Research Article

Nonlinear neural representation of emotional feelings elicited by dynamic naturalistic stimulation

*Mikko Viinikainen[1], Enrico Glerean[1], Iiro P. Jääskeläinen[*1], Juho Kettunen[2], Mikko Sams[1,3], Lauri Nummenmaa[1,3,4,5]*

[1] Brain and Mind Laboratory, Department of Biomedical Engineering and Computational Science (BECS), Aalto University School of Science, Espoo, Finland

[2] Department of Biomedical Engineering and Computational Science (BECS), Aalto University School of Science, Espoo, Finland

[3] Advanced Magnetic Imaging Centre, Aalto University School of Science, Espoo, Finland

[4] Brain Research Unit, Low Temperature Laboratory, Aalto University School of Science, Espoo, Finland

[5] Turku PET Centre, Turku, Finland

Corresponding Author & Address:

Iiro P. Jääskeläinen

Brain and Mind Laboratory, Department of Biomedical Engineering and Computational Science (BECS) Aalto University, School of Science, FIN-00076 AALTO; Email: iiro.jaaskelainen@aalto.fi; Tel: +358 50 560 9503; Fax: +358 9 470 23182

ABSTRACT

Emotions guide organisms in constantly changing dynamic environments. While the majority of previous studies have assessed neural basis of emotions elicited by impoverished stimuli (e.g., pictures or words), it has been shown that dynamic naturalistic stimuli (e.g., movies and stories) elicit stronger subjective emotional experiences. Here, we studied the neural basis of subjective feelings of pleasantness and unpleasantness (i.e., emotional valence) and emotional arousal by presenting sixteen participants with thirteen emotional and neutral movie clips during 3-Tesla fMRI scanning. After scanning, the participants viewed the clips again and rated their moment-to-moment subjective experience of valence and arousal. These participant-wise experiential time series were used to model each participant's brain activity during viewing of the movies, while factoring out contributions of physical stimulus features. The results suggest that a set of cortical and subcortical areas encode subjective feelings in nonlinear fashion; we observed a quadratic (U-shaped) dependency between the experienced emotional valence and BOLD signal in insula, somatosensory cortex, anterior and middle cingulate cortices, hypothalamus and thalamus, inferior frontal gyrus, and in medial prefrontal and orbitofrontal cortex. We propose that this network of brain areas represents the subjectively experienced valence as deviations from the neutral emotional state.

INTRODUCTION

Both early [1] and recent [2, 3, 4] models of affective processing dissociate between the initial automatic physiological and neural changes elicited by the emotional event, and subsequent conscious representation of these changes, which is called feeling or subjective emotional experience. Whereas the automatic neural and bodily emotional responses provide immediate means for protection (i.e., the "fight or flight" response), the conscious representation of these changes allows the individual to match physiological and experiential reactions with the behavioral context [5]. Consequently, this enables the individual to voluntarily fine-tune his/her behavior to better match with the changes observed in the environment.

Recent neuroimaging studies have elucidated the neural systems responsible for encoding emotional information from the sensory input [see reviews in 6, 7], however, less is known about how brain represents the subjectively experienced, pleasant and unpleasant, emotional states. A limited number of studies have assessed the brain basis of emotional feelings using self-induction of emotions [8, 9] and viewing emotional movies [10, 11, 12, 13]. However, much of what we know about the neural basis of emotional feelings stems from experiments where pictures or other relative simple stimuli have been presented to participants, even though naturalistic stimuli (e.g., movies and narrated stories) have been shown to be more robust in eliciting emotions [14]. In the present study, we aimed to reveal the neural systems that underlie emotional feelings of pleasure and displeasure (i.e., valence) and arousal during prolonged, naturalistic movie stimulation with varying affective content, and modelled the functional relationship between the experienced emotional state and the activity of these neural systems.

Neural basis of subjective emotional experience

It is a generally held view that emotional feelings arise when one becomes aware of the central and peripheral physiological changes brought about by the emotionally laden stimulus, and possibly attributes these changes to some external or internal event. Existing evidence from imaging studies suggests that emotional feelings are brought about and accessed by the coordinated activity of a neural circuit involving systems that i) evaluate and encode the affective input, ii) evaluate the rewarding versus punishing value of the stimulus and trigger corresponding autonomic changes in the observer, and iii) finally access the changes in the somatovisceral state and generate the corresponding, consciously accessible affective feeling [3, 15]. In this circuit, amygdala first encodes emotional salience of visual input [see review in 16], and the circuit comprising of amygdala, MPFC and anterior cingulate cortex (ACC) governs visceromotor control [17], with MPFC serving a critical role in triggering autonomic emotional responses to external events [18, 19]. The anterior insula might support interoceptive awareness of the bodily change [e.g. 20, 21], and the sensory representation of the homeostatic state in the anterior insula may subsequently trigger the subjective experience of emotion.

Along with the insula, the somatosensory cortices have been suggested to underlie the transformation of somatic states into subjective feelings; somatosensory cortices seem to be involved in the representation and encoding of the bodily states caused by emotions, and lesions to this region dampen subjective emotional feelings triggered by external stimuli [22]. Furthermore, lesions [15] and transcranial magnetic stimulation [23] to somatosensory cortices are known to impair recognition of facial expressions, suggesting their role in constructing the somatic representation of one's (or someone else's) emotional state. In line with this, the somatosensory cortices are activated when participants simulate others' emotional but not neutral states [24].

Both positive and negative subjective feelings seem to activate the MPFC, amygdala and thalamus, as evidenced by a handful of studies using emotional movies [11, 12, 13, 25]. In addition, studies using emotional self-induction have observed activations related to negative and positive feelings in the amygdala [8, 9, 26]. In a study investigating fear, sadness, anger, and happiness, recall-based emotion induction caused partly different activations during the different emotions but also conjoint patterns of activation and deactivation in the OFC, right insula, and right second somatosensory cortex [27]. In a recent

fMRI study, subjective emotional experience was separated from the perception of emotional stimuli [28]. In this study, blocks of aversive vs. neutral pictures were presented to subjects who were to rate their subjective emotional experience four times on 6s intervals after the presentation of each block. Whereas a large number of regions, including the amygdala, were activated during perception of aversive vs. neutral picture blocks, only some of them remained active during subsequent 26s (including 2s transition) period, suggesting that these regions contributed to the subjective emotional experience. These regions included left hippocampus, thalamus, cerebellum, and right lateral OFC. In other studies, the OFC has been suggested to link an object's value (reward or punishment) to subjective emotional experience [29], and it has also been suggested to play a key role in accessing the subjective emotional experience, as evidenced by lesions in the bilateral OFC severely altering emotional feelings [30].

Neural representation of valence and arousal

So-called categorical emotion models maintain that there exist discrete "basic" emotions, which are evolutionary scripts with distinct neural and physiological basis, that enable directing one's behavior in the most suitable and profitable way when one encounters challenges in the environment [31]. On the contrary, the dimensional models posit that the whole emotional space covering the discrete emotions can be represented by linear combinations of a limited set vectors, the most salient being valence (unpleasantness vs. pleasantness) and arousal [32, 33]. In terms of motivation, valence refers to avoidance vs. approach, and arousal refers to the intensity of activation, ranging from calm to highly tense. A bulk of neuroimaging studies implementing parametric designs have addressed how valence and arousal of pictures (including faces), words, scents and sounds are represented in the brain [34, 35, 36, 37, 38, 39, 40, 41, 42]. These studies have consistently shown that valence modulates responses particularly in the prefrontal cortical (PFC) regions and insula, whereas arousal modulates activity in the amygdala. Interestingly, some studies have suggested that valence is represented by separate positive and negative dimensions, rather than a single dimension ranging from negative to positive

[43, 44]. More detailed analysis of the response properties of the brain circuits encoding valence has suggested that there may actually exist a quadratic (X^2) rather than linear relationship between valence and BOLD signal intensity [39, 40, 41, 42]. These data suggest that separate neural populations could actually encode negatively and positively valenced events [cf. 44]. However, these experiments have focused on the sensory evaluation of the emotional stimulus qualities, and currently it remains elusive how subjective experiences of valence and arousal are represented in the brain.

Using cinema to study emotional feelings in naturalistic contexts

Recent advances in neuroimaging data analysis techniques have made it possible for neuroscientists to study brain function in settings that resemble the complexity and unpredictability of real life. Interestingly, such studies have revealed that natural dynamic stimuli activate the brain more strongly and reliably than the conventional well-controlled but often very unnatural stimuli (for a review see [45]). From experimental point of view, cinema also provides an excellent condensed simulation of emotions in real life, as most movies describe human interactions and environments in naturalistic conditions, yet movies can be used to elicit emotions in highly standardized settings. Importantly, reviews on emotion induction have consistently found that films are the most effective way to induce emotional states in human participants [46, 47]. Whereas brief sensory stimuli such as still pictures, faces and words are well suited for studying the sensory and evaluative processing of emotions, films elicit robust and genuine emotional feelings [48]. Importantly, even a short one-minute movie clip can trigger a multitude of affective experiences in the observer, and such experiences can be measured in real time. As emotional experiences unfold over time while watching films, such an approach enables powerful parametric designs for studying the affective experiences elicited by different events in the movies.

The present study

At present, studies addressing the neural systems encoding subjective moment-to-moment

emotional experiences from dynamic scenes are sparse, as well as studies addressing the cerebral mechanisms underlying subjective experience of emotional valence and arousal. In this study we characterized the neural systems supporting subjective emotional experiences of pleasantness and unpleasantness as well as arousal in a naturalistic setting. Participants viewed a set of film clips with varying valence and arousal while their brain activity was measured with fMRI. After scanning, they viewed the movies again and evaluated their moment-to-moment experience of valence and arousal. The participant-wise valence and arousal time series were then used in general linear model (GLM) to predict neural responses to subjective experiences of valence and arousal while viewing the movies. On the basis of previous studies on the neural representation of valence [39, 40, 41, 42] we predicted that we would observe a quadratic dependency between BOLD signal and valence in the core network of brain areas that give rise to emotional experiences. More specifically, U-shaped valence dependency

was expected in the insula [27, 40, 49], medial prefrontal cortex [11, 12, 13, 25, 40, 41, 50], somatosensory cortex [27, 40], and ACC [26, 39, 49, 50], as well as sub-cortical structures in the limbic system and thalamus [12, 25, 26, 41].

MATERIALS AND METHODS

Participants

The Ethics Committee of the Helsinki and Uusimaa Hospital District approved the study protocol, and the study was conducted in accordance with the Declaration of Helsinki. Sixteen volunteers (3 females and 13 males, ages 25-49 years, mean age 32 years) with normal or corrected to normal vision participated in the study. Individuals with a history of neurological or psychiatric disease or currently taking medication affecting the central nervous system were excluded. All participants were compensated for their time and travel costs and signed ethical committee-approved informed consent forms.
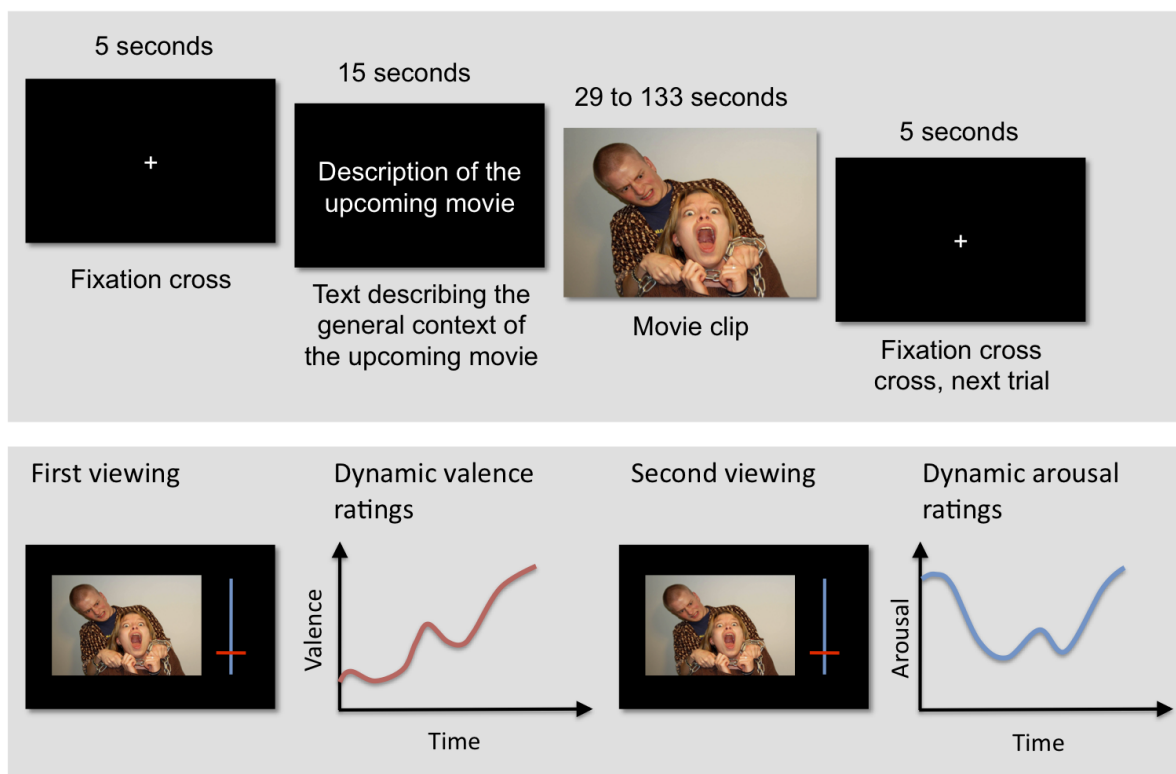

Figure 1. Experimental design. Participants watched short (29–133 s) movie clips eliciting pleasant, neutral and unpleasant emotional feelings. The movies were preceded by a 5-s presentation of a fixation cross, and 15-s presentation of a text that described the general context of the upcoming movie without revealing details of its actual events. After scanning, participants watched the movies again and rated their moment-to-moment experiences of valence and arousal on a continuous scale by moving a slider bar at the right side of the screen using a mouse.

Stimuli and experimental design

Stimuli, design, and the stimulus rating system are summarized in Figure 1. The video stimuli were thirteen approximately 90-s segments (M$_{duration}$ = 92 s, SD$_{duration}$ = 30 s) cut from Hollywood feature films such as When Harry Met Sally and The Godfather eliciting strong positive, neutral or negative emotional feelings. Most of the stimuli (See Appendix 1) were selected from the affective films database devised by Hewig and colleagues [48]. All movies were presented without sound in order to reduce the potential confounds associated with the English speech in the movies, as all participants were native Finnish speakers. Also, importantly, valence and arousal processing has been found to vary depending on the stimulus modality (e.g.,[34, 38, 39, 40, 41, 51, 52]), so we did not want complicate the interpretation of results by mixing two stimulus modalities. While being scanned, the participants watched all the films twice in a fixed order. They were instructed to watch the movies similarly as if they were watching movies from TV or at cinema. Each movie was preceded by a 5-s presentation of a fixation cross followed by 15-s presentation of a short, emotionally neutral text that explained the general setting of the forthcoming film without revealing its actual content. This served both as a washout period for the emotion elicited by the previous film, and also provided a context for the forthcoming film segment. Total task duration was 48 minutes. All stimuli were presented via an angled mirror above the participant's eyes, which reflected images projected onto a translucent screen in the bore of the magnet behind the participant's head.

Behavioural measurements

After scanning, the participants viewed the movie clips again and rated their moment-to-moment subjective emotional experience. Ratings for valence and arousal were acquired on separate runs, the former for valence and the latter for arousal. While viewing each movie, participants used a mouse to move a cursor up and down on a valence (or arousal) scale shown at the edge of the screen according to their current emotional feeling. We used the mouse instead of a slider, since it has been found to be faster (and as accurate) response method [53], and continuous rating demands fast responses. Responses were

sampled at 5 Hz. For fMRI data analyses, the responses were rescaled to range from one (negative valence; low arousal) to nine (positive valence; high arousal). This resulted in participant-wise time series of experience of valence and arousal during each movie clip that were subsequently used to model corresponding BOLD signal changes.

Controlling low-level visual features

To control for confounds arising from low-level sensory features, moment-to-moment low-level visual features were analyzed from the movies at a rate of 0.59 fps (equaling one TR) and modeled as nuisance covariates in the 1st-level fMRI data analysis (see below). The properties of the color profile were represented with hue-saturation-value (HSV) color model. For detection of edges in the movie frames, we used Gabor-filters [54] due to their similarity with the receptive fields found in the human visual system. Twenty-four Gabor filters with three receptive field sizes and eight orientations were used to filter the movie frames, accommodating a wide range of edge characteristics. By averaging over each edge type we obtained an edge profile, a single value representing the amount of edges in the current frame of the movie. Movement was calculated by first estimating the optical flow for the video stimuli by calculating the movement of each pixel from one video frame to the next one. From this optical flow vector map we calculated the mean length of vectors and used it as a measure of movement [55].

fMRI acquisition and analysis

MR imaging was performed with General Electric Signa 3 Tesla MRI scanner with Excite upgrade at Advanced Magnetic Imaging Centre at the Aalto University School of Science. Whole-brain data were acquired with T2*-weighted echo-planar imaging (EPI), sensitive to blood oxygen level-dependent (BOLD) signal contrast (27 axial slices, 3 mm slice thickness; 2 mm slice gap; time repetition = 1737 ms; time echo = 32 ms; field of view = 192 mm; voxel size: 3 X 3 X 3 mm). A total of 1700 volumes were acquired, and the first 5 volumes were discarded to allow for equilibration effects. T1-weighted structural images were acquired at a resolution of 1 X 1 X 1 mm.

Data were preprocessed and analyzed using SPM5 software (www.fil.ion.ucl.ac.uk/spm/). The EPI images were sinc interpolated in time to correct for slice time differences and realigned to the first scan by rigid body transformations to correct for head movements. EPI and structural images were coregistered and normalized to the T1 standard template in MNI space (Montreal Neurological Institute (MNI) – International Consortium for Brain Mapping) using linear and non-linear transformations, and smoothed with a Gaussian kernel of full width at half maximum of 8-mm.

A random effects model was implemented using a two-stage process (first and second level). This random-effects analysis assessed effects on the basis of inter-participant variance and thus allowed inferences about the population that the participants were drawn from. For each participant, we used a GLM to assess regional effects of valence and arousal on BOLD indices of activation. Time series of subjective valence and arousal ratings during movie viewing were down-sampled to 1 TR, and modeled as parametric modulators by convolving them with the standard hemodynamic response function. Individual ratings were used for each subject instead of the group averages of the ratings. Both first and second order modulations were modeled for orthogonalized valence and for arousal; when modeling for valence, arousal scores were modeled as nuisance effects and vice versa. In a separate analysis, we also tested linear valence and arousal effects for either negative or positive parts of the valence / arousal dimensions. Low-level visual parameters were included as nuisance covariates in all first-level models. Low-frequency signal drift was removed using a high-pass filter (cutoff 128 sec) and AR(1) modeling of temporal autocorrelations was applied. The individual contrast images were generated for the positive and negative first and second order effects of valence and arousal as well as for their first order effects restricted to either negative or positive valences. The second level analysis used these contrast images in new GLMs from which the statistical images, i.e. SPM-t maps, were generated. With balanced designs at first level (i.e. similar events for each participant, in similar numbers) this second level analysis closely approximates a true mixed effects design, with both within and between subject variance. The statistical threshold was set at $p < 0.05$, with False Discovery Rate (FDR) correction applied in order to control for false positives.

RESULTS AND OBSERVATIONS

Valence and arousal ratings of the film clips were consistent between participants (average standard deviation for valence 1.22 and for arousal 1.68), indicating that these measures were reliable. Figure 2 shows the means and 95% confidence intervals for the ratings of each film. Mean valence for the neutral films was 4.60, for the negative films 3.39, and for the positive films 6.77 (see Appendix 1 for details). Self-reported valence correlated positively with color saturation and value, whereas arousal correlated negatively with the amount of edges and hue (Table 1). Modeling the BOLD signal with linear effects of valence or arousal failed to reveal any sites of activity at $p < 0.05$ FDR-corrected statistical threshold. This was true also when nuisance covariates (i.e., low-level visual features) were excluded from the analysis. Thus, the lack of linear valence or arousal effects was not due to correlated nuisance covariates cutting down the real effects.

Table 1. Correlations between valence and arousal time series and the visual parameters extracted from the movies. Effective sample sizes for the statistical tests have been calculated with a method presented in [83], taking into account the temporal autocorrelations. Note: * = $p < .05$, ** = $p < .001$.

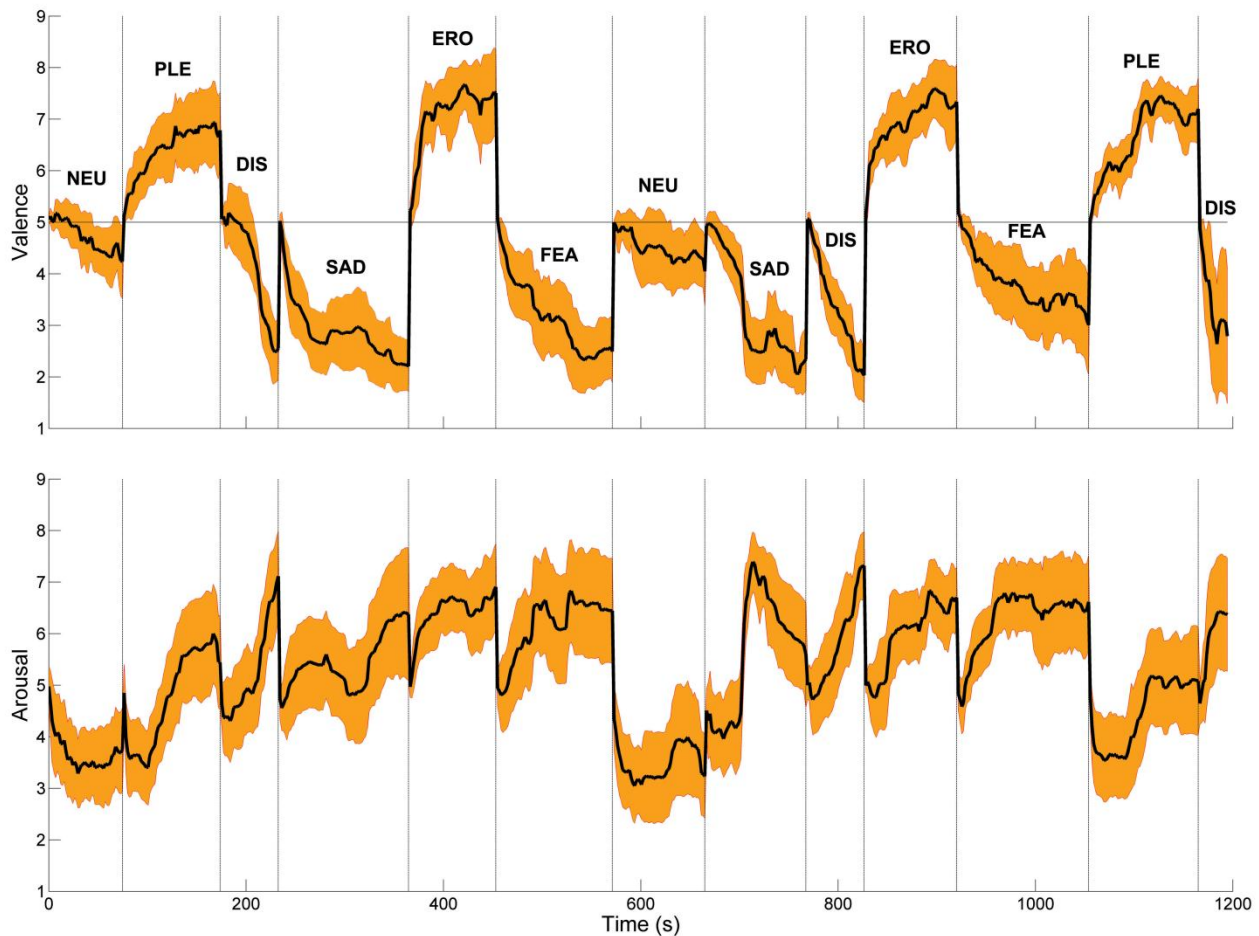|	Arousal	Movement	Egdes	Hue	Saturation	Value
Valence	-0.1976	0.0232	0.2983	-0.1705	0.4836**	0.4127*
Arousal		0.0578	-0.6270**	-0.4020*	0.2622	-0.2053
Movement			-0.0943	-0.0811	0.0293	0.0925
Edges				0.3501	-0.2397	0.5650
Hue					-0.3683**	0.2422*
Saturation						0.0718

Figure 2. Means (black) and 95% confidence intervals (orange) of self-reported dynamic valence (top) and arousal (bottom) ratings. Vertical lines denote breaks between movie clips. Horizontal line at valence 5 denotes neutral. Target emotions: NEU = neutral, PLE = pleasure (happiness), DIS = disgust, SAD = sadness, ERO = erotic (sexual arousal), FEA = fear.

Significant positive quadratic (U-shaped) effects for valence were observed in multiple brain regions (Figures 3-4). The regions included bilaterally the insula, orbitomedial prefrontal cortex (OMPFC) and VMPFC, precuneus, inferior frontal gyrus (IFG), middle cingulate cortex, precentral gyrus, somatosensory cortex (postcentral gyrus, supramarginal gyrus (SMG)), and hypothalamus. Other regions with significant positive quadratic valence dependency included the right superior temporal gyrus (STG), left caudate nucleus, left retrosplenial cortex, right anterior and posterior cingulate cortex, and left thalamus. Full summary of clusters showing significant positive quadratic dependencies with

valence is presented in Table 2. There were neither significant negative quadratic (inverted U-shaped) effects of valence, nor any significant quadratic effects of arousal. In a complementary approach, we divided the valence dimension from neutral (5) into two separate parts (positive and negative), and modeled the effects of positive and negative valence on BOLD signal separately. In other words, analysis was restricted to either negative or positive parts of the movies, as evaluated by each participant. In this analysis, we failed to find significant correlations between BOLD signal and valence or arousal at $p < 0.05$ FDR-corrected statistical threshold.

Table 2. Brain regions showing increased activity as a second-order (X^2) function of valence ($p < 0.05$, FDR corrected). Coordinates are in the MNI space.

Region	Laterality	X	Y	Z	T
Precuneus	L/R	12	-62	34	7.10
Inferior frontal gyrus (Ventrolateral prefrontal cortex), Insula	R	40	26	8	6.23
Inferior frontal gyrus (Ventrolateral prefrontal cortex)	L	-48	14	8	4.73
Insula	L	-38	2	20	4.00
Postcentral gyrus (Somatosensory cortex)	R	52	-26	48	4.13
Postcentral gyrus (Somatosensory cortex)	L	-32	-36	48	5.92
Supramarginal gyrus (Somatosensory cortex)	L	-66	-26	36	6.81
Supramarginal gyrus (Somatosensory cortex), Superior temporal gyrus	R	58	-34	23	5.38
Inferior temporal gyrus	R	52	-50	-8	6.19
Precentral gyrus (Motor cortex)	L	-58	-22	26	4.46
Precentral gyrus (Motor cortex)	R	52	0	44	3.59
Superior orbital gyrus (Orbitomedial prefrontal cortex)	L	-18	58	-4	4.51
Orbitomedial prefrontal cortex	R	18	62	6	4.13
Anterior cingulate cortex	R	11	38	30	3.85
Middle cinculate cortex	L/R	2	-20	30	3.87
Middle cinculate cortex	L	-6	8	44	3.43
Posterior cingulate cortex	R	14	-38	40	3.12
Retrosplenial cortex	L	-8	-42	28	3.58
Hypothalamus	R	8	-4	-6	3.73
Hypothalamus	L	-6	-4	-6	3.42
White matter posterior to lentiform nucleus	R	32	-20	0	3.73
Middle frontal gyrus (Ventrolateral prefrontal cortex)	L	-42	42	10	3.55
Ventromedial prefrontal cortex	L	-18	38	16	3.13
Ventromedial prefrontal cortex	R	10	55	16	3.19
Caudate nucleus	L	-16	-12	30	3.10
Calcarine sulcus	L	-24	-70	10	3.33
Thalamus	L	-16	-22	12	3.09
Supplementary motor area	L/R	-6	-10	68	3.03
Cerebellar vermis	L/R	0	-62	-14	3.11
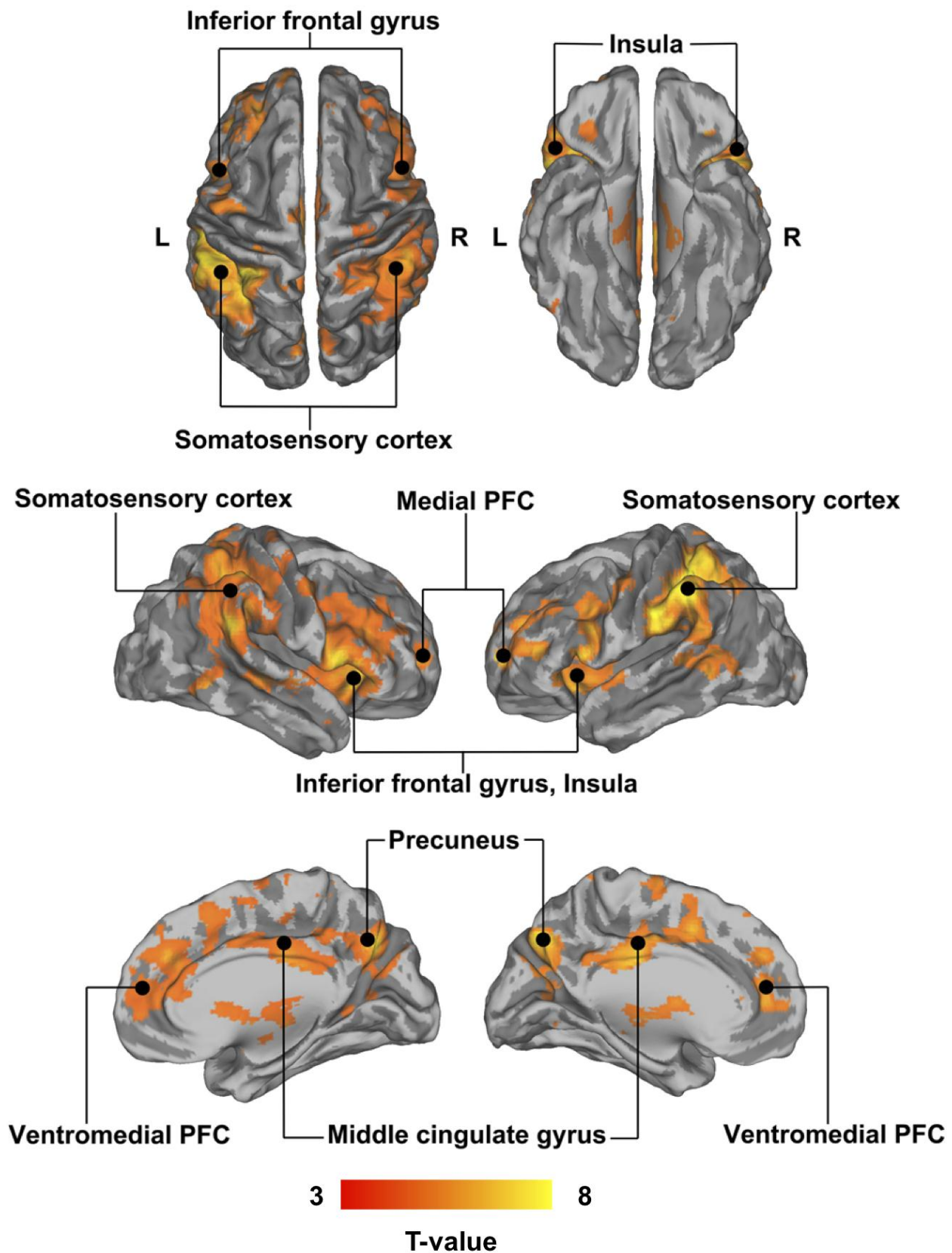
Figure 3. Brain regions encoding subjective emotional state in quadratic (X^2) fashion ($p < 0.05$ FDR corrected). PFC = prefrontal cortex.
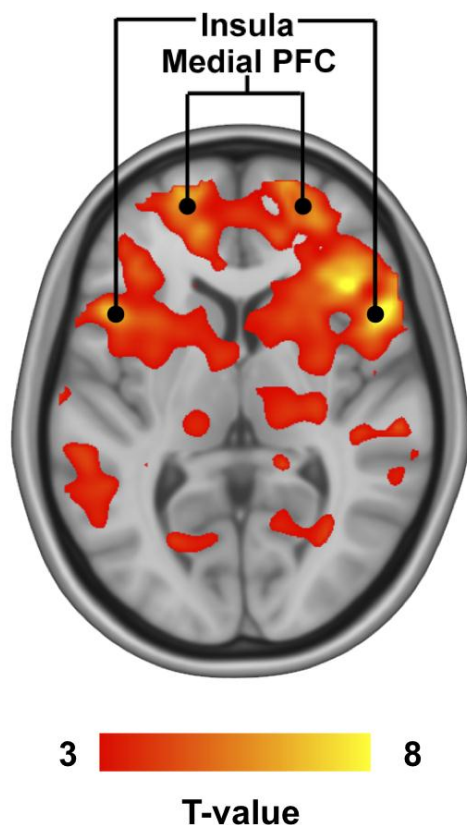
Figure 4. Axial section of the brain showing quadratic (X^2) responses to valence ($p < 0.05$ FDR corrected).

DISCUSSION

Our results reveal how the brain continuously tracks the affective valence of sensory input during extended dynamic natural stimulation, and generates corresponding subjective feelings of pleasantness and unpleasantness. The data show how moment-to-moment fluctuations in the experienced valence of emotions modulate brain responses in limbic (thalamus, hypothalamus, insula), somatosensory, (postcentral gyrus, supramarginal gyrus), and frontocortical (lateral and medial prefrontal cortex) components of the circuit encoding emotional feelings. Critically, we were able to establish that the subjective emotional experiences of valence and the BOLD responses in the affect circuits had a U-shaped rather than linear relationship, with both unpleasant and pleasant emotional feelings leading to increased brain activity. These effects were observed while controlling for low-level visual features of the movie stimulus, thus suggesting that the valence-modulated effects were not confounded with mere sensory properties of the films but, rather, that they reflect genuine effects brought about by

the subjective emotional experiences.

Brain systems underlying subjective emotional experience

Previous imaging and lesion studies suggest that subjective emotional states arise and are accessed by a coordinated cortical-subcortical network comprising of amygdala, thalamus and hypothalamus, insula and somatosensory cortices, anterior cingulate cortex (ACC), and dorsal and ventral medial prefrontal cortex (VMPFC), as well as orbitofrontal cortex (OFC) [3, 15]. We found that subjective feelings of pleasantness versus unpleasantness (valence) significantly modulated the activity of these circuits in a quadratic fashion during prolonged, naturalistic emotional stimulation. First, self-reported valence significantly modulated BOLD responses in regions encoding emotional salience and regulating autonomic nervous system (ANS) including hypothalamus, thalamus and caudate nucleus. As hypothalamus regulates the functioning of ANS [56], it is understandable that it showed increased activation towards both negative and positive valence events, as both types of events require adjustments in the ANS activity. This is also in accordance with findings from previous fMRI studies that have established that hypothalamic activity is increased for both pleasant and unpleasant emotional stimuli [57]. Thalamus has been associated with numerous emotion-related functions such as integrated autonomic expression of emotions [58], and several earlier studies, using emotional movie stimuli, have reported increased thalamus responses to both pleasant and unpleasant emotional stimulation [12, 25]. Thalamus is also known to regulate and mediate interoceptive awareness of arousal [59, 60]. In line with this, thalamus is activated by both observing others' pain as well as rating the intensity of painful experiences [61]. The present results, showing U-shaped valence dependency in the thalamus, suggest that thalamus has potentially an important role also in interoceptive awareness of emotion-induced mental and bodily states.

The models of brain basis of emotional feelings have attributed VMPFC, insula and somatosensory cortices a special role in the generation of emotion-related physiological states and corresponding emotional feelings [3, 62]. We

found significant, quadratic valence-modulated BOLD responses in all these regions. The frontal cortex is centrally involved in the processing of emotions, with VMPFC regions serving as a high-level trigger for autonomic emotional responses to external events [4, 18, 19]. Consistent with this, VMPFC responses showed U-shaped dependency of the self-reported valence of the movies. Importantly, similar left-hemispheric region of the VMPFC showed U-shaped valence dependency also in an earlier study using auditory emotional stimuli [41], suggesting that the VMPFC may encode emotional valence irrespective of stimulus modality.

The anterior insula supports interoceptive awareness, enabling subjective feelings from the body to be transformed into conscious experiences of emotions [21, 63]. Subjective emotional feelings often involve awareness of the emotion-triggered bodily changes, and it has been proposed that emotional and interoceptive states might actually share an integrated representation in the insula [62, 64]. The insula is also reliably activated by emotion imagery without any sensory input, highlighting its role in generating affective feelings [65]. Further support for this notion comes from research involving alexithymic autists, who show reduced activation in the anterior insula when evaluating their subjective feelings induced by emotionally evocative pictures [66]. Together with ACC, the insula is an important facilitator in distinguishing the most relevant/salient internal and environmental stimuli [67]. This could in part explain the U-shaped valence dependency found in these regions (see also [39, 40, 49, 50]).

It has been proposed that somatosensory cortices access the somatovisceral state brought about by emotions, and that they might be crucial for generating the subjective emotional feelings on the basis of feedback from the body [3, 15]. Consistent with this, we observed that the magnitude of the somatosensory responses were contingent on the affective valence, both positive and negative deviations from neutral valence leading to strongest somatosensory responses. Interestingly, we also found that that one key component of the putative mirror neuron circuit – inferior frontal gyrus [IFG; 68] – exhibited U-shaped dependency on valence. Although activation of the mirror-neuron system probably is

not a prerequisite for generating physiological emotional states in humans (consider, for example, the case of experience of disgust upon smelling rotten meat), some studies suggest that they might be involved in emotional contagion from others' emotional expressions: when we grasp our emotional states from others' emotional behaviour, mirroring systems might provide more detailed representation of others' action tendencies, and this premotor code might also contribute to the emotional experience [69, 70]. One must be cautious, however, when interpreting the role of IFG activity, since this region serves multiple purposes in addition mirroring.

Significant U-shaped dependency with subjectively experienced valence was also observed in cortical midline structures belonging to the 'default mode' network [71]; most notably in the posterior and retrosplenial parts of the cingulate cortex and the precuneus. The activity of the default-mode network is typically suppressed during external stimulation [72], but here we found that default-mode network activity was enhanced when participants were experiencing either positive or negative emotions. This corroborates recent findings suggesting that the default-mode network may actually be involved in evaluating of potentially survival-salient information from the body and the environment [72, 73]. These processes might be suppressed during free exploration of the environment, but are rapidly engaged when highly relevant information such as intense emotional responses need to be consciously accessed. In line with this, quite a few previous studies have reported particularly precuneus activations to pleasant [74, 75] and unpleasant [74, 76] emotional stimulation. Further, in our earlier study we observed that valence of emotional sounds modulates the activity of precuneus in a U-shaped fashion [41]. Precuneus has been proposed to underlie consciousness [77] and self-consciousness [78], and its activity is increased for example when participants recall how they rated several attributes to describe themselves [79]. As emotional feelings are brought about by the conscious representation of the neural and bodily changes triggered by the emotion, it is likely that self-referential encoding or self-awareness would be increased when (pleasant or unpleasant)

emotional states are brought about. This is in line with findings showing that the precuneus has functional connections to the key regions encoding emotional feelings, that is, the sensorimotor cortex and prefrontal cortex [80]. We thus propose that the precuneus might contribute to emotional feelings by increasing the level of self-consciousness when emotional states are brought about in the observer.

Quadratic Versus Linear Representation of Valence

Contrary to some earlier studies [34, 35, 36, 37, 38, 50, 51, 81], we failed to observe significant linear relationships between valence and BOLD responses elicited by emotional stimulation (with $p < 0.05$, FDR-corrected). Instead, we found that activity in the brain regions underlying subjective emotional feelings was the highest when the subjective experience of valence was strong (either negative or positive) and the lowest during neutral subjective experience. During recent years evidence for non-linear valence dependency of brain activity has been accumulating [39, 40, 41, 42], and our results give further support for this view using naturalistic and dynamic stimulation conditions that closely mimic emotional events one encounters in daily life. The quadratic (U-shaped) response profiles of the brain regions involved in emotional processing suggest that there might actually be partially separable neural systems that encode pleasant and unpleasant valence. The idea of two distinct systems relating to approach and withdrawal situations is old. Already in the 1950s, Miller [82] demonstrated that rats can exhibit separate approach and withdrawal gradients if closeness of reward versus punishment is modulated. In similar vein, single-cell recordings have established that individual cells in the monkey amygdala respond to either positive or negative value, but not both [44]. Functional imaging studies showing U-shaped valence dependency have also shown independent negativity and positivity processing mechanisms and support separate representations for positive and negative valence in the emotion circuit [39, 40, 42]. Such bivariate valence representation probably serves partially independent pleasantness and unpleasantness evaluations, which in turn enables separate approach and withdrawal behaviors [43].

The quadratic valence-contingent response profile of the emotion circuit naturally raises the question of whether the observed effects could actually be explained by a linear relationship between BOLD response and arousal, as both strongly negative and positive emotional states are associated with elevated arousal [33]. Importantly, we found no evidence of arousal-modulated BOLD responses at the set a priori threshold ($p < 0.05$, FDR-corrected), providing further support for the notion that valence representation in the brain is indeed quadratic rather than linear. Only when more lenient threshold ($p < 0.001$, uncorrected) was applied, we observed linear modulation of BOLD signal by arousal in the precuneus.

CONCLUSION

We conclude that during extended naturalistic stimulation, a widespread cortical-subcortical network of brain areas, extending from the thalamus and hypothalamus to the insula, somatosensory and medial prefrontal cortices, encodes subjectively felt emotional valence in a quadratic fashion. These results suggest that under natural dynamic conditions with constantly changing emotional events these neuronal populations encode felt valence in a non-linear fashion. Accordingly, our data cast doubts on the linear, bipolar valence models and suggest that approach and avoidance tendencies might activate independently and possibly sometimes even simultaneously. Importantly, our study takes a new step towards studying the brain basis of emotional reactions under highly naturalistic conditions and confirms that such approach is both feasible and reliable way of studying the emotional brain under conditions that resemble the unpredictability and complexity of real life.

APPENDIX

Descriptions of the films used in the experiment

Durations, valences, arousals, basic emotions and target emotions have been described. Valence and arousal scores range from 1 (unpleasant / calm) to 9 (pleasant / aroused). The evaluations of basic emotions, given as one number after presentation of each film, range from 0.0 to 1.0. The actual order of the films in the fMRI experiment was 11-13-5-10-3-6-7-2-8-4-12-

1-9 and in the behavioral part outside the scanner 3-4-8-5-9-12-6-1-13-11-7-2-10.

1. **An Officer And a Gentleman 1**

   Paula works in a factory. She has met a young officer Zack. He does not yet know where the acquaintance will lead. (Duration = 111s, $M_{valence}$ = 6.66, $M_{arousal}$ = 4.46, M_{anger} = 0.077, $M_{disgust}$ = 0.109, M_{fear} = 0.045, $M_{pleasure}$ = 0.711, $M_{sadness}$ = 0.079, $M_{surprise}$ = 0.401, target emotion: pleasure/happiness).

2. **An Officer And a Gentleman 2**

   Zack and Paula are looking for their friend Sid. They knock on the door of his motel room. As no one answers they enter the room. (Duration = 80s, $M_{valence}$ = 3.27, $M_{arousal}$ = 5.64, M_{anger} = 0.202, $M_{disgust}$ = 0.458, M_{fear} = 0.356, $M_{pleasure}$ = 0.163, $M_{sadness}$ = 0.646, $M_{surprise}$ = 0.522, target emotion: sadness).

3. **Emmanuelle 1**

   Emmanuelle meets her lover in his home. (Duration = 88s, $M_{valence}$ = 7.11, $M_{arousal}$ = 6.41, M_{anger} = 0.026, $M_{disgust}$ = 0.070, M_{fear} = 0.040, $M_{pleasure}$ = 0.754, $M_{sadness}$ = 0.038, $M_{surprise}$ = 0.292, target emotion: erotic).

4. **Emmanuelle 2**

   A couple spends holiday in a hotel. They have just woken up. (Duration = 93s, $M_{valence}$ = 6.96, $M_{arousal}$ = 5.99, M_{anger} = 0.025, $M_{disgust}$ = 0.061, M_{fear} = 0.028, $M_{pleasure}$ = 0.762, $M_{sadness}$ = 0.059, $M_{surprise}$ = 0.306, target emotion: erotic).

5. **Godfather**

   Jack, a wealthy film producer, lives in an ostentatious villa. One morning he wakes up in his bed. (Duration = 59s, $M_{valence}$ = 4.15, $M_{arousal}$ = 5.27, M_{anger} = 0.296, $M_{disgust}$ = 0.671, M_{fear} = 0.452, $M_{pleasure}$ = 0.129, $M_{sadness}$ = 0.272, $M_{surprise}$ = 0.574, target emotion: disgust).

6. **Halloween**

   Laurie is working as a babysitter at her parents' friends. When she arrives there one evening she does not find anybody on the ground floor and she goes upstairs. (Duration = 116s, $M_{valence}$ = 3.17, $M_{arousal}$ = 6.15, M_{anger} = 0.355, $M_{disgust}$ = 0.505, M_{fear} = 0.667, $M_{pleasure}$ = 0.164, $M_{sadness}$ = 0.282, $M_{surprise}$ = 0.522, target emotion: fear).

7. **Hannah and her sisters**

   Hannah and Holly are shopping. They talk about last night. (Duration = 92s, $M_{valence}$ = 4.50, $M_{arousal}$ = 3.49, M_{anger} = 0.094, $M_{disgust}$ = 0.199, M_{fear} = 0.092, $M_{pleasure}$ = 0.217, $M_{sadness}$ = 0.139, $M_{surprise}$ = 0.215, target emotion: neutral).

8. **Maria's lovers**

   Ivan spends a night in a cheap hotel. At night he is dreaming. (Duration = 58s, $M_{valence}$ = 3.39, $M_{arousal}$ = 5.78, M_{anger} = 0.303, $M_{disgust}$ = 0.719, M_{fear} = 0.471, $M_{pleasure}$ = 0.091, $M_{sadness}$ = 0.218, $M_{surprise}$ = 0.456, target emotion: disgust).

9. **Pink Flamingos**

   John is making unusual video films. One morning he films a transvestite and a poodle. (Duration = 29s, $M_{valence}$ = 3.47, $M_{arousal}$ = 5.92, M_{anger} = 0.229, $M_{disgust}$ = 0.802, M_{fear} = 0.170, $M_{pleasure}$ = 0.199, $M_{sadness}$ = 0.147, $M_{surprise}$ = 0.548, target emotion: disgust).

10. **The Champ**

    Billy is seriously wounded in a boxing match. He summons his son. (Duration = 130s, $M_{valence}$ = 2.89, $M_{arousal}$ = 5.44, M_{anger} = 0.225, $M_{disgust}$ = 0.417, M_{fear} = 0.356, $M_{pleasure}$ = 0.134, $M_{sadness}$ = 0.737, $M_{surprise}$ = 0.295, target emotion: sadness).

11. **The Last Emperor**

    The heir to the throne of China meets his new British teacher. They talk about the studies together. (Duration = 75s, $M_{valence}$ = 4.72, $M_{arousal}$ = 3.67, M_{anger} = 0.158, $M_{disgust}$ = 0.169, M_{fear} = 0.109, $M_{pleasure}$ = 0.226, $M_{sadness}$ = 0.126, $M_{surprise}$ = 0.220, target emotion: neutral).

12. **Silence of the Lambs**

    Clarice, a young FBI agent, is searching for a serial killer. In her investigation she questions the tailor James, whom she suspects as the murderer. (Duration = 133s, $M_{valence}$ = 3.81, $M_{arousal}$ = 6.29, M_{anger} = 0.369, $M_{disgust}$ = 0.445, M_{fear} = 0.622, $M_{pleasure}$ = 0.223, $M_{sadness}$ = 0.166, $M_{surprise}$ = 0.434, target emotion: fear).

13. **When Harry met Sally**

    Harry and Sally are sitting at a cafe. They discuss about whether Harry would notice if a woman faked an orgasm. (Duration = 100s, $M_{valence}$ = 6.42, $M_{arousal}$ = 4.78, M_{anger} = 0.050, $M_{disgust}$ = 0.068, M_{fear} = 0.078, $M_{pleasure}$ = 0.720, $M_{sadness}$ = 0.053, $M_{surprise}$ = 0.417, target emotion: pleasure/happiness).

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ACKNOWLEDGEMENTS

REFERENCES

[1] James W. What is an emotion? *Mind.* **1884;** 9: 188-205.

[2] Damasio AR. Emotion in the perspective of an integrated nervous system. *Brain Res Brain Res Rev.* **1998;** 26: 83-6.

[3] Barrett LF, Mesquita B, Ochsner KN, Gross JJ. The experience of emotion. *Annu Rev Psychol.* **2007;** 58: 373-403.

[4] Tsuchiya N, Adolphs R. Emotion and consciousness. *Trends Cogn Sci.* **2007;** 11: 158-167.

[5] Damasio AR. The somatic marker hypothesis and the possible functions of the prefrontal cortex. *Philos Trans R Soc Lond B Biol Sci.* **1996;** 351: 1413-20.

[6] Adolphs R. Recognizing emotion from facial expressions: Psychological and neurological mechanisms. *Behav Cogn Neurosci Rev.* **2002;** 1: 21-62.

[7] Vuilleumier P. How brains beware: neural mechanisms of emotional attention. *Trends Cogn Sci.* **2005;** 9: 585-94.

[8] Posse S, Fitzgerald D, Gao K, Habel U, Rosenberg D, Moore GJ, Schneider F. Real-time fMRI of temporolimbic regions detects amygdala activation during single-trial self-induced sadness. *Neuroimage*. **2003;** 18: 760-8.

[9] Schneider F, Grodd W, Weiss U, Klose U, Mayer KR, Nägele T, Gur RC. Functional MRI reveals left amygdala activation during emotion. *Psychiatry Res.* **1997;** 76: 75-82.

[10] Harrison NA, Gray MA, Gianaros PJ, Critchley HD. The embodiment of emotional feelings in the brain. *J Neurosci.* **2010;** 30: 12878-84.

[11] Aalto S, Naatanen P, Wallius E, Metsahonkala L, Stenman H, Niem PM, Karlsson H. Neuroanatomical substrata of amusement and sadness: a PET activation study using film stimuli. *Neuroreport.* **2002;** 13: 67-73.

[12] Goldin PR, Hutcherson CA, Ochsner KN, Glover GH, Gabrieli JD, Gross JJ. The neural bases of amusement and sadness: a comparison of block contrast and subject-specific emotion intensity regression approaches. *Neuroimage.* **2005;** 27: 26-36.

[13] Hutcherson CA, Goldin PR, Ochsner KN, Gabrieli JD, Barrett LF, Gross JJ. Attention and emotion: does rating emotion alter neural responses to amusing and sad films? *Neuroimage.* **2005;** 27: 656-68.

[14] Westermann R, Spies K, Stahl G, Hesse FW. Relative effectiveness and validity of mood induction procedures: A meta-analysis. *Eur J Soc Psychol.* **1996;** 26: 557-80.

[15] Adolphs R, Damasio H, Tranel D, Cooper G, Damasio AR. A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *J Neurosci.* **2000;** 20: 2683-90.

[16] Sander D, Grafman J, Zalla T. The human amygdala: an evolved system for relevance detection. *Rev Neurosci.* **2003;** 14: 303-16.

[17] Devinsky O, Morrell MJ, Vogt BA. Contributions of anterior cingulate cortex to behaviour. *Brain*. **1995;** 118: 279-306.

[18] Gray JR, Braver TS, Raichle ME. Integration of emotion and cognition in the lateral prefrontal cortex. *Proc Natl Acad Sci USA.* **2002;** 99: 4115-20.

[19] Etkin A, Egner T, Kalisch R. Emotional processing in anterior cingulate and medial prefrontal cortex. *Trends Cogn Sci.* **2011;** 15: 85-93.

[20] Craig AD. Human feelings: why are some more aware than others? *Trends Cogn Sci.* **2004;** 8: 239-41.

[21] Critchley HD, Wiens S, Rotshtein P, Ohman A, Dolan RJ. Neural systems supporting interoceptive awareness. *Nat Neurosci.* **2004;** 7: 189-95.

[22] Johnsen EL, Tranel D, Lutgendorf S, Adolphs R. A neuroanatomical dissociation for emotion induced by music. *Int J Psychophysiol.* **2009;** 72: 24-33.

[23] Pourtois G, Sander D, Andres M, Grandjean D, Reveret L, Olivier E, Vuilleumier P. Dissociable roles of the human somatosensory and superior temporal cortices for processing social face signals. *Eur J Neurosci.* **2004;** 20: 3507-15.

[24] Nummenmaa L, Hirvonen J, Parkkola R, Hietanen JK. Is emotional contagion special? An fMRI study on neural systems for affective and cognitive empathy. *Neuroimage.* **2008;** 43: 571-80.

[25] Reiman EM, Lane RD, Ahern GL, Schwartz GE, Davidson RJ, Friston KJ, Yun LS, Chen K. Neuroanatomical correlates of externally and internally generated human emotion. *Am J Psychiatry.* **1997;** 154: 918-25.

[26] Habel U, Klein M, Kellermann T, Shah NJ, Schneider F. Same or different? Neural correlates of happy and sad mood in healthy males. *Neuroimage.* **2005;** 26: 206-14.

[27] Damasio AR, Grabowski TJ, Bechara A, Damasio H, Ponto LL, Parvizi J, Hichwa RD. Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nat Neurosci.* **2000;** 3: 1049-56.

[28] Garrett AS, Maddock RJ. Separating subjective emotion from the perception of emotion-inducing stimuli: an fMRI study. *Neuroimage.* **2006;** 33: 263-74.

[29] Kringelbach ML. The human orbitofrontal cortex: linking reward to hedonic experience. *Nat Rev Neurosci.* **2005;** 6: 691-702.

[30] Hornak J, Bramham J, Rolls ET, Morris RG, O'Doherty J, Bullock PR, Polkey CE. Changes in emotion after circumscribed surgical lesions of the orbitofrontal and cingulate cortices. *Brain.* **2003;** 126: 1691-712.

[31] Ekman P. An argument for basic emotions. *Cogn Emot.* **1992;** 6: 169-200.

[32] Russell JA. A Circumplex Model of Affect. *J Pers Soc Psychol.* **1980;** 39: 1161-78.

[33] Lang PJ. The Emotion Probe - Studies of Motivation and Attention. *Am Psychol.* **1995;** 50: 372-85.

[34] Anderson AK, Christoff K, Stappen I, Panitz D, Ghahremani DG, Glover G, Gabrieli JD, Sobel N. Dissociated neural representations of intensity and valence in human olfaction. *Nat Neurosci.* **2003;** 6: 196-202.

[35] Colibazzi T, Posner J, Wang Z, Gorman D, Gerber A, Yu S, Zhu H, Kangarlu A, Duan Y, Russell JA, Peterson BS. Neural systems subserving valence and arousal during the experience of induced emotions. *Emotion.* **2010;** 10: 377-89.

[36] Grabenhorst F, Rolls ET, Margot C, da Silva MA, Velazco MI. How pleasant and unpleasant stimuli combine in different brain regions: odor mixtures. *J Neurosci.* **2007;** 27: 13532-40.

[37] Gerber AJ, Posner J, Gorman D, Colibazzi T, Yu S, Wang Z, Kangarlu A, Zhu H, Russell J, Peterson BS. An affective circumplex model of neural systems subserving valence, arousal, and cognitive overlay during the appraisal of emotional faces. *Neuropsychologia.* **2008;** 46: 2129-39.

[38] Grimm S, Schmidt CF, Bermpohl F, Heinzel A, Dahlem Y, Wyss M, Hell D, Boesiger P, Boeker H, Northoff G. Segregated neural representation of distinct emotion dimensions in the prefrontal cortex-an fMRI study. *Neuroimage.* **2006;** 30: 325-40.

[39] Lewis PA, Critchley HD, Rotshtein P, Dolan RJ. Neural correlates of processing valence and arousal in affective words. *Cereb Cortex.* **2007;** 17: 742-8.

[40] Viinikainen M, Jaaskelainen IP, Alexandrov Y, Balk MH, Autti T, Sams, M. Nonlinear relationship between emotional valence and brain activity: evidence of separate negative and positive valence dimensions. *Hum Brain Mapp.* **2010;** 31: 1030-40.

[41] Viinikainen M, Kätsyri J, Sams M. Representation of perceived sound valence in the human brain. *Hum Brain Mapp.* **2011**.

[42] Viinikainen M, Jaaskelainen IP, Balk MH, Autti T, Sams M. Neural processing of emotional valence of facial expressions. *Open J Neurosci.* **2012;** 2: 3.

[43] Cacioppo JT, Berntson GG. Relationship Between Attitudes and Evaluative Space: A Critical Review, With Emphasis on the Separability of Positive and Negative Substrates. *Psychol Bull.* **1994;** 115: 401-23.

[44] Paton JJ, Belova MA, Morrison SE, Salzman CD. The primate amygdala represents the positive and negative value of visual stimuli during learning. *Nature.* 2006; 439: 865-70.

[45] Hasson U, Malach R, Heeger DJ. Reliability of cortical activity during natural stimulation. *Trends Cogn Sci.* 2010; 14: 40-8.

[46] Gerrards-Hesse A, Spies K, Hesse FW. Experimental inductions of emotional states and their effectiveness: A review. *Br J Psychol.* **1994;** 85: 55-78.

[47] Rottenberg J, Ray RD, Gross JJ: Emotion elicitation using films. In Coan JA, Allen JJB, ed. *The handbook of emotion elicitation and assessment.* London: Oxford University Press, **2007**.

[48] Hewig J, Hagemann D, Seifert J, Gollwitzer M, Naumann E, Bartussek D. A revised film set for the induction of basic emotions. Cogn Emot. 2005; 19: 1095-109.

[49] Small DM, Gregory MD, Mak YE, Gitelman D, Mesulam MM, Parrish T. Dissociation of neural representation of intensity and affective valuation in human gustation. *Neuron.* **2003;** 39: 701-11.

[50] Posner J, Russell JA, Gerber A, Gorman D, Colibazzi T, Yu S, Wang Z, Kangarlu A, Zhu H, Peterson BS. The neurophysiological bases of emotion: an fMRI study of the affective circumplex using emotion-denoting words. *Hum Brain Mapp.* **2009;** 30: 883-95.

[51] Heinzel A, Bermpohl F, Niese R, Pfennig A, Pascual-Leone A, Schlaug G, Northoff G. How do we modulate our emotions? Parametric fMRI reveals cortical midline structures as regions specifically involved in the processing of emotional valences. *Brain Res Cogn Brain Res.* **2005;** 25: 348-58.

[52] Anders S, Eippert F, Weiskopf N, Veit R. The human amygdala is sensitive to the valence of

pictures and sounds irrespective of arousal: an fMRI study. *Soc Cogn Affect Neurosci.* **2008;** 3: 233-43.

[53] Dünser A, Looser J, Grasset R, Seichter H, Billinghurst M. Evaluation of Tangible User Interfaces for Desktop AR. *2010 International Symposium on Ubiquitous Virtual Reality*, Gwangju.

[54] Daugman JG. Uncertainty relation for resolution in space, spatial frequency, and orientation optimized by two-dimensional visual cortical filters. *J Opt Soc Am A.* **1985;** 2: 1160-9.

[55] Brox T, Bruhn A, Papenberg N, Weickert J. High Accuracy Optical Flow Estimation Based on a Theory for Warping. *European Conference on Computer Vision (ECCV).* **2004;** pp 25-36.

[56] Elmquist JK. Hypothalamic pathways underlying the endocrine, autonomic, and behavioral effects of leptin. *Physiol Behav.* **2001;** 74: 703-8.

[57] Lane RD, Reiman EM, Bradley MM, Lang PJ, Ahern GL, Davidson RJ, Schwartz GE. Neuroanatomical correlates of pleasant and unpleasant emotion. *Neuropsychologia.* **1997;** 35: 1437-44.

[58] Bard P. A diencephalic mechanism for the expression of rage with special reference to the sympathetic nervous system. *Am J Physiol.* **1928;** 84: 490-515.

[59] McCormick DA, Bal T. Sleep and arousal: Thalamocortical mechanisms. *Annu Rev Neurosci.* **1997;** 20: 185-215.

[60] Pollatos O, Schandry R, Auer DP, Kaufmann C. Brain structures mediating cardiovascular arousal and interoceptive awareness. *Brain Res.* **2007;** 1141: 178-87.

[61] Jackson PL, Meltzoff AN, Decety J. Neural circuits involved in imitation and perspective-taking. *Neuroimage.* **2006;** 31: 429-39.

[62] Craig AD. How do you feel? Interoception: the sense of the physiological condition of the body. *Nat Rev Neurosci.* **2002;** 3: 655-66.

[63] Gray MA, Harrison NA, Wiens S, Critchley HD. Modulation of emotional appraisal by false physiological feedback during fMRI. *PLoS One.* **2007;** 2: e546.

[64] Phillips ML, Gregory LJ, Cullen S, Coen S, Ng V, Andrew C, Giampietro V, Bullmore E, Zelaya F, Amaro E, Thompson DG, Hobson AR, Williams SC, Brammer M, Aziz Q. The effect of negative emotional context on neural and behavioural responses to oesophageal stimulation. *Brain.* **2003;** 126: 669-84.

[65] Phan KL, Wager T, Taylor SF, Liberzon I. Functional neuroanatomy of emotion: A meta-analysis of emotion activation studies in PET and fMRI. *Neuroimage.* **2002;** 16: 331-48.

[66] Silani G, Bird G, Brindley R, Singer T, Frith C, Frith U. Levels of emotional awareness and autism: an fMRI study. *Soc Neurosci.* **2008;** 3: 97-112.

[67] Menon V, Uddin LQ. Saliency, switching, attention and control: a network model of insula function. *Brain Struct Funct.* **2010;** 214: 655-67.

[68] Rizzolatti G, Craighero L. The mirror-neuron system. *Annu Rev Neurosci.* **2004;** 27: 169-92.

[69] Wicker B, Keysers C, Plailly J, Royet JP, Gallese V, Rizzolatti G. Both of us disgusted in My insula: the common neural basis of seeing and feeling disgust. *Neuron.* **2003;** 40: 655-64.

[70] Carr L, Iacoboni M, Dubeaut MC, Mazziotta JC, Lenzi GL. Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proc Natl Acad Sci U S A.* **2003;** 100: 5497-502.

[71] Raichle ME. Two views of brain function. *Trends Cogn Sci.* **2010;** 14: 180-90.

[72] Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL. A default mode of brain function. *Proc Natl Acad Sci U S A.* **2001;** 98: 676-82.

[73] Schilbach L, Eickhoff SB, Rska-Jagiela AR, Fink GR, Vogeley K. Minds at rest? Social cognition as the default mode of cognizing and its putative relationship to the "default system" of the brain. *Conscious Cogn.* **2008;** 17: 457-67.

[74] Paradiso S, Johnson DL, Andreasen NC, O'Leary DS, Watkins GL, Ponto LL, Hichwa RD. Cerebral blood flow changes associated with attribution of emotional valence to pleasant, unpleasant, and neutral visual stimuli in a PET study of normal subjects. *Am J Psychiatry.* **1999;** 156: 1618-29.

[75] Teasdale JD, Howard RJ, Cox SG, Ha Y, Brammer MJ, Williams SC, Checkley SA. Functional MRI study of the cognitive generation of affect. *Am J Psychiatry.* **1999;** 156: 209-15.

[76] Morris JS, Friston KJ, Buchel C, Frith CD, Young AW, Calder AJ, Dolan RJ. A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain.* **1998;** 121: 47-57.

[77] Cavanna AE. The precuneus and consciousness. *CNS Spectrums.* **2007;** 12: 545-52.

[78] Cavanna AE, Trimble MR. The precuneus: a review of its functional anatomy and behavioural correlates. *Brain.* **2006;** 129: 564-83.

[79] Lou HC, Luber B, Crupain M, Keenan JP, Nowak M, Kjaer TW, Sackeim HA, Lisanby SH. Parietal cortex and representation of the mental self. *Proc Natl Acad Sci U S A.* **2004;** 101: 6827-32.

[80] Margulies DS, Vincent JL, Kelly C, Lohmann G, Uddin LQ, Biswal BB, Villringer A, Castellanos FX, Milham MP, Petrides M. Precuneus shares intrinsic functional architecture in humans and monkeys. *Proc Natl Acad Sci U S A.* **2009;** 106: 20069-74.

[81] Cunningham WA, Raye CL, Johnson MK. Implicit and explicit evaluation: FMRI correlates of valence, emotional intensity, and control in the processing of attitudes. *J Cogn Neurosci.* **2004;** 16: 1717-29.

[82] Miller NE. Liberalization of basic S-R concepts: Extensions to conflict behavior, motivation and social learning; Koch S, ed. New York: McGraw-Hill. **1959**, pp. 198-292.

[83] Dawdy DR, Matalas NC: Statistical and probability analysis of hydrologic data, part III: Analysis of variance, covariance and time series. In Chow VT, ed. *Handbook of Applied Hydrology, A Compendium of Water-Resources Technology.* New York: McGraw-Hill, **1964;** 68-90.