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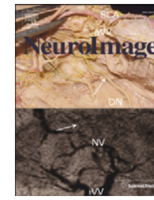

The neural correlates of subjective pleasantness

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ABSTRACT

Processing of subjective pleasantness is essential in daily life decision making, particularly in the context of cognitive and environmental factors. Pleasure is mediated by a neural network and this network has been suggested to be the biological basis of pleasure including a whole range of different modalities and domains of pleasantness. This quantitative meta-analysis of brain imaging data focuses on studies 1) based on correlations between self-reported judgements of pleasantness and brain regions and investigates whether 2) immediate (during scanning) versus subsequent judgements (after scanning) differ in brain activity.

We investigated concurrence across 40 studies reporting brain regions correlated with self-reported judgements of subjective pleasantness (attractiveness, liking or beauty) by means of activation likelihood estimation (ALE). Positive correlates of subjective pleasantness were found in mOFC, ventromedial prefrontal cortex, left ventral striatum, pregenual cortex, right cerebellum, left thalamus and the mid cingulate cortex. Negative correlates were found in left precentral gyrus, right cerebellum and right inferior frontal gyrus. A comparison of studies with subjective pleasantness judgement during or after scanning revealed no significant differences in brain activation.

We conclude that subjective pleasantness judgements are directly related to brain regions that have been described as part of the reward circuitry (mOFC, ventral striatum). The results suggest that the evaluation of likability or pleasure is an automatic process and that it is neither elicited nor enhanced by instructions to report the outcome of these judgements.

Introduction

In daily life we frequently encounter situations in which we have to make choices based on our subjective pleasantness processing, e.g. when buying fruits in a grocery store. In order to decide between different options the brain computes the values associated with stimuli and integrates it with motivational, cognitive and contextual needs (Kable and Glimcher, 2009). We might therefore choose oranges instead of cherries because we strive for something sweet but are thirsty at the same time. Neuroimaging research has made advances in understanding how the brain implements positive value processing and represents subjective pleasantness. In particular the medial prefrontal cortex (orbitofrontal (mOFC) and ventromedial prefrontal cortex), the ventral striatum and the amygdala have been implicated in reward processing (Burgdorf and Panksepp, 2006; Grabenhorst and Rolls, 2011; Liu et al., 2011; Peters and Büchel, 2010). In order to systematically explore brain regions involved in subjective pleasure processing we conducted a meta-analysis using the activation likelihood estimation (ALE) approach (Eickhoff et al., 2009; Laird et al., 2005; Turkeltaub et al., 2002). ALE allows disclosure of statistically significant concordance of activated voxels across numerous studies while controlling for chance clustering. By seeking concordance at the voxel level, ALE tests for statistically reliable clustering of activations in standardised locations, which avoids spatial distinction errors and incongruence of labelling across studies that can befall narrative-based reviews.

A recent ALE meta-analysis reported common brain activation of positive-valence neuroaesthetic processing across different sensory modalities in the right anterior insula (Brown et al., 2011). This meta-analysis included multiple studies in which positive valence was only implicitly assumed and not substantiated by participants' subjective reports. The analysis comprised investigations in which pictures of participants' offspring were shown and compared with pictures of other peoples' offspring. Alternatively, pictures of naked individuals compared with dressed individuals were presented on the assumption that naked bodies do elicit positively valenced emotions (e.g. Bocher et al., 2001; Ferretti et al., 2005; Leibenluft et al., 2004). Since many of the studies lack the association with participants' subjective pleasantness it is not clear what participants actually experienced during scanning. In order to address this problem we present a quantitative meta-analysis on coordinates of neuroimaging studies in which

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participants indicate how pleasant or attractive they regard certain experiences such as odour, taste, music or visual stimuli. We were particularly interested in the neural correlates of subjective pleasantness across various domains; we therefore selected studies in which 1) participants themselves judged pleasantness and 2) brain signal was reported as correlations or contrasts based on these individual judgements.

Recently research has been undertaken to explore whether choices or obtainable rewards need to be real in order to activate brain regions such as mOFC and ventral striatum. Bray et al. (2010) demonstrated that the experience of real as well as imagined rewards engages the mOFC. Furthermore, Kang et al. (2011) have shown mOFC and ventral striatal activation during real as well as hypothetical choices. From these studies one may conclude that activation within pleasure related brain regions does not depend on the reality of the outcome. Within the present meta-analysis we want to take the exploration of boundary conditions of hedonic brain activation one step further by asking the question whether the instruction to think about pleasantness or likability during scanning is required to elicit mOFC activation. Since it has been proposed that the mOFC represents the affective or so called goal value of stimuli (Grabenhorst and Rolls, 2011; Kringelbach, 2005) we set out to investigate whether mOFC is only engaged when an explicit judgement is required. In order to explore to what extent these areas are dependent on explicit instructions and to rate subjective pleasantness, we subdivided studies into those that afforded judgements during scanning itself and those in which the judgement was assessed before or after scanning.

Methods

Selection of studies

Studies were selected using a systematic search process. Peer-reviewed articles published in English until July 2011 were selected from the search results of two separate databases (Pubmed, ISI Web of Knowledge). Keyword searches were conducted using the following terms: (1) "neuroimaging" <OR> "fMRI" <OR> "PET," and (2) "pleasantness" <OR> "attractiveness" <OR> "preference" <OR> "liking" <OR> "reward value". From the resulting papers we selected those that presented cues (e.g. faces, objects, music, taste) that had to be judged according to subjective pleasantness (most frequently labelled as "pleasantness", "attractiveness" or "liking"). The reference lists of the selected papers were searched for additional studies that fit these criteria. Finally we included all studies of which we were able to obtain MNI or Talairach (Talairach and Tournoux, 1988) coordinates of whole-brain correlations with subjective pleasantness or contrasts between preferred and non-preferred cues. We only included coordinates resulting from analyses computed across the whole brain and excluded restricted analyses based on data with partial coverage, regions of interest or small volume correction. We included data from functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies despite the fact that they have a different physiological basis, because both methods have been used to identify the neural correlates of subjective pleasantness. Our rationale was to provide an all-embracing overview over the attempts to identify the neural correlates of pleasantness. In total there are a number of 39 studies with 237 foci of altogether 635 participants (Table 1A).

Creation of ALE maps

The ALE method provides a voxel-based meta-analytic technique for neuroimaging data (Eickhoff et al., 2009; Turkeltaub et al., 2002). By means of the software Brainmap GingerALE (http://brainmap.org/ale/), statistically significant concordance in the pattern of brain activity among several independent experiments was computed. ALE maps display regions in the brain that comprise statistically significant peak activation locations from multiple studies. Coordinates reported in Talairach were converted to MNI using Lancaster et al. (2007) (icbm2tal). In the approach taken by ALE, localization probability distributions for the foci are modelled as the centre of 3-D Gaussian functions. Gaussian distributions are summed across the experiments to generate a map of inter-study consistencies that estimate the likelihood of activation for each voxel, the ALE statistic, as determined by the entire set of studies. The false discovery rate (FDR) method was employed to correct for multiple comparisons at a significance threshold of $p<0.01$ and a cluster threshold of 100 mm³. For the ALE maps of subsamples of these studies we used a more lenient threshold, FDR at a significance threshold of $p<0.05$ and a cluster threshold of 100 mm³. The FDR thresholding procedure controls the expected proportion of incorrectly rejected null hypotheses (type I errors) and the cluster threshold ensures that the clustering of the significant voxels observed is above chance.

Contrast analyses were calculated by means of ALE subtraction analysis (GingerALE version 2.1a3), accounting for potential differences in sample size. To increase the specificity of the results, the analysis of differences was restricted to those voxels that showed an effect in the two main meta-analyses that were compared. The reported contrasts analyses were thresholded at FDR corrected $p<0.05$ and a cluster threshold of 100 mm³.

Results

ALE maps of subjective pleasantness and non-pleasantness

Positive correlates of subjective pleasantness were found in mOFC, ventromedial prefrontal cortex, left ventral striatum, pregenual cortex, right cerebellum, left thalamus and the mid cingulate cortex. Negative correlates were found in left precentral gyrus, right cerebellum and right inferior frontal gyrus. The results of the quantitative meta-analysis on positive correlates of subjective pleasantness can be found in Fig. 1A and Table 2a; the results on negative correlates of subjective pleasantness can be found in Fig. 1B and Table 2b.

ALE maps of subjective pleasantness while judgement was obtained during or not during scanning

In order to explore the dependency of neural correlates of subjective pleasantness on the judgement process itself, we subdivided coordinates of the positive correlation with subjective pleasantness into those in which the judgement was obtained during scanning (30 studies) and those in which the judgement was not obtained during scanning (11 studies, one study acquired judgements during and after scanning) (Fig. 1C, Table 2c,d). When contrasting studies with judgement during and not during scanning (FDR $p<0.05$, cluster extend threshold >100 mm^3) no difference between both classes of studies was found. Interestingly, concurrence within left amygdala was only observed across studies in which participants evaluated subjective pleasantness during scanning.

Discussion

Within the scope of the present quantitative meta-analysis we aimed at investigating common brain activations in neuroimaging studies assessing associations between subjective pleasantness ratings (mostly ratings of pleasantness, attractiveness or beauty) and brain responses. For positive correlation of subjective pleasantness we found concurrence in mOFC, left ventral striatum, ventromedial prefrontal cortex, pregenual cortex, right cerebellum, left thalamus and the mid cingulate cortex. For the negative correlation with subjective pleasantness we found left precentral gyrus, right cerebellum and right inferior frontal gyrus.

Table 1
List of included studies.

Study	Modality	N	Foci positive/negative	Stimuli	Rating	Time of rating	Reported analysis
Amemiya and Ohtomo (in press)	fMRI (3 T)	32	12	Faces	Attractiveness	Not during scanning	Correlation
Anderson et al. (2003)	fMRI (3 T)	16	1	Odour	Pleasantness	Not during scanning	Correlation
Berns et al. (2001)	fMRI (1.5 T)	25	1	Juice	Preference	Not during scanning	Contrast: preferred vs. nonpreferred
Blood et al. (1999)	PET (rCBF)	10	2/2	Music	Pleasantness	During scanning	Correlation
Blood and Zatorre (2001)	PET (rCBF)	10	9/6	Music	Pleasantness	Not during scanning	Correlation
Chatterjee et al. (2009)	fMRI (3 T)	13	14	Artificial faces	Attractiveness	During scanning	Correlation
Chatterjee et al. (2009)	fMRI (3 T)	13	3	Artificial faces	Attractiveness	Not during scanning	Correlation
Cloutier et al. (2008)	fMRI (3 T)	48	18/8	Faces	Attractiveness	During scanning	Correlation
Cunningham et al. (2011)	fMRI (3 T)	13	5/4	Thoughts of objects, persons, situations	Liking	Not during scanning	Contrast: liked vs. disliked
De Araujo et al. (2003a)	fMRI (3 T)	11	3	Water	Pleasantness	During scanning	Correlation
De Araujo et al. (2003b)	fMRI (3 T)	12	3	Odour	Pleasantness	During scanning	Correlation
Dio et al. (2007)	fMRI (3 T)	14	–/1	Sculptures	Beauty	During scanning	Contrast: ugly vs. beautiful
Grabenhorst et al. (2007)	fMRI (3 T)	14	2/2	Odour	Pleasantness	During scanning	Correlation
Grabenhorst and Rolls (2008)	fMRI (3 T)	12	1	Taste	Pleasantness	During scanning	Correlation
Grabenhorst et al. (2010)	fMRI (3 T)	14	1/3	Taste	Pleasantness	During scanning	Correlation
Heinzel et al. (2005)	fMRI (1.5 T)	13	4	IAPS pictures	Pleasantness	During scanning	Correlation
Iaria et al. (2008)	fMRI (3 T)	11	1	Faces	Attractiveness	During scanning	Contrast: attractive vs. unattractive
Jacobsen et al. (2006)	fMRI (3 T)	15	1	Abstract figures	Beauty	During scanning	Contrast: beautiful vs. not beautiful
Kawabata and Zeki (2004)	fMRI (2 T)	10	1/1	Paintings	Beauty	Not during scanning	Contrast: beautiful vs. not beautiful
Kirk (2008)	fMRI (1.5 T)	15	4/4	Photos (objects)	Pleasantness	During scanning	Correlation
Kornysheva et al. (2010)	fMRI (3 T)	17	9/–	Rhythms	Beauty	During scanning	Contrast: beautiful vs. not beautiful
Lebreton et al. (2009)	fMRI (3 T)	9	5	Photos (faces, houses, paintings)	Pleasantness	During scanning	Correlation
McCabe and Rolls (2007)	fMRI (3 T)	12	1	Taste, odour	Pleasantness	During scanning	Correlation
O'Doherty et al. (2003)	fMRI (3 T)	25	–/1	Faces	Attractiveness	During scanning	Correlation
O'Doherty et al. (2006)	fMRI (3 T)	13	3	Faces	Attractiveness	Not during scanning	Correlation
Pereira et al. (2011)	fMRI (1.5 T)	14	8/2	Music	Liking	Not during scanning	Contrast: liked vs. disliked
Piech et al. (2009)	fMRI (1.5 T)	8	2	Menu reading	Pleasantness	During scanning	Contrast: high vs. low pleasantness
Plassmann et al. (2008)	fMRI (3 T)	20	2	Wine	Pleasantness	Not during scanning	Correlation
Rolls and McCabe (2007)	fMRI (3 T)	16	1	Chocolate	Pleasantness	During scanning	Correlation
Rolls et al. (2008)	fMRI (3 T)	12	2	Temperature on hand	Pleasantness	During scanning	Correlation
Rolls et al. (2010)	fMRI (3 T)	12	6	Odour	Pleasantness	During scanning	Correlation
Royet et al. (2003)	fMRI (1.5 T)	28	3/2	Odour	Pleasantness	both	Contrast: pleasant vs. unpleasant
Shirao et al. (2005)	fMRI (1.5 T)	13	–/8	words concerning interpersonal relationships	Pleasantness	During scanning	Correlation
Small et al. (2001)	PET (H_2 ^{15}O)	9	18/11	Chocolate	Pleasantness	During scanning	Correlation
Small et al. (2003)	fMRI (1.5 T)	9	3/4	Taste	Pleasantness	During scanning	Correlation
Suzuki et al. (2008)	PET (H_2 ^{15}O)	13	1/3	Music	Pleasantness	During scanning	Contrast: pleasant vs. unpleasant, Correlation
Tsukiura and Cabeza (2011a,b)	fMRI (4 T)	22	5	Faces	Attractiveness	During scanning	Correlation
Tsukiura and Cabeza (2011a,b)	fMRI (4 T)	22	2/4	Faces, moral actions	Attractiveness	During scanning	Correlation
Vartanian and Goel (2004)	fMRI (4 T)	12	9	Paintings	Pleasantness	During scanning	Correlation
Winston et al. (2007)	fMRI (1.5 T)	28	5	Faces	Attractiveness	During scanning	Correlation

Our results are partly in line with a previous meta-analysis conducted on positive-valence neuroaesthetic processing by Brown et al. (2011). Similar to their results we found a positive association between subjective pleasantness judgements and brain activity in mOFC, ventral striatum, pregenual cortex, thalamus and the mid cingulate cortex. The observed overlap between brain regions derived from individuals' subjective pleasantness correlates in our present study and the brain regions Brown et al. (2011) associated and defined as likable conditions, in the previous meta-analysis, provide evidence for the validity of findings reported in Brown et al. (2011) although participants have not judged each target of interest. Albeit in stark contrast to our present findings Brown et al. (2011) report overlaps across all four investigated modalities (auditory, visual, gustatory, olfactory) in right anterior insula and in bilateral anterior insula when focussing on the overlap of only three modalities. Whereas the present meta-analysis on correlates of subjective pleasantness yielded no concurrence in the insula. The absence of overlap in the anterior insula across studies focusing on correlates of subjective pleasantness judgements provides a strong argument against the important roles of the anterior insula in interoceptive awareness or insight (Critchley et al., 2004), meta-representations of the state of the body (Craig, 2003) or particularly in the individuals' subjective awareness (Craig, 2004) of subjective pleasantness.

Another prominent interpretation of the function of insula in the literature is its involvement in processing of negatively valenced emotions such as disgust, sadness (Coan et al., 2006; Craig, 2005; Slavich et al., 2010), and sensations of pain or internal discomfort (Lamm et al., 2011; Singer et al., 2004). Since the subjects in Brown's study have not been consistently asked to report their subjective pleasantness, the overlap observed in the insula could be due to ambivalent feelings towards the stimulus-category externally classified as positive. For example, observing sexual stimuli could elicit repulsion instead of attraction or seeing pictures of own offspring could be associated with more complex feelings than purely pleasure.

The neural correlates of self-reported subjective pleasantness observed in the current study, in particular mOFC/ventromedial prefrontal cortex and the ventral striatum, are in line with previous studies that describe the medial prefrontal cortex involvement in processing of

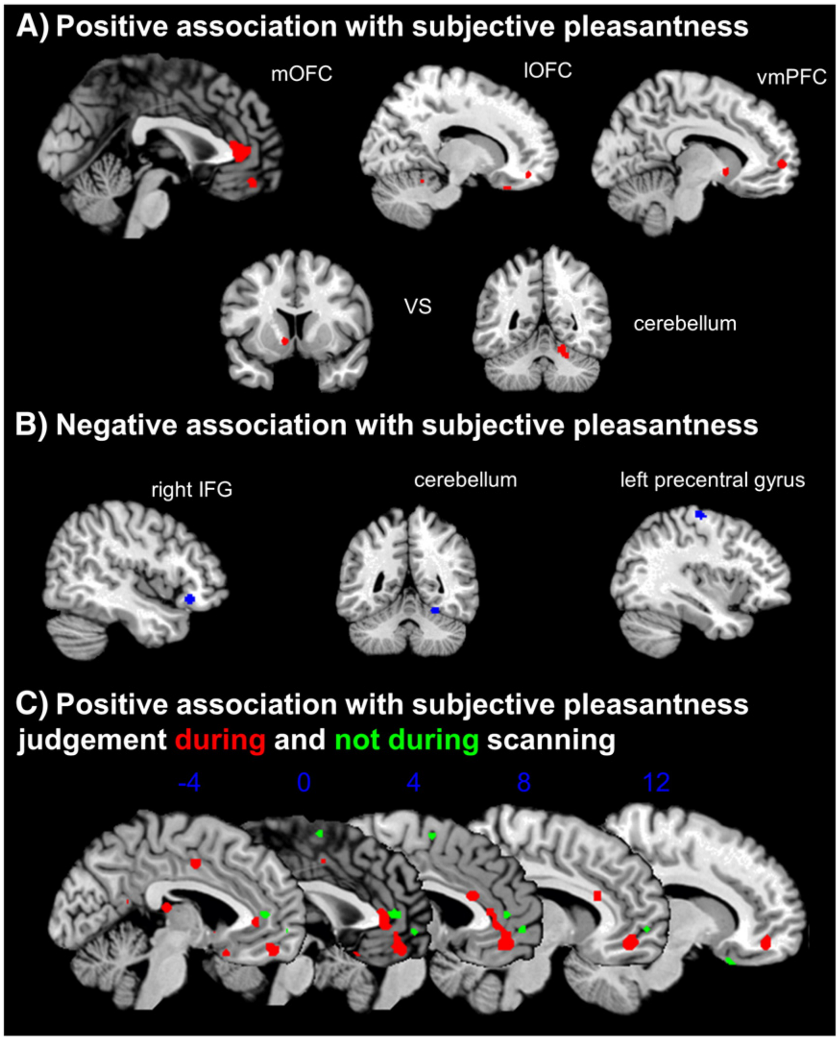

Fig. 1. ALE meta-analysis maps for (A) positive association with subjective pleasantness (FDR $p<0.01$, cluster >100 mm^3), (B) negative association with subjective pleasantness (FDR $p<0.01$, cluster >100 mm^3), (C) positive association with subjective pleasantness judgement during (red) and not during (green) scanning (FDR $p<0.05$, cluster >100 mm^3). IFG = inferior frontal gyrus, mOFC = medial orbitofrontal cortex, vmPFC = ventromedial prefrontal cortex, VS = ventral striatum, pgPFC=pregenual prefrontal cortex.

expected value, reward outcome, experienced pleasure on a common value scale (for an overview Grabenhorst and Rolls, 2011) and the ventral striatum as the hedonic "hot spot" of the brain (Pecina et al., 2006; Smith et al., 2010). Moreover the ventromedial prefrontal cortex has been implicated in self-referential processing (Kelley et al., 2002; Northoff et al., 2006; Wicker et al., 2003) and might be activated because the content of the judgements given is self-relevant.

The right cerebellar activity observed in the meta-analysis on positive as well as negative correlates of subjective pleasantness partly overlaps and is located in lobule VI. This cerebellar cluster is bigger when participants give their pleasantness judgement during scanning, compared to those studies where the rating is acquired at a later stage. We therefore speculate that the cerebellar convergence is rather related to the rating process than to the pleasantness judgement itself.

We strictly focus on correlates of reported subjective pleasantness, spanning a broad range of different stimuli to be judged. Our results are in accordance with previous meta-analyses including studies on reward-related decision making tasks, in which primarily monetary incentives were used to manipulate reward value and usually no direct association between the subjective evaluation and brain activity was made (Knutson and Greer, 2008; Liu et al., 2011; Peters and Büchel, 2010). In light of this similarity we conclude that the judgement of subjective pleasantness is indeed directly derived and reflected in brain regions known to be involved in reward representation.

The second question we aimed to address is whether the instruction to judge pleasantness may have an influence on brain activity. We reasoned that distinct brain regions associated with the conscious evaluation of presented stimuli could be identified by comparing the results of a meta-analysis on studies where participants had to judge during scanning with results of a meta-analysis where participants judged the stimuli outside the scanner. Since mOFC has been suggested to play a role in evaluating the appetitive and aversive reinforcement value of stimuli (Rolls, 1999) this was our target of interest. Additionally, based on a study reporting that OFC was more strongly activated when subjects made explicit judgements (Royet et al., 2003), we hypothesised that hedonic decisions themselves could be a decisive component determining brain activation. Contrary to this hypothesis we found concurrence in mOFC for both types of studies. Most important, no significant difference was found between the meta-analysis maps of studies in which participants performed subjective pleasantness judgements during versus not during scanning. Unfortunately, only 11 studies assessed liking judgements outside the scanner but if anything this should have biased our results to find distinct activation in the 30 studies included liking judgements inside the scanner.

From the present finding we conclude that subjective pleasantness judgements are directly related to brain regions that have been described as part of the reward circuitry itself. Furthermore, we suggest that the evaluation of likability or pleasure is an automatic process that

Table 2
Statistical concurrence observed across studies.

Anatomical region	Brodmann area	Coordinates (mni)			Volume (mm^3)
		x	*y*	*z*	
a) Positive association with subjective pleasantness (FDR, p<0.01, cluster>100 mm³)					
Medial orbitofrontal cortex	10/32	6	46	−15	1208
Pregenual prefrontal cortex	32/24	0	39	5	1208
Right cerebellum		20	−52	−23	1032
Ventromedial prefrontal cortex	10/32	−12	56	1	608
Left ventral striatum		−9	8	−6	208
Anterior cingulate cortex	24	5	22	19	168
Medial orbitofrontal cortex		16	27	−27	160
Left thalamus		−4	−25	11	136
Mid cingulate cortex	24	−4	−5	42	128
b) Negative association with subjective pleasantness (FDR, p<0.01, cluster>100 mm³)					
Right inferior frontal gyrus	47	46	27	−13	312
Right cerebellum		26	−53	−20	296
Left precentral gyrus	4	−35	−21	62	152
c) Positive association with subjective pleasantness — rating during scanning (FDR, p<0.05, cluster>100 mm³)					
Medial orbitofrontal cortex, Ventromedial prefrontal cortex	11	3	44	−11	4072
Right cerebellum		21	−54	−24	1020
Left ventral striatum		−9	9	−5	592
Anterior cingulate cortex	24	5	22	19	424
Mid cingulate cortex		−4	−5	42	392
Posterior cingulate cortex	30	−8	−53	15	352
Left thalamus		−6	−25	11	344
Left amygdala		−17	−3	−21	304
Left cerebellum		−25	−55	−22	280
Ventromedial prefrontal cortex	32/10	−16	53	−1	208
Subcallosal gyrus	25	−3	17	−21	152
Ventromedial prefrontal cortex	10	18	55	−5	144
Left frontal pole	10	−31	55	−1	120
Right inferior frontal gyrus	47	16	31	−26	112
d) Positive association with subjective liking — rating not during scanning (FDR, p<0.05, cluster>100 mm³)					
Ventromedial prefrontal cortex	32	0	44	6	448
Ventromedial prefrontal cortex	10	−11	55	2	440
Medial orbitofrontal cortex	10	3	57	−5	336
Supplementary motor area	6	2	−7	61	248
Medial orbitofrontal cortex	25	14	21	−27	240
Right middle temporal gyrus	22, 21	57	−41	4	240
Left cerebellum		−8	−84	14	136
Right cerebellum		20	−64	−14	136
Left lingual gyrus	18	−10	−82	−5	104

does not need to be prompted by instructions to report the outcome of these judgements. We deduce that there is a sensible biological mechanism necessary to generate evaluative responses towards stimuli in the world surrounding us without being asked for and most likely without the costs in terms of additional attentional resources.

Although, no significant differences were found when directly contrasting both classes of studies, one interesting aspect of our results is the concurrence found within left amygdala that was exclusively observed across studies in which participants evaluated subjective pleasantness during data acquisition. In general, negative emotional stimuli have been shown to be more effective in increasing amygdala activity than positive ones in fMRI studies (Burgdorf and Panksepp, 2006; Zald, 2003). Future research may clarify whether the amygdala involvement in judgement of pleasantness could be due to ambivalent and conflicting processes evoked by the situation of having to evaluate stimuli in question.

To summarise, the present study identified brain regions of concurrence across studies on the neural basis of subjective pleasantness by means of ALE. Positive correlates of subjective pleasantness were found in mOFC/ventromedial prefrontal cortex, left ventral striatum, pregenual cortex, right cerebellum, left thalamus and the mid cingulate cortex; negative correlates in left precentral gyrus, right cerebellum and right inferior frontal gyrus. A separate analysis on studies with subjective pleasantness judgement inside versus outside the scanner revealed no differences in brain activation. We therefore conclude that the subjective pleasantness judgement is directly related to brain regions that have been described as part of the reward circuitry. Furthermore, our results suggest that the evaluation of likability or pleasure is an automatic process that is neither elicited nor enhanced by the instructions to report the outcome of these judgements.

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