontal, parietal, and middle temporal cortex, and in the posterior cingulate gyrus and medial prefrontal cortex. Subcortically, there was a deactivation in the posterior amygdaloid region. When data from males and females were analysed separately, both had the same activation and deactivation patterns as found for the whole group. However, the limited number of male subjects did not allow for a statistical population comparison between the genders.

We further analysed each subject with an independent component analysis (ICA) [18,19], which is capable of determining brain areas that are coactive and therefore have an activity timecourse that differs from the remaining activity in the brain [17,21,35]. In most subjects ICA isolated the insula and the anterior cingulate cortex bilaterally in independent components that did not include other regions, indicating that while left and right insula were active cooperatively, their activity and that of the cingulate cortex was comparatively distinct from each other and from that in other regions (Fig. 1c). The characteristic activity timecourse of each of these areas suggests that each has a distinct role.

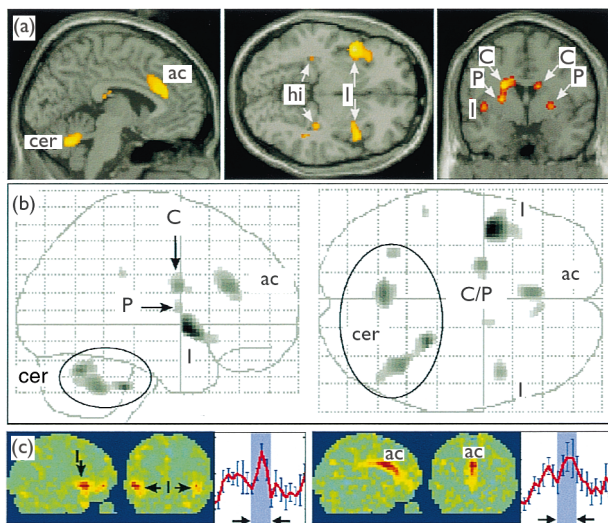
## DISCUSSION

In this study, we used a novel way of studying the neural bases of affective states in a broader sense. Previous studies have induced emotions through the use of visual

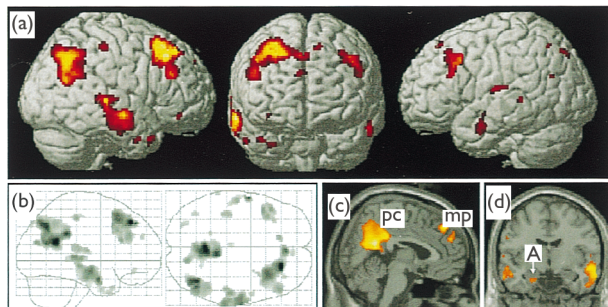
**Table 1.** Talairach coordinates of activations and deactivations when the 17 subjects viewed pictures of their loved partners and of friends.

	Left				Right			
	x	y	z	Z	x	y	z	Z
<b>Activations</b>								
Middle insula BA 14	-44	6	-4	6.82	44	10	-6	4.54
Anterior cingulate BA 24	-4	30	24	5.07	6	34	16	4.15
Caudate nucleus (dorsal head)	-22	-2	24	4.90	14	4	22	3.94
Putamen (medial dorsal)	-22	0	10	4.20	26	0	2	3.60
Posterior hippocampus	-38	-34	-10	3.66	36	-30	-2	4.04
<b>Cerebellum</b>								
Vermis	-4	-60	-28	5.49				
Middle cerebellar peduncle					40	-50	-38	5.16
Middle cerebellar peduncle					26	-34	-38	5.72
<b>Deactivations</b>								
<b>Prefrontal cortex</b>								
Superior frontal gyrus BA 9					22	36	46	7.96
Medial frontal gyrus BA 9					4	42	44	6.29
Middle frontal gyrus BA 9	-44	16	42	5.16	32	20	50	6.29
BA 9/46	-44	24	24	5.12	50	34	30	5.11
<b>Parietal cortex</b>								
Parallel sulcus/MT gyrus BA 39					46	-64	20	6.52
Intraparietal sulcus BA 19/39					40	-64	40	7.01
<b>Temporal cortex</b>								
Superior gyrus BA 21/22					66	-12	-12	6.10
BA 22					66	-30	4	5.68
BA 22					54	-24	2	5.28
Middle gyrus/pole BA 20/21	-58	-2	-22	6.31	56	2	-34	4.15
<b>Posterior cingulate</b>								
BA 29/30					8	-40	32	6.84
BA 23	0	-54	22	7.54	4	-52	22	7.58
Caudate nucleus	-10	10	4	4.01				
Amygdaloid region*	-22	-10	-26	3.69	22	-8	-22	5.06

\*Only the left amygdaloid region was active in the whole group. Coordinates for the right are shown for the 11 females, where activation was bilateral. (x,y,z): Talairach coordinates of peak activation. Z: Z-score;  $p < 0.001$  uncorrected corresponds to Z-score of 3.69. BA: Brodmann area.



**Fig. 3.** Activity elicited when subjects viewed pictures of their loved partner compared to that produced when they viewed pictures of their friends. The activity, restricted to only a few areas, is shown in sagittal ( $x = -4$  mm), transverse ( $z = -6$  mm), and coronal sections ( $y = 0$  mm) superimposed on slices taken through a template brain in (a) and in glassbrain projections in (b). ac, anterior cingulate; cer, cerebellum; I, insula; hi, posterior hippocampus and the coronal section activity in caudate nucleus (C) and putamen (P). Data are from a SPM random effects group analysis of 17 subjects (glassbrains:  $p < 0.001$  ( $Z = 3.69$ ), sections:  $p < 0.005$  ( $Z = 2.92$ ), both uncorrected with an extent threshold of 6 voxels. (c) An independent component analysis applied to single subjects isolated activity in the insula and the anterior cingulate cortex separately, and in 9 of 11 the components did not involve any other regions. Shown are two independent components from a single subject, in which the one containing the insula included also a more frontal region. The associated activity timecourses are stimulus triggered averages, averaged for all nine repeats and time-locked around the 'love' condition (blue bar: 17.4 s). Error bars = s.e.



**Fig. 4.** Deactivations revealed by a comparison of brain activity elicited when subjects viewed pictures of their friends with that produced when they viewed pictures of their loved partner. Cortically, deactivations were right-lateralized within the prefrontal cortex, the middle temporal gyrus and the parietal cortex, as is apparent (a) in the projections onto the cortical surfaces in side and front views of a template brain and (b) in glassbrain projections. (c) The sagittal section ( $x = 4$  mm) shows deactivations in the posterior cingulate gyrus (pc) and in the medial prefrontal cortex (mp). (d) The coronal section ( $y = -8$  mm) shows deactivation in the left amygdaloid region (A). Thresholding: as in Fig. 3, with (a) thresholded as (b).

scenes, or, less commonly, through autobiographic events. As well, they have compared positive emotional states with negative ones. Here we have for the first time tried to explore the neural correlates of personal relationships; in

addition, we have compared two positive emotional states. This study is therefore an initial attempt to explore the neurological bases of one of the most important ingredients in human interaction, that of personal relationships, which we hope future studies will extend.

Given the complexity of the sentiment of romantic love, it was not surprising to find that the activity was within regions of the brain found to be active in other emotional states, even if the pattern of activity evoked here is unique. This raises the question of the degree of overlap in sites of activity between this and previous studies. The cortical and sub-cortical structures involved are large and many previously reported activations lie in subdivisions of these structures which are distinct from ours. Where there is a suspected overlap of activation (see later), its extent is difficult to determine from the anatomical information available in many previous studies. What seems to be certain is that, even allowing for possible overlap, the pattern of activation obtained here was nevertheless unique, both in the identity and combination of sites involved. To us, the surprise was to find that the activity was restricted to so few areas with such a small spatial extent, given that romantic love involves several not easily dissociable components.

**Faces, familiarity and attention:** By restricting the experiment to views of faces alone, we hoped to minimize the differences in visual stimulation, and thus concentrate on a difference in emotional attachment. This approach may be complicated by two potentially confounding variables, of familiarity and attention. Even though all the faces were highly familiar to our subjects, it is not unreasonable to assume that the face of a loved person is likely to be more familiar than that of friends. But imaging studies reassure us that familiarity with a face leads to heightened activity within the part of the visual cortex specialized for face processing in the fusiform gyrus, and other areas not activated here [22]. Similarly, it is plausible to suppose that the loved face attracts more of the subjects attention than the faces of friends. But previous studies show that attention to faces or even features associated with them leads to increased activity in the fusiform gyrus and in other, non-visual areas, none of which were activated here [20]. We thus conclude that neither variable influenced our results.

**Activations:** The insula is related to a variety of emotional functions [23]. Lesions in it can have severe emotional consequences, among them those related to the interpretation of visual input. Imaging studies of various negative emotional experiences have localized activity to a region of the anterior insula that is distinct from our medial one [23]. Interestingly, attractiveness of unfamiliar faces was reported to correlate positively with blood flow in the left insula [24], in a region that does seem to overlap with ours.

The large anterior cingulate cortex consists of several functionally distinct components [25]; several of its subdivisions play an important role in emotional function. Whilst previous imaging experiments involving different emotions have attributed activity to 'the anterior cingulate', they almost certainly activated different subdivisions within it. In particular, the anterior cingulate cortex includes

regions implicated in happy states [6], attention to one's own emotional state and especially social interactions which involve assessing one's own and other people's emotions and states of mind [25,26]. The locus activated in our study is small and localized to a ventral region distinct from the regions activated in most studies mentioned above, which are often restricted to dorsal parts of the anterior cingulate (BA 32), which is unfortunately not usually distinguished from the more ventral region (BA 24) involved here. The distinction between the (dorsal) region of the anterior cingulate activated in many studies of emotion and the ventral one activated here argues for functional subdivisions related to emotions within the anterior cingulate too.

The two subcortical zones activated, the caudate nucleus and putamen, are also amongst the most commonly activated regions in studies involving both positive [11–13,24,27,28] and negative emotions [5,6,8] (see also [29]), probably in different subdivisions. Both have been considered to be part of the extrapyramidal motor system, raising the question whether the activity we observed is related to increased motor planning or imagery associated with a loved person. This is unlikely because studies on motor imagery, mental rotation and motor execution typically do not activate either structure, while activating other regions not implicated in this study [30]. In contrast, it is noteworthy that dopamine release due to success in a video game has been localised to a broad region in the striatum that overlaps at least with the activity reported here in the putamen [31]. Collectively, these results call for a reappraisal of the role of the putamen and the caudate in emotional states and as parts of the extrapyramidal motor system.

**Deactivations:** In charting the neural basis of so complex an emotion, the deactivations are also important, since the nature and strength of the emotion itself may be dictated in part at least by a complex balance between the two. The widespread deactivations that we have observed have their counterpart in previous studies which have shown that happiness correlates with deactivations in the right prefrontal and bilateral parietal and temporal cortices [5]. Conversely, it is striking to note that sadness and depression correlate with activation in some of the cortical regions deactivated in our study, especially the right prefrontal cortex [10], whose artificial inactivation by means of transcranial magnetic stimulation has proven to result in successful treatment against depression [32]. The posterior cingulate cortex is one of the most commonly activated region in emotional studies [29], but its exact function remains poorly understood. The deactivation of the amygdaloid region is of special interest, since activity in it correlates with fear, sadness and aggression, and is thought to mediate emotional learning [33]; activity in it increases from the most happy to the most fearful facial expression viewed [28]. This differential response is further emphasised by our results which show that, within experienced positive emotions, the amygdaloid region is more active when viewing friends than the loved partner.

**Studies of sexual arousal:** Sexual arousal is of course never far from romantic love, making it especially interest-

ing to consider the degree to which the two are neuronally entangled. Two studies on sexual arousal [11,12] reported no activations that overlapped with ours, but both activated regions adjacent to ours in the anterior cingulate gyrus, one in the left caudate nucleus and the right insula [11], and the other in the right globus pallidus [12]. Deactivations were reported in the posterior cingulate cortex [11] and in the right hemisphere [12], the latter overlapping with ours in BA 8. It is however striking that studies of cocaine- and mu-opioid agonist-induced euphoria have shown increased activity in foci that seem to overlap with all foci activated in our study: the anterior cingulate cortex [27,34], the insula, the caudate nucleus and the putamen [27]. This suggests a potentially close neural link between romantic love and euphoric states.

## CONCLUSION

We have tried to identify the cortical activity associated with the state of romantic love, by comparing one positive emotion (romantic love) with another one (friendship). Our stimuli were emotionally indistinguishable to an external observer: the difference between the partner and friends was an emotional one, apparent to the subject concerned alone. By showing that a unique set of interconnected areas becomes active when humans view the face of someone who elicits a unique and characteristic set of emotions, we have shown that underlying one of the richest experiences of mankind is a functionally specialised system of the brain. It is perhaps surprising that so complex and overwhelming a sentiment should correlate differentially with activity in such restricted regions of the brain, and fascinating to reflect that the face that launched a thousand ships should have done so through such a limited expanse of cortex. Given the complexity of the sentiment of romantic love, and its capacity to exhilarate, arouse and disturb and thus influence so much of our behaviour, it would be surprising if these areas act in isolation. The widespread cortical connections of the areas differentially activated here is no doubt a means of recruiting more areas during this complex emotional state, with a pattern of activity that may differ between individuals and situations, which future studies will no doubt unravel. Given the uniqueness of the pattern of activity evoked, it is not unreasonable to suppose that other unique emotional states will correlate with activity in other functionally specialized subsystems of the brain.

## REFERENCES

1. Sternberg RJ. *Psychol Rev* **93**, 119–135 (1986).
2. Hazan C and Shaver P. *J Pers Soc Psychobiol* **52**, 511–524 (1987).
3. Sternberg RJ and Barnes ML. *The Psychology of Love*. New Haven, CT: Yale University Press; 1988.
4. Kimbrell TA, George MS, Parekh PI *et al.* *Biol Psychiatry* **46**, 454–465 (1999).
5. George MS, Ketter TA, Parekh PI *et al.* *Am J Psychiatry* **152**, 341–351 (1995).
6. Lane RD, Reiman EM, Ahern GL *et al.* *Am J Psychiatry* **154**, 926–933 (1997).
7. Reiman EM. *J Clin Psychiatry* **58**, 4–12 (1997).
8. Teasdale JD, Howard RJ, Cox SG *et al.* *Am J Psychiatry* **156**, 209–215 (1999).
9. Paradiso S, Johnson DL, Andreasen NC *et al.* *Am J Psychiatry* **156**, 1618–1629 (1999).

10. Beauregard M, Leroux JM, Bergman S *et al.* *Neuroreport* **9**, 3253–3258 (1998).
11. Stoleru S, Gregoire MC, Gerard D *et al.* *Arch Sex Behav* **28**, 1–21 (1999).
12. Rauch SL, Shin LM, Dougherty DD *et al.* *Psychiatry Res* **91**, 1–10 (1999).
13. Lane RD, Reiman EM, Bradley MM *et al.* *Neuropsychologia* **35**, 1437–1444 (1997).
14. Zeki S and Bartels A. *Eur J Neurosci* **12 (Suppl. 11)** 88 (2000).
15. Hatfield E and Sprecher S. *J Adolescence* **9**, 383–410 (1986).
16. Friston KJ, Holmes AP, Poline JB *et al.* *NeuroImage* **2**, 45–53 (1995).
17. Bartels A and Zeki S. *European Journal of Neuroscience* **12**, 172–193 (2000).
18. Bell AJ and Sejnowski TJ. *Neural Computation* **7**, 1129–1159 (1995).
19. McKeown MJ, Jung TP, Makeig S *et al.* *Proc Natl Acad Sci USA* **95**, 803–810 (1998).
20. Wojculik E, Kanwisher N and Driver J. *Journal of Neurophysiology* **79**, 1574–1578 (1998).
21. Zeki S and Bartels A. *Phil Trans R Soc Lond B* **354**, 1371–1382 (1999).
22. Leveroni CL, Seidenberg M, Mayer AR *et al.* *J Neurosci* **20**, 878–886 (2000).
23. Flynn FG, Benson DF and Ardila A. *J Aphasiol* **13**, 55–78 (1999).
24. Nakamura K, Kawashima R, Ito K *et al.* *J Neurophysiol* **82**, 1610–1614 (1999).
25. Devinsky O, Morrell MJ and Brent AV. *Brain* **118**, 279–306 (1995).
26. Frith CD and Frith U. *Science* **286**, 1692–1695 (1999).
27. Breiter HC, Gollub RL, Weisskoff RM *et al.* *Neuron* **19**, 591–611 (1997).
28. Morris JS, Frith CD, Perrett DI *et al.* *Nature* **383**, 812–815 (1996).
29. Maddock RJ. *Trends Neurosci* **22**, 310–316 (1999).
30. Decety J and Grezes J. *Trends Cogn Sci* **3**, 172–178 (1999).
31. Koepp MJ, Gunn RN, Lawrence AD *et al.* *Nature* **393**, 266–268 (1998).
32. Menkes DL, Bodnar P, Ballesteros RA *et al.* *J Neurol Neurosurg Psychiatry* **67**, 113–115 (1999).
33. LeDoux J. *The Emotional Brain*. New York: Simon and Schuster; 1996.
34. Schlaepfer TE, Strain EC, Greenberg BD *et al.* *Am J Psychiatry* **155**, 470–473 (1998).
35. Bartels A and Zeki S. *Soc Neurosci Abstr* **766.5** (1999).

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