

Modulation of aesthetic value by semantic context: An fMRI study

Ulrich Kirk^{a,b,*}, Martin Skov^{c,1}, Oliver Hulme^{a,b,1}, Mark S. Christensen^{c,d}, Semir Zeki^{a,b}

^a Wellcome Laboratory of Neurobiology, Anatomy Department, University College London, Darwin Building, Gower Street, London WC1E 6BT, UK

^b Wellcome Department of Imaging Neuroscience, University College London, Darwin Building, Gower Street, London WC1E 6BT, UK

^c Danish Research Centre for Magnetic Resonance, Copenhagen University Hospital, Hvidovre, DK-2650, Denmark

^d Department of Exercise and Sport Sciences, University of Copenhagen, The Panum Institute, DK-2200, Denmark

ARTICLE INFO

Article history:

Received 14 April 2008

Revised 1 August 2008

Accepted 13 October 2008

Available online 29 October 2008

ABSTRACT

Aesthetic judgments, like most judgments, depend on context. Whether an object or image is seen in daily life or in an art gallery can significantly modulate the aesthetic value humans attach to it. We investigated the neural system supporting this modulation by presenting human subjects with artworks under different contexts whilst acquiring fMRI data. Using the same database of artworks, we randomly labelled images as being either sourced from a gallery or computer generated. Subjects' aesthetic ratings were significantly higher for stimuli viewed in the 'gallery' than 'computer' contexts. This contextual modulation correlated with activity in the medial orbitofrontal cortex and prefrontal cortex, whereas the context, independent of aesthetic value, correlated with bilateral activations of temporal pole and bilateral entorhinal cortex. This shows that prefrontal and orbitofrontal cortices recruited by aesthetic judgments are significantly biased by subjects' prior expectations about the likely hedonic value of stimuli according to their source.

© 2008 Elsevier Inc. All rights reserved.

Introduction

It is known, both anecdotally and experimentally, that aesthetic value is influenced by context. Behavioural studies have shown that presenting artworks accompanied with titles, text, and other forms of cognitive information can significantly influence an observer's reported evaluation of the artwork (e.g., Cupchik et al., 1994; Leder et al., 2006; Russell, 2003). However, the neural sources of this context specific modulation remain uncharted.

Recently, neuroimaging studies have investigated the neural correlates of aesthetic evaluation. Experiments using musical sequences as stimuli (Blood et al., 1999; Blood and Zatorre, 2001; Brown et al., 2004; Menon and Levitin, 2005; Koelsch et al., 2006) have found that post-hoc ratings of subjective pleasantness correlate with activity in the striatum (dorsal and ventral), amygdala, parahippocampal gyrus, insula, orbitofrontal cortex (OFC), and the anterior cingulate cortex (ACC). A similar finding was reported in two studies using paintings as stimuli (Vartanian and Goel, 2004; Kawabata and Zeki, 2004). The main effect of the subjects' aesthetic appreciation of the images (as determined by subjective ratings) resulted in activity in the caudate nucleus, OFC and ACC. The network recruited during an aesthetic judgment (when compared to a symmetry judgment) includes enhanced activity in frontomedian cortex, lateral OFC,

inferior frontal gyrus, posterior cingulate, temporal pole, and temporoparietal junction (Jacobsen et al., 2006). Together, these studies suggest that subjective assessment of the aesthetic value of works of art, engage a network of brain structures known to be involved in the processing of reward, perceptual processing, and decision-making.

The question we address here is whether explicit contextual information influences activity in specific part of this extended network of areas. Since previous studies have demonstrated that activity in the medial OFC is modulated by contextual information in experimental conditions where subjects evaluate their preference for liquids or odours, we hypothesized that the medial OFC would be the most likely target of such contextual modulation. de Araujo et al. (2005) demonstrated that human subjects will rate a test odour as significantly more pleasant when it is paired with a pleasant visual word as when paired with an unpleasant one. They observed a neural correlate of this behavioural modulation in medial OFC. This shows that high-level cognitive input such as word labels influence brain activity in medial OFC. Similarly, McClure et al. (2004) investigated the neural systems involved in generating preferences produced by two different brands of soft drinks (Coca-Cola and Pepsi) and found that the rated preference of unlabelled drinks (i.e. without cognitive influences) was reflected in activations of the ventromedial part of the prefrontal cortex (VMPFC), whereas brand knowledge modulated dorsolateral prefrontal cortex, visual cortex, midbrain and hippocampus. This result was recently extended by Plassmann et al. (2008) who showed that knowledge of the monetary value of a wine increases subjects' reports of preference, and reported a neural correlate of this effect in medial OFC. However, no neuroimaging study has charted the

* Corresponding author. Wellcome Laboratory of Neurobiology, Anatomy Department, University College London, Darwin Building, Gower Street, London WC1E 6BT, UK
E-mail address: ulrich.kirk@uclmail.net (U. Kirk).

¹ These authors contributed equally to this work.

neural correlates of contextual modulation of subjective preference for visual stimuli, including visual works of art.

To test this hypothesis subjects were asked to aesthetically rate a series of abstract paintings while in the scanner. We manipulated the context under which subjects viewed the artworks by labelling 50% as being from a prestigious gallery ('gallery' label) and 50% as being generated by the experimenters using a computer program ('computer' label) (see Fig. 1). This prevented any systematic difference in visual stimulation between the two conditions and thus controlled only the prior expectation by changing the context. Our aim was to test which areas were significantly modulated by context alone, and which were modulated by both context and aesthetics ratings. Pre-

screening of subjects and post-hoc testing confirmed that subjects had no prior knowledge or familiarity of the paintings.

We hypothesized that the context in which subjects viewed artworks would significantly affect both their aesthetic evaluation in terms of their behavioural rating as well as the neural processing supporting this change. We base our hypothesis on the assumption that the context associated with the 'gallery' label would induce a higher expectation of reward than the context associated with the 'computer' label, and that this difference in reward expectation would be reflected in the ratings and in the neural activity of the reward system.

Materials and methods

Subjects

Fourteen subjects (5 females; mean age 26.3 years, age range 23–29 years, 4 left-handed) participated in the study. They were all undergraduate or graduate students and all had normal or corrected-to-normal vision, and none had a history of neurological or psychiatric disorders. We excluded subjects with a formal education in any art-related field in order to reduce the familiarity effect of the stimulus class. Written informed consent from all subjects and ethical approval (KF-01-131/03) were obtained before the experiment.

fMRI task

Visual chromatic reproductions of original abstract paintings served as stimuli. In total 200 stimuli were selected from online sources (see Supplementary material for a complete list of stimulus material). Labels accompanied stimulus-presentation and were presented below each visual stimulus (see Fig. 1). We manipulated the context in which the stimuli were presented by applying one of two labels in different blocks: Half the stimuli were labelled as belonging to the Louisiana Museum of Modern Art, Denmark, corresponding to 'gallery' conditions, while the other half were labelled as 'computer' (implying that the experimenters generated the stimuli through a computer program, Photoshop). Prior to scanning, subjects were instructed in the use of the aesthetic rating scale. No reference was made to the labelling manipulation of the stimulus material. In support of the experimental manipulation subjects were given the following instruction: "Inside the scanner you will be presented with 200 abstract paintings. There are two types of paintings. 50% of the paintings have been borrowed from the Louisiana Museum of Modern Art (Copenhagen, Denmark). The other 50% have been generated by the experimenter by means of a computer program (Photoshop)". All subjects had prior knowledge of the existence and prestige of Louisiana Museum of Modern Art. All labels were counterbalanced across subjects, such that visual parameters were balanced across label conditions. Since systematic differences in visual stimulation between the two conditions were controlled only the prior expectations of the subjects varied by changing the context.

Prior to scanning, stimuli were rated according to an aesthetic rating scale in a behavioural pilot study by a separate cohort of subjects (9 subjects; 3 females; mean age 25.3 years; age range 24–28 years). Level of appeal was rated using a scale from 1 to 5, where 1: "very unappealing" and 5: "very appealing". Based on these results, we found that the reports conformed to an approximately uniform balanced distribution across the aesthetic rating scale.

The experimental protocol consisted of a block-design with 5 presentations in each block with identical labels making a total of 20 blocks for each context. A block design was used in order to minimize the number of task switches required of subjects. On each trial, a fixation cross appeared for 1000 ms on a grey background followed by a stimulus presentation for 5000 ms. Following the appearance of each stimulus, subjects were instructed, within the 5000 ms stimulus

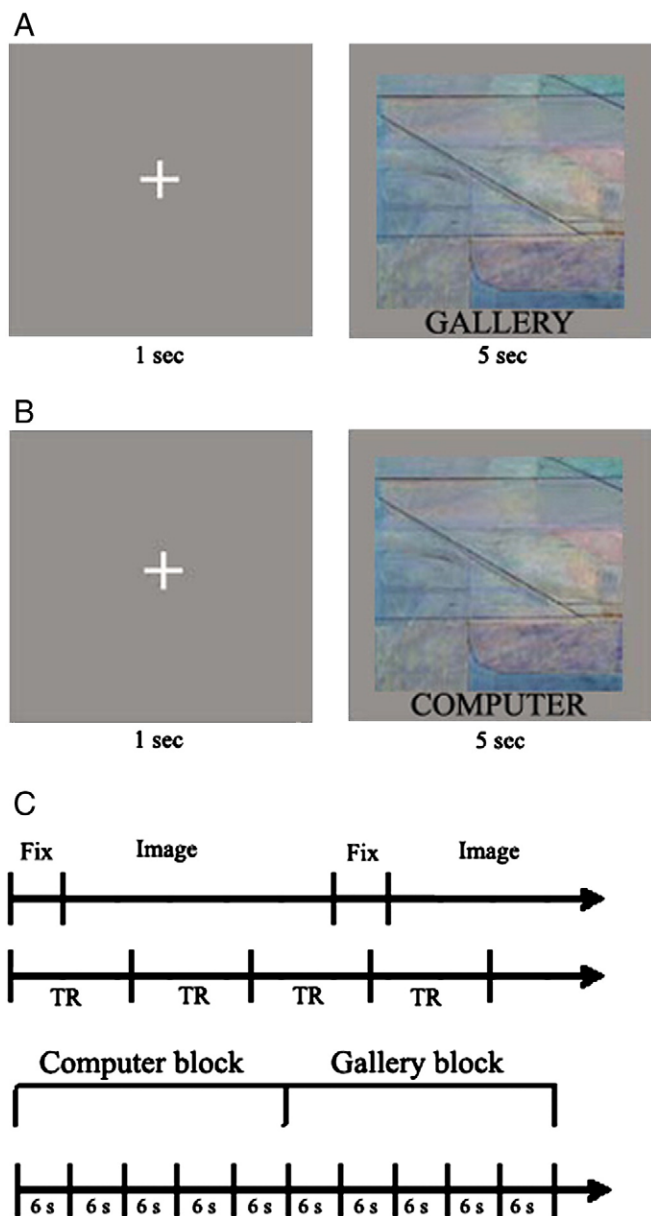


Fig. 1. Displays experimental paradigm where a fixation cross was shown for 1 s followed by a block of 5 presentations of 'gallery' labelled conditions (A) or 'computer' labelled conditions (B), which was presented for 5 s in which the subjects were instructed to indicate the level of aesthetic appeal by means of button-press on a scale from 5 (highest appeal) to 1 (lowest appeal). The inter-trial interval was 1 s (fixation cross) between the presented images. (C) The experimental protocol consisted of a block-design with 5 presentations in each block. The 5 trials within every block had duration of 6 s (fixation+stimulus). The TR was 2400 ms. Labels were counterbalanced across subjects. The stimuli were all non-canonical chromatic abstract artworks.

duration, to rate the stimulus (using the same scale as mentioned above) by pressing one of five buttons on a key pad with their right hand (Fig. 1). Total scanning-time per subject was 20 min per session. Post-scanning, subjects were presented (outside the scanner) with the stimuli again and asked to rate each stimulus on a 5-step familiarity rating scale (1; not familiar – 5; very familiar). Familiarity ratings were entered into the design matrix as a parametric regressor of no interest.

The stimuli were presented at a screen resolution of 1024×768 pixels displayed at a visual angle of 24×18°, and centred in a 500×500 pixel resolution surrounded by a grey background. Stimuli were presented and responses collected using E-prime (Psychology Software Tools, Inc.). The stimuli were back-projected via an LCD projector onto a transparent screen positioned over the subjects' head and viewed through a tilted mirror fixed to the head coil.

fMRI data acquisition

The functional imaging was performed with a 3 T scanner (Siemens, Magnetom Trio, Erlangen, Germany) to acquire gradient T2* weighted echo planar images (EPI) to maximize the blood oxygen level-dependent (BOLD) contrast (echo time, TE=30 ms; repetition time, TR=2400 ms; flip angle, FA=90°). The EPI sequence was optimized in order to reduce signal drop-out in OFC (Deichmann et al., 2003). Each functional image was acquired in an interleaved way, beginning with 2nd slice (slice no. 2,4...40, 1,3...39) when counted from the bottom, comprising 40 axial slices each 3.0 mm thick, consisting of 64×64 voxels with an inplane resolution of 3×3 mm. The slices were acquired in the transverse plane and tilted around the x-axis in order to give near whole-brain coverage, excluding the cerebellum. Each session consisted of 500 volumes. The subjects' pulse and respiration were recorded using an MRI-compatible pulse oximeter, and a respiration belt, both sampled at 50 Hz. After every functional scan, a T1 weighted MPAGE structural sequence was acquired, using a phased array head coil to provide high-resolution anatomical detail.

fMRI data analysis

Image pre-processing and data analysis was performed using SPM2 (Wellcome Department of Imaging Neuroscience, London, UK). The EPI images were realigned spatially (Friston et al., 1995). This was followed by temporal realignment, which corrected for slice-time differences using the middle slice as reference slice. Images were then normalized to the Montreal Neurological Institute (MNI) template provided in SPM2. Finally a spatial filtering was performed by applying a Gaussian smoothing kernel of 8 mm FWHM (full width at half-maximum).

Following pre-processing a general linear model was applied to the fMRI time-series where stimulus onset was modelled as single impulse response functions including stimulus duration (5000 ms) and then convolved with the canonical haemodynamic response function (HRF) including its temporal and dispersion derivatives in order to capture variations in the onset and width of the BOLD responses.

A parametric regression analysis was used (Buchel et al., 1998) that allowed us to model 0th order and 1st order haemodynamic responses using orthogonalized polynomial expansion functions. This was performed for each of the two conditions (gallery and computer labels) using subject-specific aesthetic ratings in order to model parametric modulations of aesthetic ratings for the 1st order expansions. The 0th order parametric regression analysis allowed us to model the two conditions (gallery and computer) independently of the aesthetic ratings. This gave the overall design character of a mixed design incorporating the condition (gallery and computer labels) in the 0th order expansion and the aesthetic evaluation of the individual stimuli into the 1st order expansion and. Because the HRF is a smoothing filter in the temporal domain, the 0th order expansion, which was constructed as a convolution of the box-car ('on' when the

stimulus was presented and 'off' in the 1 s in between) with the HRF, was very similar to, although not identical, a traditional box-car which for the 'gallery' labelled images would be 'on' for the full 30 s and 'off' when the computer label was 'on'. The 1st order expansion on the other hand incorporates the individual aesthetic ratings in such a way that the underlying model (i.e. onset time + 5 s duration) is scaled with the aesthetic rating and then convolved with the HRF. Thereby a regressor was constructed where the expected haemodynamic signal varied for the individual images according to the aesthetic rating. First-level analysis was performed on each subject to generate a single mean image corresponding to each term of the polynomial expansion. As the behavioural data demonstrated a statistically significant difference in aesthetic ratings (see Fig. 2) between gallery and computer conditions, further regressors were applied to separate the data and control for these behavioural differences between conditions. For each subject the frequency of each of the five rating bins was balanced, such that there were no differences in mean ratings between gallery and computer conditions since such a difference would confound the 0th order parametric regression analysis with

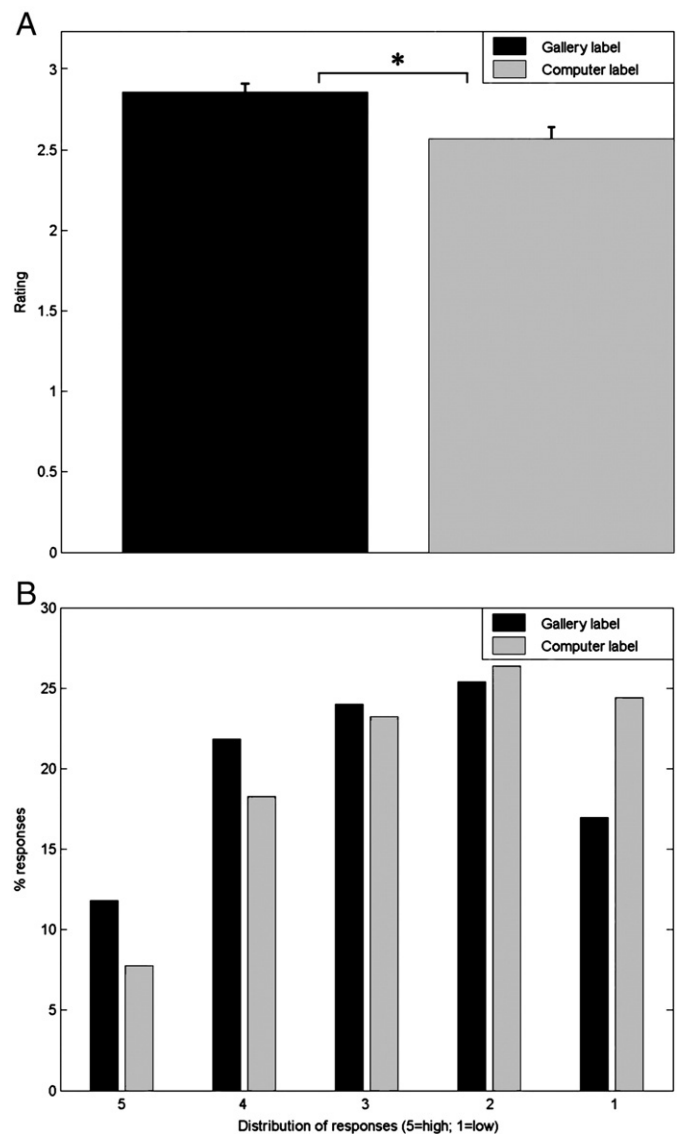


Fig. 2. Subjects' aesthetic ratings grouped according to the labelled conditions. (A) Mean aesthetic ratings across subjects for the two conditions. The SEM across subjects is shown. (B) Distribution of the frequencies of aesthetic responses across all subjects for the two conditions (5=high appeal; 1=low appeal).

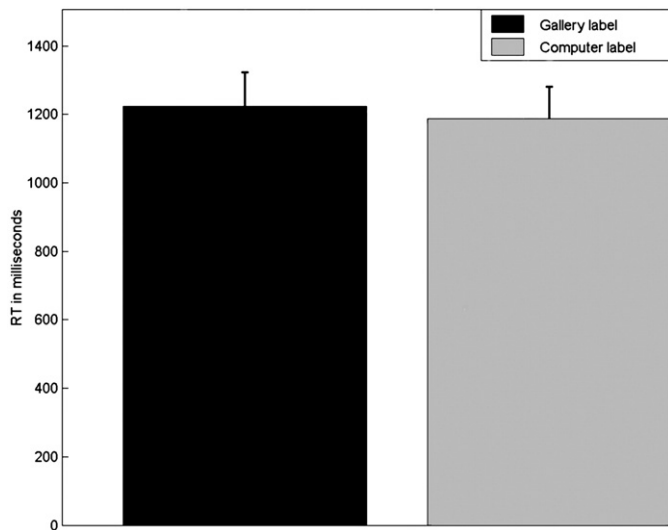


Fig. 3. Behavioural data collected during scanning. The figure shows the mean reaction-times (RT) across all subjects. Bars indicate SEM.

aesthetic ratings. For each subject the residual rating bins from this process were put in separate regressors that were applied in the subsequent 1st order parametric modulation. The mean images from the first level analysis were entered into a second-level, random effects (RFX) analysis accounting for the between subject variance. An ANOVA model using the beta-estimates of the two conditions for the 0th and 1st order expansions was applied. Equal variance was not assumed, thus SPM2's options for non-sphericity correction was applied (Glaser and Friston, 2004).

In order to correct for the structured noise induced by respiration and cardiac pulsation we included RETROICOR (RETROspective Image based CORrection method) nuisance covariates in the design matrix (Glover et al., 2000). These regressors are a Fourier expansion of the aliased cardiac and respiratory oscillations. We included six regressors for respiration and ten regressors for cardiac pulsation. We also included twenty-four regressors that remove residual movement artefacts with spin history

effects, which have been shown to remain even after image realignment (Friston et al., 1996). This set of nuisance regressors have also been shown to reduce inter and intra subject variation significantly (Lund et al., 2005). Having all four types of nuisance regressors in the design improves the assumption of independently and identically distributed errors (Lund et al., 2006). For the analysis a high pass filter with a cut-off frequency at 1/128 Hz was applied.

Using *t*-contrasts allowed us to test for correlations of the fMRI BOLD signal and the parameters of interest performed respectively as 0th order and 1st order parametric modulations. Reported *p*-values ($p < 0.05$) were controlled for false discovery rate (FDR) correction (Genovese et al., 2002). Additionally for regions which failed to reach FDR significance but for which we had a priori hypotheses, we report uncorrected *p*-values. Unless otherwise stated reported *p*-values are uncorrected for multiple comparisons. The co-ordinates of all activations are reported in MNI space.

Results

Behavioural data

The aesthetic ratings collected during scanning for the two stimulus conditions are shown in Fig. 2. The mean aesthetic rating for 'gallery' labelled conditions was 2.86 (SEM=0.05), and for 'computer' labelled conditions 2.57 (SEM=0.07). As hypothesized, statistical analysis revealed that the stimuli were rated as being significantly more aesthetically pleasing when labelled as 'gallery' than when labelled as 'computer' (ANOVA, $F(1,26)=10.49$; $p < 0.003$). Mean reaction times (RT) were 1224 ms (SEM=98.5) for gallery conditions and 1187 ms (SEM=96.5) for computer conditions (Fig. 3). The labels did not give rise to a significant difference in RT (ANOVA, $F(1,26)=0.07$; $p > 0.78$) between conditions.

fMRI data

Correlation between the BOLD signal and aesthetic ratings

To test whether aesthetic ratings differentially modulate brain activity due to the labelling of the two conditions, we employed a parametric regression analysis (Buchs et al., 1998) using the mean

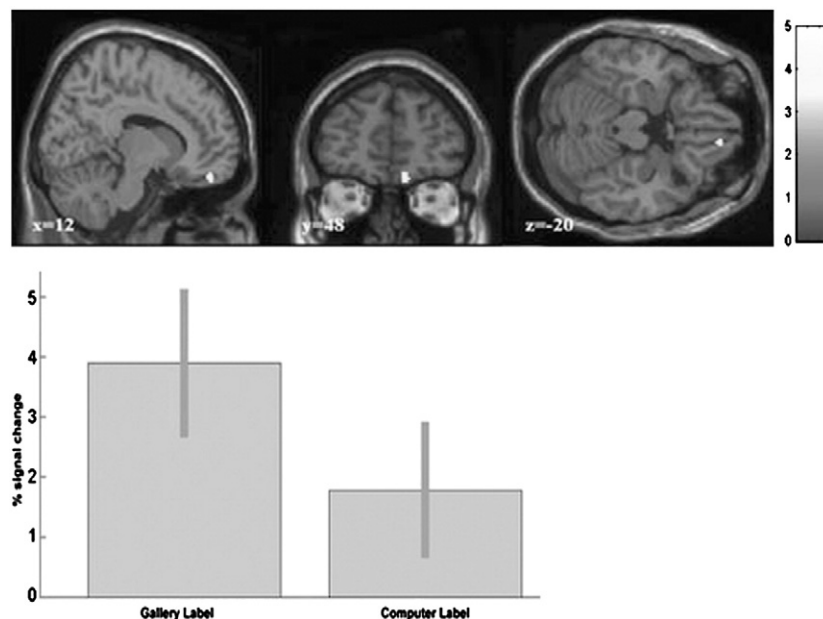


Fig. 4. Upper panel: The figure shows activation in right medial OFC where the BOLD signal correlates with the 1st order linear term for the contrast [G–C]. The activation is overlaid on sagittal, coronal and axial sections of the canonical SPM structural image. Lower panel: Parameter estimates for voxels in medial OFC for the two conditions Gallery (G) and Computer (C) where the x-axis reflects the two stimulus conditions, and the y-axis shows BOLD signal changes. Error bars indicate 90% confidence interval.

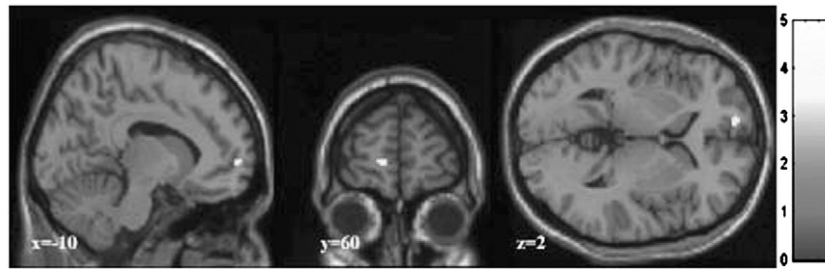


Fig. 5. Activation in left polar frontal cortex where the BOLD signal correlates with the 1st order linear term of the aesthetic ratings for the contrast [G–C]. The activation is overlaid on sagittal, coronal and axial sections of the canonical SPM structural image.

centred subject-specific behavioural responses (aesthetic judgments) as separate regressors for each label.

We identified brain areas where the 1st order parametric regression co-efficient for aesthetic ratings was greater for the gallery (G) compared to the computer (C) context. This contrast revealed significant effects in right medial OFC (12, 48, –20; $z=4.37$; $p<0.05$, corrected for multiple comparisons using false discovery rate, FDR) (Fig. 4). Although the peak voxels were located in the medial OFC of the right hemisphere (Fig. 4), significant activations were found in a corresponding region of the left OFC at a lower statistical threshold of $p<0.001$ (–14, 46, –23; $z=3.51$) (figure not shown). Furthermore, the left frontal pole on the ventral aspect of the medial prefrontal cortex (VMPFC) (–10, 60, 2; $z=3.49$; $p<0.001$) was active (Fig. 5). The converse comparison, which should show areas whose linear response to aesthetic ratings is greater for the computer context than it is for the gallery context, showed no significant regions ($p>0.001$) (figure not shown).

A conjunction analysis was performed to identify common brain regions that are linearly responsive to aesthetic ratings regardless of context. This was performed as a conjunction between the 1st order parametric regressors for both G and C conditions. This analysis did not reveal significant voxels ($p>0.001^2$).

Correlation between the BOLD signal and context irrespective of aesthetic ratings

For the main effect [G–C], which reflects brain areas which are more active in the gallery vs. computer condition irrespective of the actual aesthetic rating given, activity was found in bilateral entorhinal cortex, BA 28/34 (see Table 1 and Fig. 6A). This region, located on the parahippocampal gyrus adjacent to the hippocampus formation, is heavily interconnected with the hippocampus. Furthermore, we observed activity in bilateral temporal pole/medial temporal pole (see Table 1 and Fig. 6B) and a large cluster of voxels in bilateral visual cortex corresponding to BA 17 (see Table 1). The main effects show an effect of context even when there was no change in the visual stimulation across the two conditions.

For the converse main effect of context [C–G] we did not observe significant activations ($p>0.001$) (figure not shown).

Finally, we performed a conjunction analysis to identify areas involved in contextual processing irrespective of the two conditions. This was performed as a conjunction between G and C conditions. It

did not result in any significant activity ($p>0.001^2$), indicating that contextual processing are recruited differentially by the two labels in brain areas shown in Fig. 6.

Correlation between recognition effects and aesthetic ratings

To control whether recognition effects induced by the labels might have contributed to the results, such that the cortical differences between conditions reflected recognition effects rather than aesthetic judgments in medial OFC (Frey and Petrides, 2002), we regressed onto familiarity data (collected post-scanning for all subjects) in order to search for brain areas that showed a correlation between familiarity and aesthetic ratings. Small volume corrections (SVC) were applied constraining our analysis to the medial OFC activation (12, 48, –20 and –14, 46, –23). This analysis did not produce any supra-threshold voxels at $p>0.001$ (not shown), indicating that recognition effects did not contribute to the results in medial OFC.

Discussion

The aim of this study was to investigate the neural system supporting contextual modulation of aesthetic ratings. We presented images to subjects in two different contexts, which we hypothesized

Table 1

Location of brain regions that respond preferentially to [Gallery–Computer] irrespective of aesthetic ratings

Brain region	Peak MNI coordinates	z Score
R. entorhinalcortex,BA28/34	20, – 4, – 28	3.54
L. entorhinalcortex,BA28/34	– 18, – 8, – 28	(3.27)
R. temporalpole	32,18,– 42	3.83
L. temporalpole	– 36,14,– 36	3.41
R. visualcortex(BA17)	10,– 52,10	3.95*
L.visualcortex(BA17)	2,– 60,12	
	– 6,– 56,12	

Activations are shown at ($p<0.001$, uncorrected) and ($p<0.005$, uncorrected, in parentheses). * $p<0.003$, corrected; cluster-level. L, left hemisphere; R, right hemisphere.

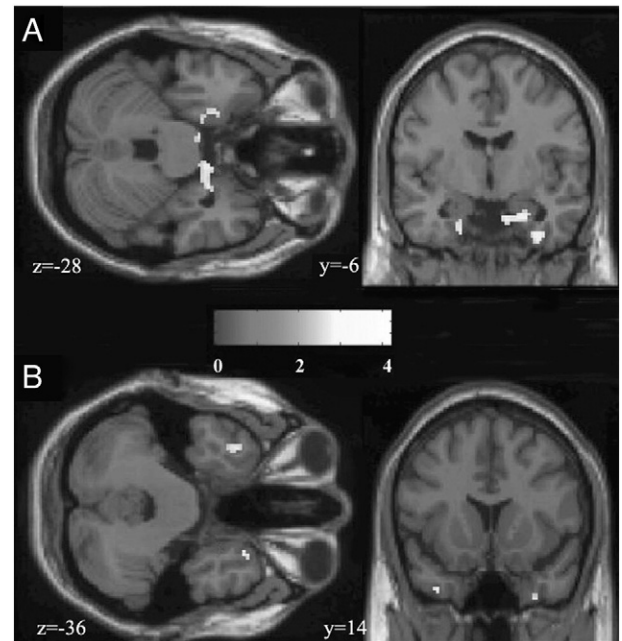


Fig. 6. The main effect of context [G–C]. (A) Significant voxels ($p<0.001$) were found in right entorhinal cortex. Activations were found in a corresponding region on the left at a lower statistical threshold ($p<0.005$). Panel A displayed at $p<0.005$ to show the extent of the activation in entorhinal cortex. (B) Activations were also found in bilateral temporal pole ($p<0.001$). The activations are overlaid on axial and coronal sections of the canonical SPM structural image.

would induce different prior expectations of the hedonic values of each image, with gallery contexts inducing a greater expectation of hedonic value than the same image presented in a computer-generated context. The behavioural results showed this hypothesis to be correct, since images under the gallery label were rated as having a significantly higher mean aesthetic value than those carrying the computer label, even in the absence of systematic differences in visual stimulation across conditions.

The fMRI data showed that activity in the medial OFC exhibited a stronger correlation with aesthetic ratings under the gallery context compared to the computer context, thus demonstrating that the aesthetic response profile in medial OFC is sensitive to context. In contrast, bilateral activations in the entorhinal cortex, adjoining the hippocampus, temporal pole and primary visual cortex showed a greater response to the gallery vs. computer context irrespective of the actual aesthetic ratings. Note that for this contrast, we controlled for the distribution of aesthetic ratings, so that the conditions used were selected to ensure that the distributions of aesthetic ratings were identical for both gallery and computer conditions. Thus differences in mean aesthetic rating cannot account for the activations reported.

The activation of medial OFC is consistent with current evidence which suggests that this region represents attributed hedonic values from a variety of sensory modalities, including gustatory (O'Doherty et al., 2001a; Small et al., 2001, 2003), olfactory (Anderson et al., 2003; Gottfried et al., 2002; Rolls et al., 2003a), somatosensory (Rolls et al., 2003b), correlated with modulated activity (Blood et al., 1999; Blood and Zatorre, 2001; Brown et al., 2004; Menon and Levitin, 2005; Koelsch et al., 2006) and vision (Aharon et al., 2001; Kawabata and Zeki, 2004; O'Doherty et al., 2003b; Vartanian and Goel, 2004) as well as for more abstract rewards such as money (Elliott et al., 2003; Knutson et al., 2001; O'Doherty et al., 2001b). As an extension of these previous findings, the present study provides evidence that the representation of hedonic value in medial OFC is modulated differently relative to cognitive and semantic input even when there are no systematic image-wise differences across the two conditions. Furthermore, the results of the present study confirm and extend earlier studies demonstrating a relation between contextual modulation of subjects' preference for perceived stimuli and medial OFC activity. Studies using brand information to influence preference for soft drinks (McClure et al., 2004), visual word descriptors to influence preference for odours (de Araujo et al., 2005), and price information to influence preference for wine (Plassmann et al., 2008) all found that this behavioural effect modulated activity in medial OFC or VMPFC. The present study extends this effect to the domain of visual processing. This generality across gustatory, olfactory and visual modalities strongly suggests that medial OFC is a common centre for the integration of different sources of information pertaining to the assessment of a stimulus' value, including sensory information, reward processing, and high-level cognitive inputs.

An interesting question is how the OFC result should be interpreted in relation to models of the neural mechanisms underlying aesthetic evaluation. The medial OFC might be involved in two functional sub-processes: (1) the evaluative categorization processes associated with making an aesthetic judgment, i.e. the subjective report; or (2) or the processes correlated with the coding of subjective pleasure, i.e. stimulus hedonic value. Results indicate a neural difference between making an active aesthetic judgment of the aesthetic value of some stimulus and attending to the same stimulus in other ways (passive viewing; symmetrical judgments) (Höfel and Jacobsen, 2007a,b; Jacobsen and Höfel, 2003; Jacobsen et al., 2006). However, no involvement of medial part of OFC was found in a neuroimaging study investigating the processes involved in making aesthetic judgments compared to making a symmetry judgment although parametric effects of stimulus complexity in aesthetic judgments were found in the lateral aspects of the OFC (Jacobsen et al., 2006). The parametric modulation of medial OFC in the present study are thus more likely to be related to the subjective coding

of hedonic valence, than mechanisms associated with the active act of making an overt judgment.

In the study by McClure et al. (2004) images of Coca-Cola vs. Pepsi cans influenced activations in areas that are traditionally considered as more cognitive than flavour related areas, including hippocampus, midbrain, primary visual cortex and dorsolateral prefrontal cortex (McClure et al., 2004). We observed bilateral activation in the entorhinal cortex in the main effect [G–C] irrespective of the actual aesthetic ratings. The entorhinal cortex adjoins and is interconnected with the hippocampus, a region that has been consistently related to processing of episodic memories (Brown and Aggleton, 2001; Eichenbaum et al., 1996, 2007). Hippocampus activation is associated with trials in which subjects correctly recollect contextual information compared to ones in which they do not (Cansino et al., 2002). Other findings suggest that midbrain dopaminergic systems involved in reward expectation could directly modulate declarative memory formation in the hippocampus (Adcock et al., 2006; Bernabeu et al., 1997; Wittmann et al., 2005). This evidence is in line with our initial hypothesis that it is the subjects' conception of the image, rather than its sensory properties, that primarily determines its hedonic value. Similarly, recent results have shown that neurons in primary visual cortex encode associations between visual stimuli and subsequent prediction of reward timing (Shuler and Bear, 2006). These data demonstrate that reward-timing activity can occur very early in the sensory-processing paths. One possible mechanism responsible for this effect might be due to subjects acquiring different prior expectations over future rewards evoked by the stimulus labels. The different expectations of hedonic value could be determined in different ways. The difference in context in this experiment straddles at least two possible factors. The first might be loosely described as a difference in prestige; the art gallery is more prestigious than the computer as a source of artworks. Accordingly the prediction of higher reward for the gallery comes from a social prior. The more prestigious the art gallery, the more competition there is for artists to display works there, therefore those that succeed will be more likely to reward viewers than those that fail. A second, closely related factor is the monetary value of the artwork. Artworks from a gallery are more likely to have a greater monetary value than those which are not (on average). Neglecting economic factors of supply and demand, one might have the simple prior that the more expensive the artwork the more likely it is to have a higher hedonic value for a given observer. The context induced changes in aesthetic modulation could be due to either or both of these factors and dissociating these two will be the focus of future work.

We adopted a blocked rather than event-related design in this study. In contrast to an event-related design in which the labelling would inevitably have introduced an element of unpredictability, our approach allowed us to look at responses to cognitive labels that were fully predictable within blocks. It has been suggested that block designs is confounded by reward expectation (O'Doherty et al., 2003a; Winston et al., 2007). Accordingly activity observed in the present study could possibly be due to reward expectation induced by the block design rather than being driven by the assessment of aesthetic value. However, we argue against this possibility in that evidence suggests that ventral striatum is involved in reward expectancy, rather than being involved in stimulus hedonic value (e.g. Berridge 1996; Knutson et al., 2001; Schultz et al., 1992). OFC, on the other hand, is known to be involved in representing the hedonic value of a stimulus (O'Doherty et al., 2003a; Tremblay and Schultz, 1999; Winston et al., 2007). Hence, OFC responses in the present study can be attributed to the hedonic value of the stimuli themselves and it is likely that responses were not observed in ventral striatum because there was no confound of reward expectation.

Although the entorhinal cortex and temporal pole (BA 38) are associated with different roles in declarative memory (Kroll et al. 1997; Nakamura and Kubota 1995; Sargolini et al. 2006), our data suggest a connection between them. The temporal pole is thought to be implicated in semantic memory retrieval (Damasio et al., 1996; Mummery et al., 2000). This region is involved in the storage and recall

of contextual information, particularly when affectively salient (Lane et al., 1997; Smith et al., 2004). The temporal poles have also been reported to be active in tasks that require explicit evaluation judgments such as emotional intensity (Cunningham et al., 2004), and aesthetic judgments (Jacobsen et al., 2006). Our data fits with these prior findings and raise the possibility that the entorhinal cortex and temporal pole may be engaged during recollection of art-related and cultural information that influence aesthetic judgments during gallery conditions, while VMPFC and medial OFC are more involved in attaching hedonic properties to them. These two systems do not appear to function independently of each other but are modulated and cooperate to influence aesthetic judgments induced by semantic context.

Acknowledgments

We thank Dr. T. Lund for helpful discussions. T. Ramsøy provided useful comments on the manuscript. U. Kirk was supported by a PhD scholarship from the Danish Medical Research Council; M. Skov was supported by Hvidovre Hospital's research foundation; O. Hulme was supported by the Medical Research Council, United Kingdom; M.S. Christensen was supported by the Faculty of Science, University of Copenhagen and the Danish Medical Research Council; S. Zeki was supported by a grant from the Wellcome Trust, London. The MR-scanner was donated by the Simon Spies Foundation.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2008.10.009.

References

- Adcock, R.A., Thangavel, A., Gabrieli, A.W., Knutson, B., Gabrieli, J.D.E., 2006. Reward-motivated learning: mesolimbic activation precedes memory formation. *Neuron* 50, 507–517.
- Aharon, I., Etcoff, N., Arieli, D., Chabris, C.F., O'Connor, E., Breiter, H.C., 2001. Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron* 32, 537–551.
- Anderson, A.K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D.G., Glover, G., Gabrieli, J.D.E., Sobel, N., 2003. Dissociated neural representations of intensity and valence in human olfaction. *Nat. Neurosci.* 6, 196–202.
- Bernabeu, R., Bevilaqua, L., Ardenghi, P., Bromberg, E., Schmitz, P., Bianchin, M., Izquierdo, I., Medina, J.H., 1997. Involvement of hippocampal cAMP/cAMP-dependent protein kinase signalling pathways in a late memory consolidation phase of aversively motivated learning in rats. *Proc. Natl. Acad. Sci. U. S. A.* 94, 7041–7046.
- Berridge, K.C., 1996. Food reward: brain substrates of wanting and liking. *Neurosci. Biobehav. Rev.* 20, 1–25.
- Blood, A.J., Zatorre, R.J., 2001. Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proc. Natl. Acad. Sci. U. S. A.* 25, 11818–11823.
- Blood, A.J., Zatorre, R.J., Bermudez, P., Evans, A.C., 1999. Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. *Nat. Neurosci.* 2, 382–387.
- Brown, M.W., Aggleton, J.P., 2001. Recognition memory: what are the roles of the perirhinal cortex and hippocampus? *Nat. Rev., Neurosci.* 2, 51–61.
- Brown, S., Martinez, M.J., Parsons, L.M., 2004. Passive music listening spontaneously engages limbic and paralimbic systems. *NeuroReport* 15, 2033–2037.
- Buchel, C., Holmes, A.P., Rees, G., Friston, K.J., 1998. Characterizing stimulus response functions using nonlinear regressors in parametric fMRI experiments. *NeuroImage* 8, 140–148.
- Cansino, S., Maquet, P., Dolan, R.J., Rugg, M.D., 2002. Brain activity underlying encoding and retrieval of source memory. *Cereb. Cortex* 12, 1048–1056.
- Cunningham, W.A., Raye, C.L., Johnson, M.K., 2004. Implicit and explicit evaluation: fMRI correlates of valence, emotional intensity, and control in the processing of attitudes. *J. Cogn. Neurosci.* 16 (10), 1717–1729.
- Cupchik, G.C., Shereck, L., Spiegel, S., 1994. The effects of textual information on artistic communication. *Visual Arts Res.* 20, 62–78.
- Damasio, H., Grabowski, T.J., Tranel, D., Hichwa, R.D., Damasio, A.R., 1996. A neural basis for lexical retrieval. *Nature* 380, 499–505.
- de Araujo, I.E., Rolls, E.T., Velasco, M.I., Margot, C., Cayeux, I., 2005. Cognitive modulation of olfactory processing. *Neuron* 46, 671–679.
- Deichmann, R., Gottfried, J.A., Hutton, C., Turner, R., 2003. Optimized EPI for fMRI studies of the orbitofrontal cortex. *NeuroImage* 19, 430–441.
- Eichenbaum, H., Schoenbaum, G., Young, B., Bunsey, M., 1996. Functional organization of the hippocampal memory system. *Proc. Natl. Acad. Sci. U. S. A.* 93, 13500–13507.
- Eichenbaum, H., Yonelinas, A.P., Ranganath, C., 2007. The medial temporal lobe and recognition memory. *Annu. Rev. Neurosci.* 21, 123–152.
- Elliott, R., Newman, J.L., Longe, O.A., Deakin, J.F., 2003. 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.
- Frey, S., Petrides, M., 2002. Orbitofrontal cortex and memory formation. *Neuron* 36, 171–176.
- Friston, K.J., Ashburner, J., Frith, C.D., Poline, J.B., Heather, J.D., Frackowiak, R.S.J., 1995. Spatial registration and normalization of images. *Hum. Brain Mapp.* 2, 165–189.
- Friston, K.J., Williams, S., Howard, R., Frackowiak, R.S.J., Turner, R., 1996. Movement-related effects in fMRI time-series. *Magn. Reson. Med.* 35, 346–355.
- Genovese, C.R., Lazar, N.A., Nichols, T., 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *NeuroImage* 15, 870–878.
- Glaser, D., Friston, K.J., 2004. Variance components. In: Frackowiak, R.S.J., Friston, K.J., Frith, C.D., Dolan, R.J., Price, C.J., Zeki, S., Ashburner, J., Penny, W. (Eds.), *Human Brain Function*. Academic Press, Elsevier, pp. 781–792.
- Glover, G.H., Li, T.Q., Ress, D., 2000. Image-based method for retrospective correction of physiological motion effects in fMRI: RETROICOR. *Magn. Reson. Med.* 44, 162–167.
- Gottfried, J.A., Deichmann, R., Winston, J.S., Dolan, R.J., 2002. Functional heterogeneity in human olfactory cortex: an event-related functional magnetic resonance imaging study. *J. Neurosci.* 22, 10819–10828.
- Höfel, L., Jacobsen, T., 2007a. Electrophysiological indices of processing aesthetics: spontaneous or intentional processes? *Int. J. Psychophysiol.* 65, 20–31.
- Höfel, L., Jacobsen, T., 2007b. Electrophysiological indices of processing symmetry and aesthetics. A result of judgment categorization or judgment report? *J. Psychophysiol.* 21, 9–21.
- Jacobsen, T., Höfel, L., 2003. Descriptive and evaluative judgment processes: behavioral and electrophysiological indices of processing symmetry and aesthetics. *Cogn. Affect. Behav. Neurosci.* 3, 289–299.
- Jacobsen, T., Schubotz, R.I., Höfel, L., Von, C., Cramon, D.Y., 2006. Brain correlates of aesthetic judgment of beauty. *NeuroImage* 29, 276–285.
- Kawabata, H., Zeki, S., 2004. Neural correlates of beauty. *J. Neurophysiol.* 91, 1699–1705.
- Knutson, B., Adams, C.M., Fong, G.W., Hommer, D., 2001. Anticipation of increasing monetary reward selectivity recruits nucleus accumbens. *J. Neurosci.* 21, RC159.
- Koelsch, S., Fritz, T., Von, C., Cramon, D.Y., Müller, K., Friederici, A.D., 2006. Investigating emotion with music: an fMRI study. *Hum. Brain Mapp.* 27, 239–250.
- Kroll, N.E., Markowitsch, H.J., Knight, R.T., von Cramon, D.Y., 1997. Retrieval of old memories: the temporofrontal hypothesis. *Brain* 120, 1377–1399.
- Lane, R.D., Fink, G.R., Chau, P.M.L., Dolan, R.J., 1997. Neural activation during selective attention to subjective emotional responses. *NeuroReport* 8, 3969–3972.
- Leder, H., Carbon, C.C., Ripsas, A.L., 2006. Entitling art: Influence of title information on understanding and appreciation of paintings. *Acta Psychol. (Amst.)* 121, 176–198.
- Lund, T.E., Nørgaard, M.D., Rostrup, E., Rowe, J.B., Paulson, O.B., 2005. Motion or activity: their role in intra- and inter-subject variation in fMRI. *NeuroImage* 26, 960–964.
- Lund, T.E., Madsen, K.H., Sidaros, K., Luo, W.L., Nichols, T.E., 2006. Non-white noise in fMRI: does modeling have an impact? *NeuroImage* 29, 54–66.
- McClure, S.M., Li, J., Tomlin, D., Cypert, K.S., Montague, L.M., Montague, P.R., 2004. Neural correlates of behavioral preference for culturally familiar drinks. *Neuron* 44, 379–387.
- Menon, V., Levitin, D.J., 2005. The rewards of music listening: response and physiological connectivity of the mesolimbic system. *NeuroImage* 28, 175–184.
- Mummary, C.J., Patterson, K., Price, C.J., Ashburner, J., Frackowiak, R.S., Hodges, J.R., 2000. A voxel-based morphometry study of semantic dementia: relationship between temporal lobe atrophy and semantic memory. *Ann. Neurol.* 47, 36–45.
- Nakamura, K., Kubota, K., 1995. Mnemonic firing of neurons in the monkey temporal pole during a visual recognition memory task. *J. Neurophysiol.* 74, 162–178.
- O'Doherty, J., Rolls, E.T., Francis, S., Bowtell, R., McGlone, F., 2001a. Representation of pleasant and aversive taste in the human brain. *J. Neurophysiol.* 85, 1315–1321.
- O'Doherty, J.P., Kringelbach, M.L., Rolls, E.T., Hornak, J., Andrews, C., 2001b. Abstract reward and punishment representation in the human orbitofrontal cortex. *Nat. Neurosci.* 4, 95–102.
- O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D.M., Dolan, R.J., 2003a. Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia* 41, 147–155.
- O'Doherty, J.P., Critchley, H., Deichmann, R., Dolan, R.J., 2003b. Dissociating valence of outcome from behavioral control in human orbital and ventral prefrontal cortices. *J. Neurosci.* 23, 7931–7939.
- Plassmann, H., O'Doherty, J., Shiv, B., Rangel, A., 2008. Marketing actions can modulate neural representations of experienced pleasantness. *Proc. Natl. Acad. Sci. U. S. A.* 105, 1050–1054.
- Rolls, E.T., Kringelbach, M.L., de Araujo, I.E., 2003a. Different representations of pleasant and unpleasant odours in the human brain. *Eur. J. Neurosci.* 18, 695–703.
- Rolls, E.T., O'Doherty, J., Kringelbach, M.L., Francis, S., Bowtell, R., McGlone, F., 2003b. Representations of pleasant and painful touch in the human orbitofrontal and cingulate cortices. *Cereb. Cortex* 13, 308–317.
- Russell, P.A., 2003. Effort after meaning and the hedonic value of paintings. *Br. J. Psychol.* 94, 99–110.
- Sargolini, F., Fyhn, M., Haftin, T., McNaughton, B.L., Witter, M.P., Moser, M.B., Moser, E.I., 2006. Conjunctive representation of position, direction, and velocity in entorhinal cortex. *Science* 312, 758–762.
- Schultz, W., Apicella, P., Scarnati, E., Ljungberg, T., 1992. Neuronal activity in monkey ventral striatum related to the expectation of reward. *J. Neurosci.* 12, 4595–4610.
- Shuler, M.G., Bear, M.F., 2006. Reward timing in the primary visual cortex. *Science* 311, 1606–1609.
- Small, D.M., Zatorre, R.J., Dagher, A., Evans, A.C., Jones-Gotman, M., 2001. Changes in brain activity related to eating chocolate. *Brain* 124, 1720–1733.
- Small, D.M., Gregory, M.D., Mak, Y.E., Gitelman, D., Mesulam, M.M., Parrish, T., 2003. Dissociation of neural representation of intensity and affective valuation in human gustation. *Neuron* 39, 701–711.

- Smith, A.P., Henson, R.N., Dolan, R.J., Rugg, M.D., 2004. fMRI correlates of the episodic retrieval of emotional contexts. *NeuroImage* 22, 868–878.
- Tremblay, L., Schultz, W., 1999. Relative reward preference in primate orbitofrontal cortex. *Nature* 398, 704–708.
- Vartanian, O., Goel, V., 2004. Neuroanatomical correlate of aesthetic preference for paintings. *NeuroReport* 15, 893–897.
- Winston, J.S., O, Doherty, J., Kilner, J.M., Perrett, D.I., Dolan, R.J., 2007. Brain systems for assessing facial attractiveness. *Neuropsychologia* 45, 195–206.
- Wittmann, B.C., Schott, B.H., Guderian, S., Frey, J.U., Heinze, H.J., Düzel, E., 2005. Reward-related fMRI activation of dopaminergic midbrain is associated with enhanced hippocampus-dependent long-term memory formation. *Neuron* 45, 459–467.