NeuroImage 48 (2009) 258–268

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Different representations of relative and absolute subjective value in the human brain

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ARTICLE INFO

Article history:
Received 12 February 2009
Revised 4 June 2009
Accepted 18 June 2009
Available online 25 June 2009

Keywords:
Neuroeconomics
Emotion
Olfaction
Reward
Decision-making
fMRI
Pleasantness
Affect

ABSTRACT

Relative reward value is important for the choice between a set of available rewards, and absolute reward value for stable and consistent economic choice. It is unclear whether in the human brain subjective absolute value representations can be dissociated from relative reward value representations. Using fMRI, we investigated how the subjective pleasantness of an odor is influenced by whether the odor is presented in the context of a relatively more pleasant or less pleasant odor. We delivered two of a set of four odors separated by a delay of 6 s, with the instruction to rate the pleasantness of the second odor, and searched for brain regions where the activations were correlated with the absolute pleasantness rating of the second odor, and for brain regions where the activations were correlated with the difference in pleasantness of the second from the first odor, that is, with relative pleasantness. Activations in the anterolateral orbitofrontal cortex tracked the relative subjective pleasantness, whereas activations in the anterior insula tracked the relative subjective unpleasantness. In contrast, in the medial and midorbitofrontal cortex activations tracked the absolute pleasantness of the stimuli. Thus, both relative and absolute subjective value signals which provide important inputs to decision-making processes about which stimulus to choose are separately and simultaneously represented in the human brain.

Introduction

In economic decision-making, the brain needs to compute the subjective value of different goods in order for choices to be guided by preferences. Reward value is represented in the orbitofrontal cortex and connected areas (Rolls, 2005; Rolls and Grabenhorst, 2008) in that neuronal activity to taste, olfactory, flavor and visual food stimuli decreases as their reward value decreases to zero during feeding to satiety (Critchley and Rolls, 1996; Rolls et al., 1989), in that orbitofrontal cortex neurons are activated from brain-stimulation reward sites (Mora et al., 1980), in that orbitofrontal cortex brain-stimulation reward is decreased by feeding to satiety (Mora et al., 1979), and in that lesions of the orbitofrontal cortex impair reinforcement-related learning (Rolls et al., 1994), the ability to judge emotional and thus reward value (Hornak et al., 1996), and the subjective emotional experience of rewards (Hornak et al., 2003). Further, activations in these areas are correlated with the amount of money won or lost on an individual trial (O'Doherty et al., 2001a), and with the pleasantness (or subjective affective value) ratings made to many classes of stimuli, including taste, olfactory, flavor, thermal and visual stimuli (Grabenhorst and Rolls, 2008; Grabenhorst et al., 2007; Kringelbach et al., 2003; Rolls et al., 2008b). However, different types of value signal may be required for different types of decisions.

Relative reward value is important when choosing between a given set of rewards. A representation of relative reward value takes into account the current reward context in that it is influenced by the value of other rewards that are available. A related psychological phenomenon is positive contrast, in which animals work harder than on average for a high reward value just at the transition between the low and high reward value (Crespi, 1942; Mazur, 1998; Rolls, 2005). One example, investigated here, is that if a pleasant odor is preceded by an unpleasant odor, the pleasant odor may be perceived as more pleasant than usual. It has been shown that neurons in the orbitofrontal cortex encode the relative reward value of a food, responding for example to a symbol that indicates an apple if it was shown in a trial block where the other food was less preferred, and not responding to the apple symbol if it was shown in a trial block with a more preferred reward (Tremblay and Schultz, 1999). In addition, macaque dopamine neurons fire much more when large vs small rewards are given (Fiorillo et al., 2003).

Absolute reward value is important for stable and consistent economic choices (Lee, 2006; Muller et al., 2007; Padoa-Schioppa and Assad, 2008), and such a representation should not be influenced by the value of other available rewards. In a test of whether the absolute value of flavor stimuli is represented in the orbitofrontal cortex, some neurons coded for the value of a food reward independently of the value of the other reward presented on a given trial, and it was suggested that transitivity, a fundamental trait of economic choice, is represented by the neuronal activity (Padoa-Schioppa and Assad, 2008).

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doi:10.1016/j.neuroimage.2009.06.045

It is unclear whether both absolute and relative value signals are expressed in the brain at the same time, and separately. The aim of the present study was to compare brain representations of absolute and relative subjective reward value, to investigate whether both are represented in brain regions such as the orbitofrontal cortex and related regions at the same time, and whether these neural representations are separable. We delivered two of a set of four odors separated by a delay of 6 s, with the instruction to rate the pleasantness of the second odor, and searched for brain regions where the activations were correlated with the absolute pleasantness rating of the second odor, and for brain regions where the activations were correlated with the difference in pleasantness of the second from the first odor, that is, with relative pleasantness.

Methods

Design

We used four odors, two pleasant (citral and vanillin) and two unpleasant (hexanoic acid and isovaleric acid). Two different odors were presented separated by 6 s on each trial, and the participants rated the subjective pleasantness and intensity of the second odor. Every possible combination of odors was presented, so that sometimes a second odor was preceded by an odor of similar pleasantness, and sometimes of different pleasantness. We were then able to show that activations in some brain regions were correlated with the relative pleasantness of the odors (as influenced by the preceding odor), and in other brain regions were related to the absolute value of the pleasantness ratings. Because these analyses were based on how subjective ratings of relative and absolute pleasantness are related to brain activations, this study directly addresses the question of how relative and absolute subjective value are represented in the brain. Contrast analyses were also performed to test whether activations to a given odor were greater if it was more pleasant than the first odor (pos diff) than if it was less pleasant (neg diff). As shown in the Results, from the ratings we were able to show that the pleasantness of a second odor was increased (relative to its average value) if it was preceded by an unpleasant odor vs a pleasant odor. Further, the unpleasantness of a second odor was greater if it was preceded by a pleasant vs an unpleasant odor.

Participants

Twelve healthy volunteers (7 male and 5 female, mean age 27) participated in the study. Ethical approval (Central Oxford Research Ethics Committee) and written informed consent from all subjects were obtained before the experiment.

Stimuli

The set of olfactory stimuli used was selected based on previous fMRI studies on olfaction (Rolls et al., 2003a). The pleasant odors were 1 M citral and 4 M vanillin. The unpleasant odors were hexanoic acid (10% v/v) and isovaleric acid (15%). The odors were made up in propylene glycol.

Stimulus delivery

A purpose-built continuous airflow ten-channel computer-controlled olfactometer was used to allow odor stimuli to be delivered in the MRI scanner (Rolls et al., 2003a). The control and metal components of the system are kept outside the scanner room, and the system is free of any auditory, tactile or thermal shifts that could cue the subject to the onset of odor delivery. The flow of clean medical air is controlled using a pressure regulator and flow meter. The air is directed using solenoid-operated valves controlled by the stimulus computer using TTL pulses to either a clean air wash bottle containing only solvent, propylene glycol, or to one of four other wash bottles each containing one odorant dissolved in the propylene glycol. Each wash bottle is connected by its own Teflon tube (to provide for low adhesion) to a single delivery nozzle placed within 1 cm of the nose to minimize dead space. The delivery nozzle provided two tubes, one for each nostril, to produce birhinal stimulation. The flow rate of the air supply was kept constant at 2 l/min such that the same minimal degree of tactile somatosensory stimulation was delivered throughout. The air line was on continuously by default, and was switched off only when the solenoid directed the clean air supply to another wash bottle so that an odorant could be delivered. This resulted in a system with no perceptible pressure change when the air was replaced during stimulus delivery by an odor for 2 s. This system was used in previous fMRI studies of human olfaction (Rolls et al., 2003a).

Experimental protocol

The experimental protocol consisted of an event-related interleaved design presenting in random permuted sequence the 12 different pairs of olfactory stimuli, which represented all possible combinations of the four olfactory stimuli in which the second and first odors were different. Each trial started at $t=0$ s with the first odor being delivered for 2 s accompanied by a visual label stating "Sniff first stimulus". There was then a 6 s period during which clean air was delivered. In this period at $t=7$ s a visual label was displayed stating "Rate stimulus". At $t=8$ s the second odor was presented for 2 s accompanied by a visual label stating "Sniff Rate stimulus". There was then a 6 s period during which clean air was delivered. At $t=16$ s the subjective ratings were made. The first rating was for the pleasantness of the second odor on a continuous (analogue) visual scale with markers from −2 (very unpleasant), through 0 (neutral), to +2 (very pleasant) at intervals of 1.0. The second rating was for the intensity of the second odor on a scale from 0 (very weak) to 4 (very intense). The ratings were made with a visual rating scale in which the subject moved the bar to the appropriate exact point on the continuous scale using a button box. (The values on this continuous scale were processed with an accuracy of 0.1 divisions on the scale.) There was 4 s for each rating. Subjects were pre-trained outside the scanner in the whole procedure and use of the rating scales. There was an inter-trial interval of 2 s. Each of the odors was presented in the second position 9 times, and the trials were delivered in a random permuted sequence. This general protocol and design have been used successfully in previous studies to investigate activations and their relation to subjective ratings in cortical areas (de Araujo et al., 2005; Grabenhorst et al., 2008a; Grabenhorst et al., 2007; Rolls et al., 2003a,b). These trials were interspersed with other trials in which decision-making was investigated as part of a separate investigation (Rolls et al., 2009b).

fMRI data acquisition

Images were acquired with a 3.0-T VARIAN/SIEMENS whole-body scanner at the Centre for Functional Magnetic Resonance Imaging at Oxford (FMRIB), where 27 T2* weighted EPI coronal slices with in-plane resolution of 3×3 mm and between plane spacing of 4 mm were acquired every 2 s ($TR=2$). We used the techniques that we have developed over a number of years (de Araujo et al., 2003; O'Doherty et al., 2001b), and as described in detail by Wilson et al. (2002) we carefully selected the imaging parameters in order to minimize susceptibility and distortion artefact in the orbitofrontal cortex. The relevant factors include imaging in the coronal plane, minimizing voxel size in the plane of the imaging, as high a gradient switching frequency as possible (960 Hz), a short echo time of 28 ms, and local shimming for the inferior frontal area. The matrix size was 64×64 and the field of view was 192×192 mm. Continuous coverage was

obtained from +62 (A/P) to −46 (A/P). A whole brain T2* weighted EPI volume of the above dimensions, and an anatomical T1 volume with coronal plane slice thickness 3 mm and in-plane resolution of 1 × 1 mm were also acquired.

fMRI data analysis

The imaging data were analysed using SPM5 (Statistical Parametric Mapping, Wellcome Trust Centre for Neuroimaging, London). Preprocessing of the data used SPM5 realignment, reslicing with sinc interpolation, normalisation to the MNI coordinate system (Montreal Neurological Institute) (Collins et al., 1994), and spatial smoothing with a 6 mm full width at half maximum isotropic Gaussian kernel. The time series at each voxel were low-pass filtered with a haemodynamic response kernel. Time series non-sphericity at each voxel was estimated and corrected for (Friston et al., 2002), and a high-pass filter with a cut-off period of 128 s was applied. In the single event design, a general linear model was then applied to the time course of activation where the onset of the second odor (at $t = 8$ s in each trial) was modelled with an impulse response function and then convolved with the canonical haemodynamic response function (Friston et al., 1994). Linear contrasts were defined to test specific effects. Time derivatives were included in the basis functions set. Following smoothness estimation (Kiebel et al., 1999), in the first stage of analysis condition-specific experimental effects (parameter estimates, or regression coefficients, pertaining to the height of the canonical HRF) were obtained via the general linear model (GLM) in a voxel-wise manner for each subject. In the second (group random effects) stage, subject-specific linear contrasts of these parameter estimates were entered into a series of one-sample *t*-tests, each constituting a group-level statistical parametric map. The correlation analyses of the fMRI BOLD (blood oxygenation-level dependent) signal with given parameters of interest (e.g. the pleasantness ratings) were performed at the second level through applying one-sample *t*-tests to the first-level subject-specific statistical parametric maps resulting from performing linear parametric modulation as implemented in SPM5. We report results for brain regions where there were prior hypotheses as described in Design, under Methods section, and applied small volume (false discovery rate) corrections for multiple comparisons (Genovese et al., 2002) with a radius corresponding to the full width at half maximum of the spatial smoothing filter used. These brain regions with prior hypotheses identified in this way were as follows: anterolateral orbitofrontal cortex [−42 42 −12] (Grabenhorst et al., 2007; Royet et al., 2003); medial orbitofrontal cortex [2 52 −18] (Rolls et al., 2003a); midorbitofrontal cortex [40 28 −8] (Royet et al., 2003); anterior insula [36 12 14] (Royet et al., 2003). In addition to the statistical criterion just described for a significant effect calculated for the peak voxel of a region of activation in an a priori defined region based on earlier findings, we used the additional statistical test (see Gottfried et al., 2002b; O'Doherty et al., 2006, 2003c) that the results reported were in global contrast and/or correlation analyses significant using the criterion of $p < 0.001$ uncorrected for multiple comparisons, and these additional statistics confirmed the same effects in the a priori regions in all cases in this paper.

To show the change in the % BOLD signal, for the areas with significant activations, we extracted from the fitted time course the event-related responses from the peak voxel for each subject. These peaks of the single-subject time courses were then averaged across subjects.

For voxels where significant correlations were found between the % BOLD signal and the ratings, we produced graphs to show how the ratings were related to the % BOLD signal. These were produced for each subject by taking the average of the BOLD response in the 3 time bins at 4, 6 and 8 s post stimulus onset (when the haemodynamic response function has high values), on each trial, and the corresponding rating. For each subject the means were calculated in discretized ranges of the rating function (e.g. −2 to −1.75, −1.75 to −1.5, etc.), and then these values were averaged across subjects.

For every brain area considered, the same analyses were performed, as follows. First, a correlation (i.e. SPM regression) analysis was performed (separately for each second odor) between the BOLD signal and the difference between the pleasantness rating of the second odor, and the mean pleasantness rating of the first odor obtained from the trials on which it was being rated. These correlations were combined across odors in the second level (group) analyses. Second, a correlation analysis was performed between the BOLD signal and the absolute pleasantness rating given to the (second) odor. Third, a contrast was performed (separately for each second odor) for all trials on which the relative difference in pleasantness for the second odor compared to the first odor was positive (pos diff) compared with when it was negative (neg diff). For all analyses the activations were measured at the time of delivery of the second odor. Fourth, a correlation analysis was performed between the BOLD signal and the intensity rating given to the (second) odor. In addition, we checked and confirmed that the results described were not due to any trial-by-trial variation in for example the pleasantness ratings and the BOLD signal, by using for the correlation analyses the mean of the rating given across trials to the second odor, and by statistically comparing the regression analyses for relative and absolute pleasantness for different brain regions. The results within the a priori regions of interest defined above are described in the paper. Activations or correlations outside the a priori regions of interest were few as shown by the global analyses over the whole brain, and are shown in the tables in the Supplementary material.

Results

Behavioural ratings of pleasantness and intensity

The ratings of the pleasantness and intensity of the four odor stimuli obtained during the neuroimaging are shown in Fig. 1. The absolute ratings of the pleasantness of the odors shown in Fig. 1a indicate, as per the design, that the citral and vanilla were rated as pleasant, and the hexanoic acid and isovaleric acid were rated as unpleasant. (The one way ANOVA indicated significant differences in pleasantness ($F_{(3,44)} = 46.3$, $p << 0.001$).) Also as per the design, the intensity ratings were relatively similar to each other, as shown in Fig. 1b. To investigate whether the subjective pleasantness of the second odor was different depending on the pleasantness of the first odor that was presented earlier in a given trial, we grouped the ratings into trials where the rating of the second odor on that trial was more pleasant than the average rating of the first odor (pos diff) (which was always different); and into trials where the second odor on that trial was less pleasant (neg diff). Fig. 1c shows that for every odor (citral, vanillin, hexanoic acid, and isovaleric acid) the rating of pleasantness of the second odor was greater if the second odor was more pleasant than the first odor (pos diff), compared to the rating given if the second odor was less pleasant than the first (neg diff). This effect, whereby the rating of pleasantness of the first odor depends on the relative pleasantness of the preceding odor, was significant in a two-way within-subjects ANOVA ($F_{(1,3)} = 15.9$, $p = 0.028$) (with one factor the pleasantness rating, and the second the odor). In contrast, in a useful control condition, the pleasantness ratings for the second odor were little affected by whether the first odor was more or less intense (Fig. 1d) ($F_{(1,3)} = 1.86$, $p = 0.27$).

The way in which the rating of the pleasantness of the second odor is influenced by the difference in pleasantness of the first is brought out in Fig. 1e. This shows for the citral odor that it was more pleasant than the mean rating to citral if the second odor (citral) was more pleasant than the first (large positive values on the abscissa for the pleasantness difference of the second odor relative to the first); and

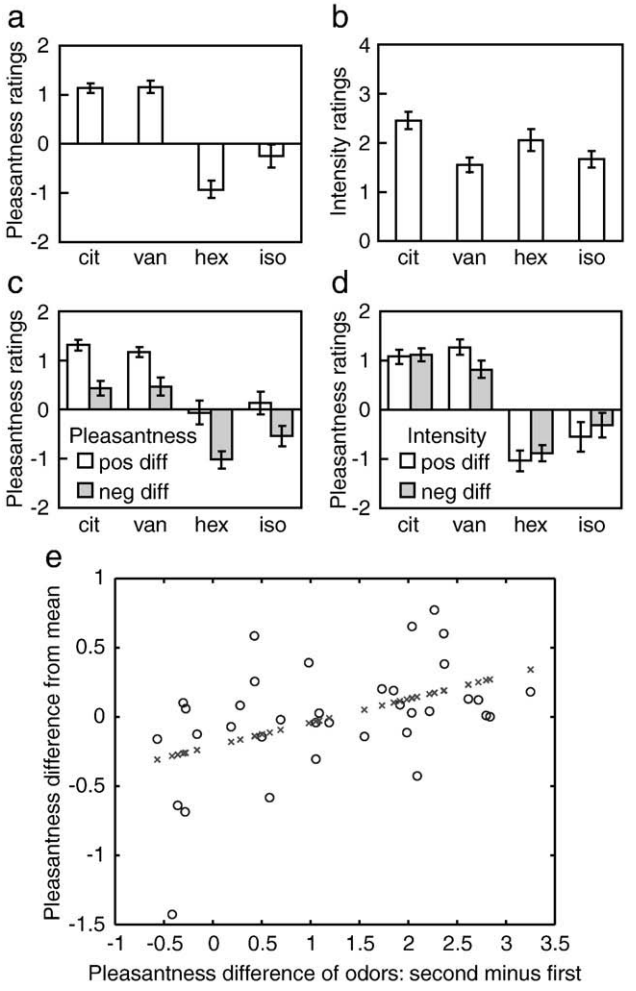

Fig. 1. Pleasantness and intensity ratings. (a) The absolute ratings of the pleasantness of the odors: cit: citral, van: vanillin, hex: hexanoic acid, iso: isovaleric acid. The mean ± sem is shown throughout. +2 is very pleasant, −2 is very unpleasant. (b) The intensity ratings of the odors were relatively similar ($F_{(3,44)} = 5.03$, $p < 0.01$). (c) The pleasantness ratings of each odor depending on whether they were more pleasant than the first odor (pos diff) or less pleasant than the first odor (neg diff). (d) The pleasantness ratings of each odor depending on whether they were more intense than the first odor (pos diff) or less intense than the first odor (neg diff). (e) The difference in the rating of the pleasantness of a citral from its mean rating as a function of how much the citral was more pleasant than the first odor (positive values on the abscissa) or was less pleasant than the first odor (negative values on the abscissa). Each point represents the average value for one subject of all trials on which the second odor (citral) was paired with one of the other three odors. The line of points shows the regression line.

was less pleasant than the mean rating to citral if the second odor was less pleasant than the first (negative values on the abscissa). (In the latter condition, if the first odor was relatively pleasant, for example vanilla, this tended to decrease the pleasantness of the second odor, the citral.) Each point in Fig. 1e represents the average value for one participant of all trials on which the second odor (citral) was paired with one of the other three odors. The correlation shown in Fig. 1e was positive and significant ($r = 0.46$, $p < 0.005$). The slope was 0.17, showing that the change in the pleasantness rating for the second odor that can be produced is 17% of the difference in the pleasantness of the first and second odors in this case. A significant relation was found when the data from all four odors in the second condition were included ($r = 0.18$, $p = 0.0275$, slope = 0.033, intercept = 0.00).

We note that these measures of the relative value of an odor being influenced by the reward value of a previous odor were based on subjective ratings. They are supported by findings that the choices made of an odor were also influenced by the pleasantness of the preceding odor on other trials included in the same investigation in which choices between the odors were made (Rolls et al., 2009a,b). In particular, the pleasant odor citral was chosen on 84 ± 4% (sem) of trials when it was preceded by an unpleasant odor, and on 39 ± 11% when it was preceded by an equally or slightly more pleasant odor (vanillin). The pleasant odor vanillin was chosen on 95 ± 2% of trials when it was preceded by an unpleasant odor, and on 70 ± 11% when it was preceded by an equally/slightly less pleasant odor (citral). The unpleasant odor hexanoic acid was chosen on 8 ± 6% or trials when it was preceded by a pleasant odor (vanillin or citral), and on 26 ± 10% when it was preceded by an equally/slightly less pleasant odor (isovaleric acid). Finally, isovaleric acid was chosen on 13 ± 6% or trials when it was preceded by a pleasant odor, and on 44 ± 13% or trials when it was preceded by an unpleasant odor (Rolls et al., 2009a,b).

The fMRI analyses focussed on brain regions where for a given second odor the activations were correlated with the absolute pleasantness rating of the second odor, and on brain regions where the activations were correlated with the difference in pleasantness of the second from the first odor, which is termed relative pleasantness.

Anterolateral orbitofrontal cortex: relative pleasantness

Fig. 2a shows a region of the anterolateral orbitofrontal cortex where there was a correlation between the BOLD signal and the relative pleasantness of the second odor compared to the first odor. This was shown in an SPM correlation analysis where the regressor was the difference in pleasantness between the ratings (the second minus the first) on a given trial [−44 48 −8] ($z = 3.35$, $p = 0.015$). The nature of the relation is illustrated in more detail by the analysis in Fig. 2b which shows the relation between the BOLD signal and the relative pleasantness of the second odor compared to the first. Fig. 2b shows that there was a positive correlation between the BOLD signal in this brain region measured at the time of the second odor and the difference in the pleasantness of the second odor compared to the first (i.e. positive values on the abscissa are when the second odor is more pleasant) ($r = 0.89$, $df = 14$, $p = 8 \times 10^{-6}$).

For comparison, Fig. 2c shows that there was only a weak correlation of the BOLD signal in this region with the absolute value of the pleasantness ratings that were given to the second odor ($r = 0.56$, $df = 15$, $p = 0.025$). (An SPM regression analysis between the BOLD signal and the absolute value of the pleasantness of the second odor did reveal a significant effect in this region [−40 48 −4] ($z = 3.14$, $p = 0.013$), though as shown by a comparison of Figs. 2b and c, the BOLD signal was more clearly related to the difference in pleasantness of the second from the first odor, rather than to the absolute value of the pleasantness of the odors, which was high for citral and vanillin, and negative for hexanoic and isovaleric. We show later, in Fig. 5a, a significant dissociation from other brain areas where the activations reflect the absolute value of the pleasantness.) An SPM regression analysis did not show any correlation with the intensity ratings in this brain area.

These findings were supported by a contrast analysis of all trials on which the relative difference in pleasantness for the second odor compared to the first odor was positive (pos diff) contrasted with when it was negative (neg diff). This contrast revealed significant effects in the anterior lateral orbitofrontal cortex at [−38 48 −12] ($z = 2.78$, $p = 0.031$) as shown in Fig. 3a (circle). All activations shown in this paper were measured at the time of presentation of the second odor. (Similar effects were found in analyses where the first odor was included as a regressor of no interest: [−38 48 −12] $z = 3.14$, $p = 0.009$.) It is important in this contrast that the activations used were always for the same odor (citral, vanillin, hexanoic or isovaleric acid), with the only difference that the odor was more pleasant than the one that had preceded it (pos diff), or was less pleasant than the one that had preceded it (neg diff). Fig. 3b shows that for each odor this region of the anterolateral orbitofrontal cortex was more strongly activated (as indicated by the % BOLD response) by the second odor

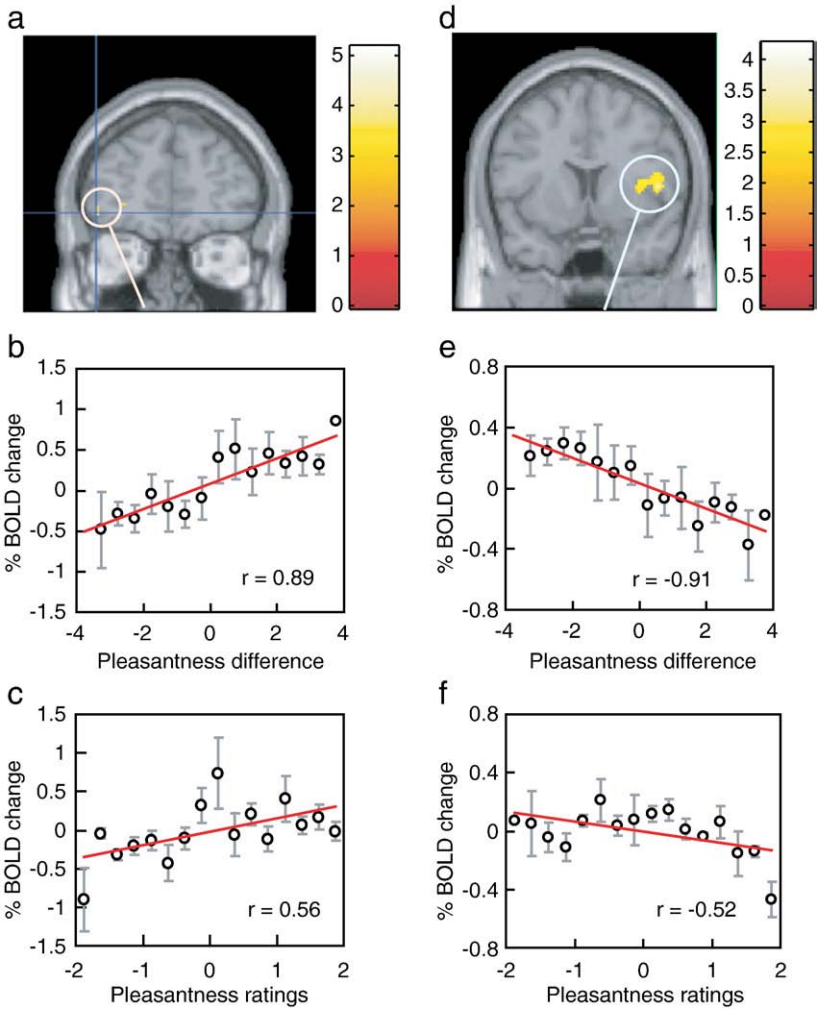

Fig. 2. (a–c) Relative pleasantness: positive correlation between the BOLD signal and the difference in pleasantness of the second odor compared to the first odor. a. A significant correlation was found in the anterior lateral orbitofrontal cortex at [−44 48 −8] ($z=3.35$, $p=0.015$) (circled). (b) There was a positive correlation between the BOLD signal in this brain region measured at the time of the second odor and the difference in the pleasantness of the second odor compared to the first (i.e. positive values on the abscissa are when the second odor is more pleasant) ($r=0.89$, $df=14$, $p=8\times10^{-6}$). (c) A weaker correlation of the BOLD signal in this region with the absolute value of the pleasantness ratings that were given to the second odor was found ($r=0.56$, $df=15$, $p=0.025$). (d–f) Relative unpleasantness: negative correlation between the BOLD signal and the difference in pleasantness of the second odor compared to the first odor. d. A significant negative correlation was found in the anterior insular/frontal opercular cortex (circled). The peak of the effect lay in the frontal operculum [46 14 16] ($z=3.61$, $p=0.007$) and extended into the anterior insular cortex with additional peaks [38 10 10] $z=2.65$, $p=0.019$ and [30 22 4] $z=3.59$, $p=0.006$. (e) There was a negative correlation between the BOLD signal in this brain region measured at the time of the second odor and the difference in the pleasantness of the second odor compared to the first (i.e. positive values on the abscissa are when the second odor is more pleasant) ($r=-0.91$, $df=14$, $p=3\times10^{-6}$). (f) There was a weaker correlation of the BOLD signal in this region with the absolute value of the pleasantness ratings that were given to the second odor ($r=-0.52$, $df=15$, $p<0.05$).

when the second odor was rated as more pleasant (pos diff) compared to when it was rated as less pleasant (neg diff) ($t_{11}=4.5$, $p<10^{-4}$).

Thus activations in the anterolateral orbitofrontal cortex were greater to an odor if it was more pleasant than the first odor, and smaller if it was less pleasant than the first odor.

Anterior insular/frontal opercular cortex: relative unpleasantness

Fig. 2d shows a region of the anterior insular/frontal opercular cortex where there was a correlation between the BOLD signal and the relative unpleasantness of the second odor compared to the first odor. This was shown in an SPM correlation analysis where the regressor was the difference in pleasantness between the ratings (the second minus the first) on a given trial ([46 14 16] ($z=3.61$, $p=0.007$). The peak of the effect lay in the frontal operculum [46 14 16] ($z=3.61$, $p=0.007$) and extended into the anterior insular cortex with additional peaks [38 10 10] $z=2.65$, $p=0.019$ and [30 22 4] $z=3.59$, $p=0.006$. (Similar effects were found in analyses where the first odor was included as a regressor of no interest: [48 14 8] $z=2.71$, $p=0.041$.) The nature of the relation is revealed in more detail by the analysis in Fig. 2e which shows the relation between the BOLD signal and the relative pleasantness of the second odor compared to the first. Fig. 2e shows that there was a negative correlation between the BOLD signal in this brain region measured at the time of the second odor and the difference in the pleasantness of the second odor compared to the first (i.e. positive values on the abscissa are when the second odor is more pleasant) ($r=-0.91$, $df=14$, $p=3\times10^{-6}$).

For comparison, an SPM regression analysis between the BOLD signal and the absolute value of the pleasantness of the second odor did not reveal a significant effect in this region. Consistently, Fig. 2f shows that there was only a weak (negative) correlation of the BOLD signal in this region with the absolute value of the pleasantness ratings that were given to the second odor ($r=-0.52$, $df=15$, $p<0.05$). An SPM regression analysis did not show any correlation with the intensity ratings in this brain area.

These findings were supported by a contrast analysis of all trials on which the relative difference in pleasantness for the second odor compared to the first odor was negative (neg diff) contrasted with when it was positive (pos diff). This contrast revealed significant

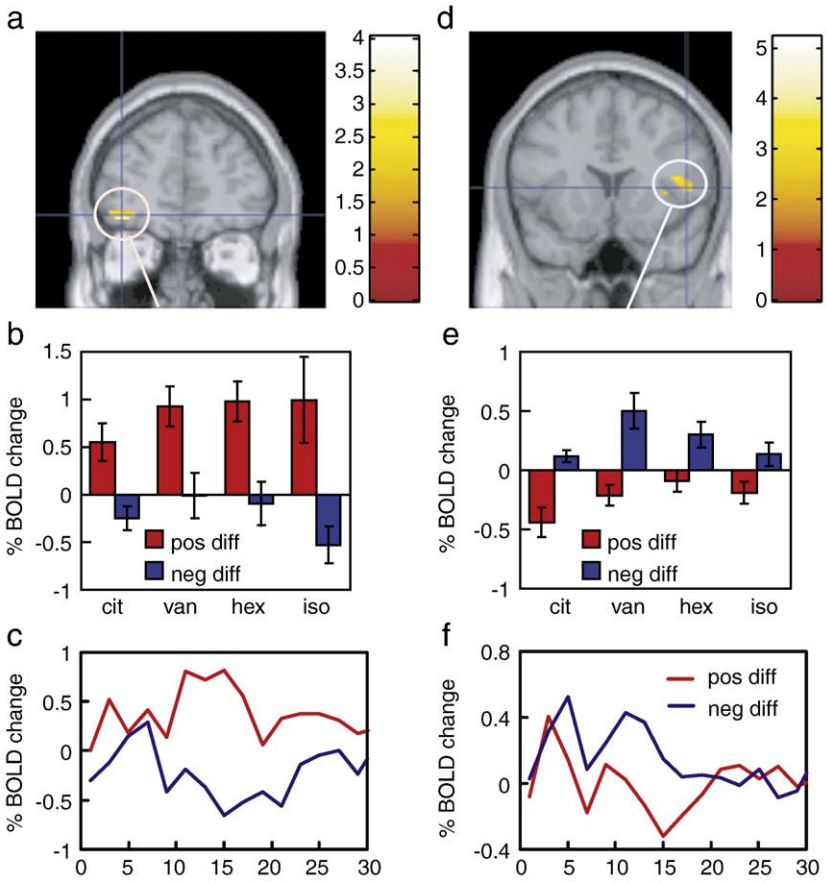

Fig. 3. (a–c) Relative pleasantness. (a) A contrast of all trials on which the relative difference in pleasantness for the second odor compared to the first odor was positive (pos diff) contrasted with when it was negative (neg diff). Significant effects were found in the anterior lateral orbitofrontal cortex at [−38 48 −12] ($z=2.78$, $p=0.031$) (circled). (b) For each odor this region was more strongly activated (as indicated by the % BOLD response) by the second odor when the second odor was rated as more pleasant than the first odor (pos diff) compared to when it was rated as less pleasant (neg diff) ($t_{11}=4.5$, $p<10^{-4}$). (c) Time courses of the effects for the anterior lateral orbitofrontal cortex for the trials on which the relative difference in pleasantness for the second odor compared to the first odor was positive (pos diff) compared with when it was negative (neg diff). The time courses were extracted as described in the Methods. (d–f) Relative unpleasantness. (d) A contrast of all trials on which the relative difference in pleasantness for the second odor compared to the first odor was negative (neg diff) contrasted with when it was positive (pos diff) revealed significant effects in the anterior insular cortex at [42 18 12] ($z=3.12$, $p=0.030$) (circled). (e) This insular region was more strongly activated (as indicated by the % BOLD response) by the second odor when the second odor was rated as less pleasant than the first (neg diff) compared to when it was rated as more pleasant (pos diff) ($t_{11}=4.7$, $p<10^{-4}$). (f) Time courses of the effects for the anterior insular cortex for the trials on which the relative difference in pleasantness for the second odor compared to the first odor was positive (pos diff) compared with when it was negative (neg diff).

effects in the anterior insular cortex at [42 18 12] ($z=3.12$, $p=0.030$) as shown in Fig. 3d (circled). Fig. 3e shows that for each odor this region of the anterior insular cortex was more strongly activated (as indicated by the % BOLD response) by the second odor when the second odor was rated as less pleasant (neg diff) compared to when it was rated as more pleasant (pos diff) ($t_{11}=4.7$, $p<10^{-4}$). (As shown in Fig. 3e the activations in this region related to differences of pleasantness were different particularly for the positive odors, but we emphasize that the results of the SPM regression analysis shown in Figs. 2e and f were based on all odors.)

Thus activations in the anterior insular cortex were greater to an odor if it was more unpleasant than the first odor, and smaller if it was more pleasant than the first odor. This brain region thus reflected conditions in which the second odor was less pleasant than the first odor.

Medial orbitofrontal cortex: absolute pleasantness

In contrast to the previous brain areas, some brain regions had activations that were much more strongly related to the absolute value of the pleasantness rating, than to the relative pleasantness of the second compared to the first odor. An example is the medial orbitofrontal cortex.

Fig. 4a (pink circles) shows that in an SPM correlation analysis there was a parametric modulation of the BOLD signal related to the absolute value of the pleasantness ratings given to the (second) odor in the medial orbitofrontal cortex [−2 50 −20] ($z=3.27$, $p=0.029$). Fig. 4d shows that the BOLD signal was clearly related to the pleasantness ratings ($r=0.78$, $df=15$, $p<10^{-4}$).

On the other hand, in the SPM analysis the contrast posdiff–negdiff (and the reverse contrast) showed no effects that reached significance in the medial orbitofrontal cortex. This evidence that the relative pleasantness difference is not so important for this brain region is illustrated further in Fig. 4b, which shows that in the medial orbitofrontal cortex there were no significant differences in the activations produced by the second odor depending on whether the first odor was more pleasant or less pleasant ($t_{11}=1.9$, $p>0.05$). Consistently, an SPM correlation analysis in which the regressor was the difference in the pleasantness of the second odor compared to the first showed no significant effects in this region, and as shown in Fig. 4c, there was little correlation between the BOLD signal and the difference in the pleasantness ratings ($r=0.25$, $df=12$, $p=0.42$). An SPM correlation analysis did not show any correlation with the intensity ratings in this brain area.

Midorbitofrontal cortex: absolute pleasantness

Activations in the midorbitofrontal cortex were also more closely related to the absolute value of the pleasantness of the odors than to

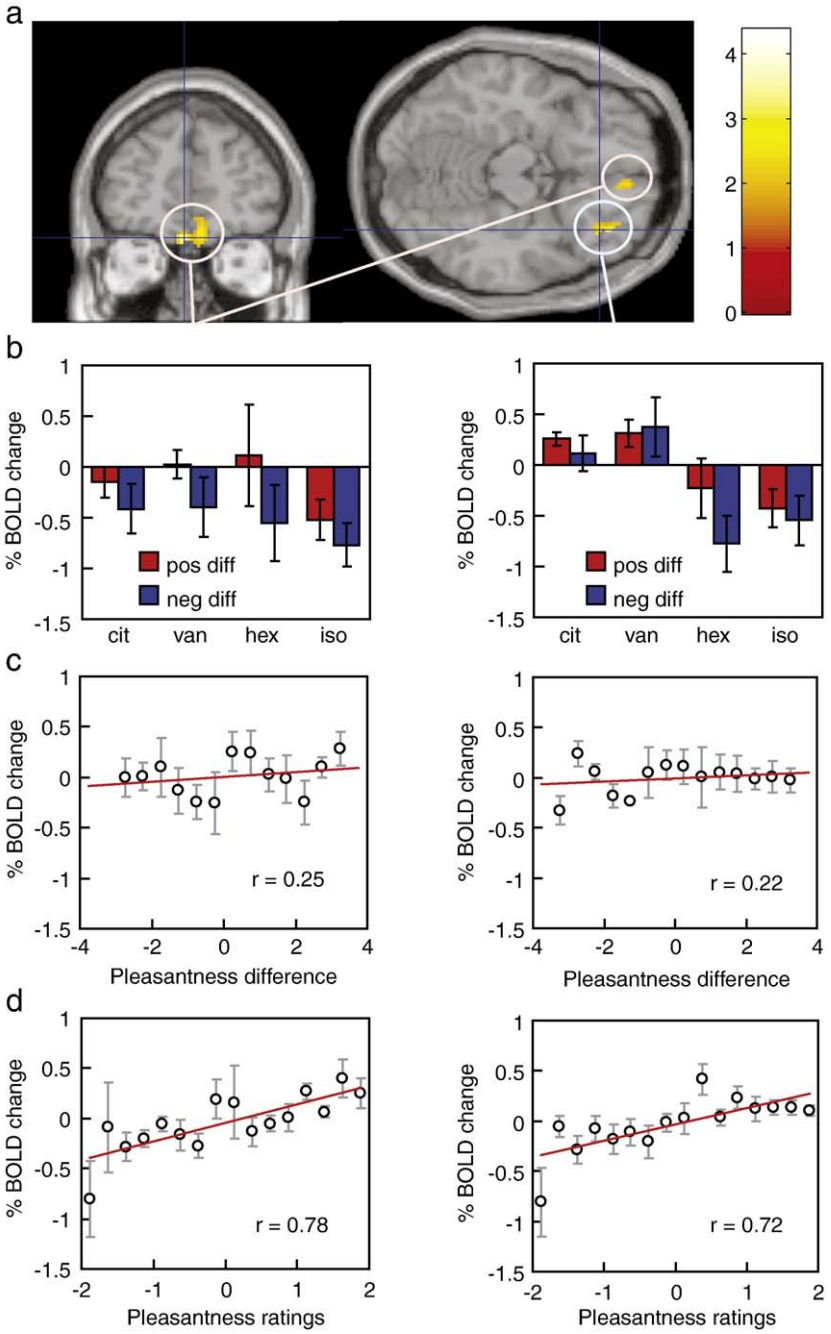

Fig. 4. (a) An SPM correlation analysis showed a parametric modulation of the BOLD signal related to the absolute value of the pleasantness ratings given to the (second) odor in the medial orbitofrontal cortex (pink circles) [−2 50 −20] ($z=3.27$, $p=0.029$); and in the midorbitofrontal cortex (blue circle) [40 36 −12] ($z=3.13$, $p=0.024$). (b–d) Medial orbitofrontal cortex. b. No significant differences in the activations produced by the second odor depending on whether the first odor was more pleasant or less pleasant were found ($t_{11}=1.9$, $p>0.05$). (c) There was little correlation between the BOLD signal and the difference in the pleasantness ratings ($r=0.25$, $df=12$, $p=0.42$). (d) The correlation between the BOLD signal and the pleasantness ratings ($r=0.78$, $df=15$, $p<10^{-4}$). (e–g) Midorbitofrontal cortex. (e) No significant differences in the activations produced by the second odor depending on whether the first odor was more pleasant or less pleasant were found ($t_{11}=1.2$, $p>0.1$). (f) There was little correlation between the BOLD signal and the difference in the pleasantness ratings ($r=0.22$, $df=13$, $p=0.45$). g. The correlation between the BOLD signal and the pleasantness ratings ($r=0.7$, $df=15$, $p=0.002$).

the relative pleasantness of the odor as influenced by whether the preceding odor was more or less pleasant.

Fig. 4a (blue circle) shows that in an SPM correlation analysis there was a parametric modulation of the BOLD signal related to the absolute value of the pleasantness ratings given to the (second) odor in the midorbitofrontal cortex [40 36 −12] ($z=3.13$, $p=0.024$). Fig. 4g shows that the BOLD signal was clearly related to the pleasantness ratings ($r=0.72$, $df=15$, $p=0.002$).

On the other hand, in the SPM analysis the contrast posdiff–negdiff (and the reverse contrast) showed no effects that reached significance in the midorbitofrontal cortex. This evidence that the relative pleasantness difference is not so important for this brain region is illustrated further in Fig. 4e, which shows that in the midorbitofrontal cortex there were no differences in the activations produced by the second odor depending on whether the second odor was more pleasant (pos diff) or less pleasant (neg diff) ($t_{11}=1.2$, $p>0.1$). Consistently, an SPM correlation analysis in which the regressor was the difference in the pleasantness of the second odor compared to the first showed no significant effects in this region, and as shown in Fig. 4f, there was little correlation between the BOLD signal and the

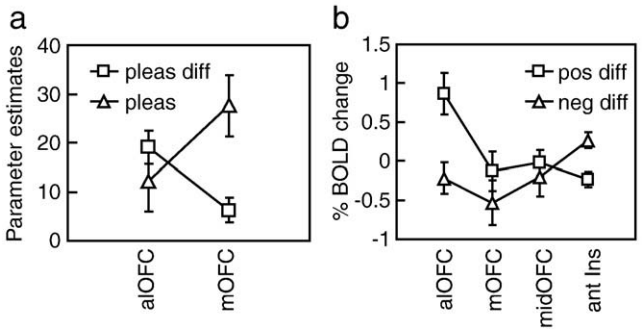

Fig. 5. (a) Parameter estimates (mean ± sem) for the correlation analyses for the anterior lateral orbitofrontal cortex (alOFC) and medial orbitofrontal cortex (mOFC) regions shown in Figs. 2a–c and 4 showing that activations in the alOFC were more related to relative pleasantness, and in the medial OFC to absolute pleasantness. The dissociation was significant, as shown by the interaction term ($F_{(1,11)} = 17.0$, $p = 0.002$). (b) BOLD signal changes for different brain regions (alOFC — anterior lateral orbitofrontal cortex; mOFC — medial orbitofrontal cortex; midOFC — midorbitofrontal cortex; ant Ins — anterior insula) for, averaged across all odors (± sem), the pos diff condition (where the second odor was more pleasant than the first) and the neg diff condition (where the second odor was less pleasant than the first).

difference in the pleasantness ratings ($r = 0.22$, $df = 13$, $p = 0.45$). An SPM correlation analysis did not show any correlation with the intensity ratings in this brain area.

Dissociations between activations in different brain areas

The evidence described above indicates that some brain areas have activations that reflect more whether a particular odor is more or less pleasant than the odor that preceded it, and thus represent relative pleasantness, rather than the absolute value of the pleasantness of the odor (which was rated by the subjects on every trial for the second odor that was presented). These areas include the anterolateral orbitofrontal cortex (relative pleasantness), and the anterior insula (relative unpleasantness). Other brain areas had activations that were more closely related to the absolute value of the pleasantness than to the relative pleasantness of an odor as influenced by which odor had preceded it. These areas included the mid and medial orbitofrontal cortex.

To test for the significance of the dissociation between brain regions where activations reflect relative pleasantness vs brain regions where activations reflect absolute pleasantness we compared the parameter estimates for the correlations with relative vs absolute pleasantness in different brain regions. Fig. 5a shows parameter estimates (mean ± sem) for the anterior lateral orbitofrontal cortex (alOFC) and medial orbitofrontal cortex (mOFC) regions shown in Figs. 2a–c and 4, showing that activations in the alOFC were more related to relative pleasantness, and in the medial OFC to absolute pleasantness. The dissociation was significant, as shown by the interaction term ($F_{(1,11)} = 17.0$, $p = 0.002$).

To further analyse these findings, Fig. 5b shows the change in the BOLD signal for trials on which a test odor was more pleasant than the preceding odor (pos diff) or less pleasant (neg diff) for different brain regions. The BOLD signals reflect the difference in pleasantness in the anterolateral orbitofrontal cortex and anterior insula, but much less in the medial and midorbitofrontal cortex. To test statistically whether there were dissociations between the brain areas in the way in which they responded to the second odor on the two different trial types, we performed a two-factor ANOVA on the % BOLD peaks (obtained from the statistically significant SPM analyses described above) where one factor was the brain area, and the other factor was the difference in pleasantness between the first and the second odor (positive or negative). Significant interactions were found in a number of these ANOVAs, including the lateral orbitofrontal cortex vs medial orbitofrontal cortex ($p = 0.036$); lateral orbitofrontal cortex vs midorbitofrontal cortex ($p = 0.002$); lateral orbitofrontal cortex vs anterior insula ($p < 10^{-4}$); anterior insula vs medial orbitofrontal cortex ($p = 0.004$); anterior insula vs midorbitofrontal cortex ($p = 0.001$); but not for medial vs midorbitofrontal cortex ($p > 0.3$). (A Fisher exact probability test (Fisher, 1932; Littell and Folks, 1971; Zaykin et al., 2002) showed that this pattern of results would have occurred by chance with $p < 10^{-10}$.) The findings show that there are differences between brain areas in how they respond to the second odor on trials where the first odor was more pleasant relative to the response to the second odor when the first odor was less pleasant.

We also checked whether the global analyses using the criterion of $p < 0.001$ uncorrected revealed other brain regions in which there were activations related to the pleasantness ratings, and where activations had significant effects in the main contrast used to define areas in this paper, pos diff–neg diff and its opposite, and found no brain areas other than those described with such effects in the global analyses. We also performed a finite impulse response (FIR) analysis to explicitly test for differences during earlier periods of the trial including the first odor period and the delay period and the results confirmed that our findings were attributable and specific to the period of the second odor (see Supplementary material).

Pyriform cortex: correlation with subjective intensity not pleasantness

To check whether relative pleasantness, or absolute pleasantness, is represented at earlier stages of cortical processing, we examined activations found in this investigation in the pyriform (primary olfactory) cortex. No correlations with relative or absolute pleasantness ratings were found, but a correlation with the rated subjective intensity of the odor presented on each trial was found ([32 8 −16] $z = 3.42$, $p = 0.014$). There was a positive correlation between the % change in the BOLD signal and the rated subjective intensity of the odor ($r = 0.86$, $p = 2 \times 10^{-5}$). These results are illustrated in the Supplementary material, and are in line with previous findings that intensity, and attention to intensity, but not pleasantness, is typically reflected in activations in the pyriform cortex (Anderson et al., 2003; Rolls and Grabenhorst, 2008; Rolls et al., 2003a, 2008a). The area in which this was found corresponds to what has been designated as posterior pyriform cortex in humans (with anterior pyriform cortex located close to $y = 12$) (Gottfried et al., 2002a), though its exact correspondence to the distinction (Haberly, 2001) made in rodents of posterior vs anterior pyriform cortex is not yet known.

Discussion

A key finding of this study is that simultaneous and separate neural representations of the relative reward value and the absolute reward value of stimuli exist in the human orbitofrontal cortex. Relative reward value was represented in the anterolateral orbitofrontal cortex. Relative negative reward value was represented in the anterior insula. Absolute reward value and its subjective correlate absolute pleasantness were represented in the medial and midorbitofrontal cortex.

The representations were simultaneous in that both the relative and the absolute value were influencing behaviour on every trial, and were evident on each trial in the brain activations described. The time course of the neuronal decision-making within a trial is on a timescale of tens to hundreds of milliseconds, and how this is affected by the difficulty of the choice, is now starting to be understood, and occurs at a finer timescale than the processes described here (Rolls and Deco, 2010; Rolls et al., 2009a). However, absolute and relative reward value were simultaneously represented in the brain in the sense that both types of representations were present in a given trial, and could thus potentially provide inputs for making a value-based choice on that trial. The findings help to reconcile neurophysiological studies with

differing results (Padoa-Schioppa and Assad, 2008; Tremblay and Schultz, 1999) by showing that both absolute and relative reward value are represented in the orbitofrontal cortex. The findings on a representation of absolute olfactory reward value are complemented by the finding of representations of absolute monetary reward value in the medial orbitofrontal cortex (O'Doherty et al., 2001a). In addition to the absolute value of olfactory and monetary reward, the absolute value of taste, flavor, thermal and visual rewards are represented in the medial and midorbitofrontal cortex (Grabenhorst and Rolls, 2008; Grabenhorst et al., 2007; Kringelbach et al., 2003; O'Doherty et al., 2003b; Rolls, 2005, 2008b; Rolls and Grabenhorst, 2008; Rolls et al., 2008b), and there is growing acceptance that the orbitofrontal cortex represents reward value (Lee, 2006; Lee et al., 2007; Muller et al., 2007).

The findings on a representation of relative reward value are complemented by the finding that activations in the ventromedial prefrontal cortex to the same perceptual stimulus were greater when the stimulus predicted the more valuable of two monetary rewards than when it predicted the less valuable (i.e. a representation of relative reward value), though absolute reward value was not investigated in that study (Elliott et al., 2008). The results are also complemented by a study of absolute and relative monetary loss, which identified a region of mid/lateral orbitofrontal cortex that was related to relative loss in a counterfactual design (Fujiwara et al., 2008).

In this study, activations related to relative pleasantness were found in the anterolateral orbitofrontal cortex [−38 48 −12], and there was a weak positive correlation with the (absolute value of) the pleasantness ratings at this site (Fig. 2c). Support for some role of the anterolateral orbitofrontal cortex in reward processing is that in an investigation with hedonically complex odor stimuli that included positive and negative components, activations were correlated with subjective pleasantness in the anterolateral orbitofrontal cortex [40 52 −6] (Grabenhorst et al., 2007). Further, activations to pleasant odors (but not to unpleasant odors) have been reported in the anterolateral orbitofrontal cortex [−42 42 −12] (Royet et al., 2003). In addition, in a monetary reward/loss task, activations in the anterolateral orbitofrontal cortex were related to reward-loss [−39 42 −15] (O'Doherty et al., 2003a). In a previous study, activations were correlated with the unpleasantness of 6 odors in different parts of the lateral orbitofrontal cortex (at [−20 54 −14] and [−16 28 −18]) (Rolls et al., 2003a).

We also found that activations in the anterior insula were related to relative unpleasantness, as shown in Figs. 2 and 3. In addition, there was a weak negative correlation with the absolute value of the pleasantness ratings in the anterior insula (Fig. 2f), and in a previous study with a larger set of odors (3 pleasant and 3 unpleasant odors), activations produced by unpleasant odors were significant in the anterior insula at [45 15 −9] (Rolls et al., 2003a) (cf. Wicker et al., 2003). Consistently, other aversive events can activate the anterior insula, including the omission of an expected monetary reward (i.e. frustrative non-reward) (Abler et al., 2005), the expectation of low monetary reward outcomes (i.e. low expected value), and the uncertainty of reward (Rolls et al., 2008c), and risk prediction and risk prediction error (Preuschoff et al., 2008). The insula may be activated by these aversive events at least partly in relation to its role in sensing visceral activity, and in producing autonomic responses (Craig, 2002, 2009; Critchley, 2005; Critchley et al., 2004), some of which may be larger to aversive stimuli, because of computations that include those described here. For example, activations in the anterior insula are related to judgements of heartbeats (Critchley et al., 2004) and the representation of changes in electrodermal activity (Critchley et al., 2000). The insula has forward projections to the orbitofrontal cortex (Price, 2006), and there will be corresponding backprojections, but the present results suggest that the functions of these regions in relative subjective value are different, with relative pleasantness represented in the orbitofrontal cortex, and relative unpleasantness in the insula. (In addition, we note that the amygdala has previously been implicated in olfactory processing (Anderson et al., 2003.) In the present study no effects for relative or absolute subjective value were found in the amygdala even at lower statistical thresholds, though it could be of interest to investigate this further, as by optimizing the shimming on the orbitofrontal cortex to increase signal from that region, there can be a tendency to reduce the signal in some parts of the medial temporal lobe.)

Why might it be useful and adaptive for the brain to represent both absolute value and relative value? The utility of representing absolute value for decision-making is that this is closely related to transitivity, a property of economic choice, in which if the reward value of A>B, and of B>C, then when a choice is made later, A will be chosen over C (Glimcher et al., 2005; Padoa-Schioppa and Assad, 2008; Tversky, 1969). Accordingly a representation of value that is invariant with respect to the current reward context provides a foundation for establishing stable preferences and consistent choice behaviour (Padoa-Schioppa and Assad, 2008). Further, when temporal discounting (the rate at which reward value decreases as a function of the delay until the reward is given) is evaluated in 'discounted utility' theory the calculations are performed with respect to the current absolute value of the goods (Doya, 2008; Kable and Glimcher, 2007). However, a representation of relative value may be useful in decision-making, for example in helping to make a choice as part of a decision-making mechanism, in which one of two rewards must be chosen over the other on an individual trial. In this situation, it may be helpful to allow the firing rates to increase to the more valued option, and to decrease to the other, as a result of competitive interactions in attractor networks that could help to make choice decisions (Deco and Rolls, 2006; Deco et al., 2009; Rolls, 2008b; Rolls and Deco, 2010; Rolls et al., 2009a; Wang, 2002). Having an overshoot of the relative reward value, as described here and as found in positive contrast (Crespi, 1942; Mazur, 1998; Rolls, 2005), may be a useful heuristic built into the brain that helps local hill-climbing up reward gradients by helping an organism lock on well to a more valuable goal if it has recently become better than other options. Conversely negative contrast in which a reward becomes transiently relatively undervalued after the reward value has decreased may be useful in helping organisms to unlock from a recently devalued goal, and this may encourage the organism to explore the environment for other alternative goals.

A neuronal mechanism that might implement relative reward could be that described above, an attractor network in which the inputs are the two rewards to be compared. But to implement the positive contrast effects over delays as in the experiment described here, a neuronal mechanism might involve some adaptation. In this situation, if there is overlap in the representations of two successive rewards, then there will be less activation to the second reward if it is preceded by another reward. On the other hand, if the reward is preceded by a punisher with no overlap in the representation, then the response to the reward will be large because there will be no adaptation of the reward representation. A system that does not show these contrast effects might have very selective tuning for different rewards, so that there is little overlap in the representation of the first and second rewards.

A strength of the present study is that it directly measures subjective value, by using subjective ratings. This is in contrast to alternative designs in which subjective value is not measured directly, but is inferred from choices made, or is taken to be monotonically related to for example monetary face value (Elliott et al., 2008; Fujiwara et al., 2008; Kable and Glimcher, 2007; Plassmann et al., 2007; Rangel et al., 2008). The present study showed that in some brain regions the activations were linearly related to a measure of relative subjective value (Fig. 2), and in other regions were linearly related to absolute subjective value (Fig. 4) where subjective value was assigned individually by each participant on a trial-by-trial basis. We note that subjective value is closely related to subjective emotional

feelings, and that there are several different systems involved in behavioural choice, only some of which will correlate with subjective value (Rolls, 2005; Rolls, 2008a). Further, we note that when decisions involving choice are taken, it is important to take into account the costs as well as the benefits (Lee et al., 2007). Indeed, we have argued that the evidence that enters an attractor network that makes a choice between rewards must take into account the cost of obtaining each reward, so that the input to the choice network is in fact the net value (i.e. the reward − the cost) for each of the possible choices (Rolls, 2009; Rolls and Grabenhorst, 2008).

An interesting aspect of the findings is that in areas that represent the relative value of a stimulus, there is also a consistent though weaker relation to absolute value. Thus in a region that represents relative pleasantness, (e.g. the anterolateral orbitofrontal cortex), there is a weaker correlation of brain activations with absolute pleasantness, and in a brain area that represents relative unpleasantness (e.g. the anterior insula), there is a weaker correlation with absolute unpleasantness. Thus the rule appears to be that relative value is represented in a region with some correlation with absolute value with the same sign. This may reflect the fact that in order to compute relative pleasantness, some evidence on the absolute pleasantness of the stimuli being compared is needed. Consistent with this point, during decision-making about vibrotactile stimuli, neurons in the ventral premotor cortex reflect at first the second stimulus, and then represent whether the second stimulus is higher or lower in frequency than the first (Romo et al., 2004).

The findings reported here indicate that representations of the reward value of olfactory stimuli in the orbitofrontal cortex can be influenced by the context in which the stimuli are presented, that is what other rewards are available at the same time. This is consistent with previous findings which showed that cognitive, linguistic level, processing can modulate neural responses to the identical olfactory, taste, or flavor stimuli in the orbitofrontal cortex, and that these activations track corresponding changes in subjective pleasantness (de Araujo et al., 2005; Grabenhorst et al., 2008a). Further, paying selective attention to the pleasantness vs the intensity of olfactory and taste stimuli can influence how the orbitofrontal cortex responds to these stimuli (Grabenhorst and Rolls, 2008; Rolls et al., 2008a). It has also been shown that activations to a bitter taste stimulus in different parts of the insula can be attenuated when the taste stimulus is preceded by a visual symbol that has been associated with a lower concentration of the taste (Nitschke et al., 2006). Together, these findings indicate that representations of affective value in the orbitofrontal cortex and anterior insula can be influenced by processing related to cognition, selective attention, and expectancy. Part of the significance of the present findings is that they show that some of these representations can also be influenced by the current reward context, which may be important in economic decision-making when the availability of other goods has to be taken into account. This type of relative reward processing, as well as the representation of absolute reward value shown also by neuronal recordings (Critchley and Rolls, 1996; Padoa-Schioppa and Assad, 2006; Rolls et al., 1989), and the negative reward prediction error computation by neurons found in the orbitofrontal cortex (Rolls and Grabenhorst, 2008; Thorpe et al., 1983), may contribute to the reward-related decision-making impairments that follow damage to the orbitofrontal/ventromedial prefrontal cortex in humans (Bechara et al., 1996; Hodges, 2001; Hornak et al., 2003, 2004; Rahman et al., 1999; Rolls, 1999, 2005; Rolls et al., 1994; Wallis, 2007).

Representing relative value is potentially important in reaching a choice between rewards (Rolls and Grabenhorst, 2008). Recently, we have been able to show that the ventromedial prefrontal cortex area 10 is more strongly activated in choice decision-making, whereas the orbitofrontal and pregenual cingulate cortices which project to medial area 10 provide a representation on a continuous value scale (Grabenhorst et al., 2008b; Rolls and Grabenhorst, 2008). Consistent with this idea, a recent study found a representation of relative value in the ventromedial prefrontal cortex in a monetary task (Elliott et al., 2008). To investigate interactions between these systems, it might be of interest to investigate whether there is functional coupling between the ventromedial prefrontal cortex area 10 and the orbitofrontal cortex regions described here during the performance of this type of task.

The findings that the activations of some brain areas, and related psychophysical effects, are influenced by the value of the stimulus that has immediately preceded it has many important implications. For example, in psychophysical testing of the pleasantness of stimuli, reliable measurements for a given stimulus are only likely to be found when careful control is provided of the pleasantness of preceding stimuli. Further, reward contrast, and changes to a better level of reward even somewhat independently of absolute reward level, may be important factors in subjective well-being and happiness, and this may be important in helping to understand mood states in what are at first glance environments in which very different absolute levels of reward are available (Rolls, 2005). Being sensitive to relative reward value may, as suggested above, be a useful heuristic in local reward gradient climbing, and this adaptive value may underlie some of the processing described in this investigation.

Acknowledgments

F.G. was supported by the Gottlieb-Daimler- and Karl Benz-Foundation, and by the Oxford Centre for Computational Neuroscience. The investigation was performed at the Centre for Functional Magnetic Resonance Imaging of the Brain (FMRIB) at Oxford University, and we thank Irene Tracey, Peter Jezzard, and Stuart Clare for their help. The investigation was supported by the Oxford Centre for Computational Neuroscience.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2009.06.045.

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