The impact of sociality and affective valence on brain activation: A meta-analysis

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Abstract

Thirty years of neuroimaging reveal the set of brain regions consistently associated with pleasant and unpleasant affect in humans—or the *neural reference space* for valence. Yet some of humans' most potent affective states occur in the context of other humans. Prior work has yet to differentiate how the neural reference space for valence varies as a product of the sociality of affective stimuli. To address this question, we meta-analyzed across 614 social and non-social affective neuroimaging contrasts, summarizing the brain regions that are consistently activated for social and non-social affective information. We demonstrate that across the literature, social and non-social affective stimuli yield overlapping activations within regions associated with visceromotor control, including the amygdala, hypothalamus, anterior cingulate cortex and insula. However, we find that social processing differs from non-social affective processing in that it involves additional cortical activations in the medial prefrontal and posterior cingulum that have been associated with mentalizing and prediction. A Bayesian classifier was able to differentiate unpleasant from pleasant affect, but not social from non-social affective states. Moreover, it was not able to classify unpleasantness from pleasantness at the highest levels of sociality. These findings suggest that highly social scenarios may be equally salient to humans, regardless of their valence.

Keywords: social, affect, valence, neuroimaging, meta-analysis

Highlights

- In humans, social stimuli are highly affective. We map how sociality and affective valence affect brain activations across the literature.
- We meta-analyzed 493 neuroimaging studies of social and non-social affective paradigms published from 1992-2019, including 7,801 participants.
- Social and non-social affective stimuli are associated with overlapping activations within visceromotor control regions.
- Social processing involves additional cortical activations previously associated with abstraction and prediction.
- Social v. non-social affective processing does not use unique circuitry but sociality relies on relatively more elaborate cortical processing.

Author contributions

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Data and Code Availability Statement

The meta-analytic database, codebook, and activation maps are available at https://osf.io/uzmxf/. Meta-analytic activation maps were produced in NeuroElf software version 1.1 https://neuroelf.net. Bayesian Spatial Point Process classification analyses were performed in C++ (for code: http://www-personal.umich.edu/~jiankang/software.html).

Author Acknowledgments

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Ethics Statement

Informed consent and institutional ethical review committee are not applicable to this study.

For over a century, scientists have rigorously studied the neurobiological basis of pleasantness and unpleasantness (Adolphs, 2010a; Blood et al., 1999; Lane et al., 1997; Lang and Bradley, 2007; LeDoux, 2012; LeDoux, 2000; LeDoux et al., 1984; Sander et al., 2003) using animal models (Knutson et al., 2002; Young, 2002), human lesion studies (Adolphs et al., 1999; Adolphs et al., 2003; Craig, 2005; Craig, 2003), and neuroimaging of healthy, awake, humans [for meta-analyses (Bartra et al., 2013; Clithero and Rangel, 2014; Lindquist et al., 2016)]. The dimension that ranges from pleasantness to unpleasantness is known as "valence," and is thought to serve as a signal as to whether objects, people, or situations are valuable to an organism and should be approached or avoided in the future (Barrett and Bliss-Moreau, 2009). In humans, valence is thought to infuse every moment of conscious experience and to serve as a "common currency" for comparing the value of otherwise disparate objects, people, and places (Cabanac, 2002).

It is thus not surprising that decades of research using neuroimaging have attempted to reveal the *neural reference space* for valence (Lindquist et al., 2016). A neural reference space is the set of neurons that probabilistically realize a class of mental events (Edelman, 1989). Such meta-analyses (Bartra et al., 2013; Clithero and Rangel, 2014; Lindquist et al., 2016) build on the human lesion and non-human animal literature to reveal sets of brain regions that are consistently activated during paradigms that elicit both pleasant and unpleasant affect (see Table 1). For instance, recent meta-analyses show that brain regions involved in visceromotor control (midbrain, nucleus accumbens, amygdala, ventromedial prefrontal cortex, supplementary motor area, dorsal anterior cingulate cortex, ventral anterior insula), representation of bodily states (dorsal anterior insula), heightened sensory processing (fusiform gyrus), and representation of and access to semantic knowledge (middle temporal gyrus, superior temporal gyrus, dorsomedial prefrontal cortex, inferior frontal gyrus) show consistent activation to both pleasant and unpleasant stimuli (Bartra et al., 2013; Lindquist et al., 2016). Amongst these valence-general regions, there is convergent evidence that left amygdala and insula show preferential activation to unpleasantness (Lindquist et al., 2016; Liu et al., 2011) and OFC and ventral striatum show preferential activation to pleasantness (Bartra et al., 2013; Lindquist et al., 2016; Liu et al., 2011).

Although this research has been informative, it has been largely agnostic about how other qualities of human experience may influence the function of the neural reference space for valence. It is not uncommon in the neuroimaging literature to manipulate pleasantness by showing participants images of smiling babies and fireworks, asking them to recall a beautiful sunset, presenting them with the smell of chocolate, or having them listen to a friendly voice. In contrast, studies manipulate unpleasantness by showing images of human violence and striking snakes, asking participants to imagine the death of a loved one, presenting them with the smell of vomit, or having them listen to screeching sirens. As a highly social species, it is not difficult to imagine that humans might represent images of smiling babies, memories of a loved one's death, or hearing a friendly voice as equally affectively evocative —if not more so—than images of cute puppies, memories of seeing roadkill, or hearing a babbling stream. The idea that social information is processed by social species in a distinct manner from non-social information is referred to as the "*social saliency*" hypothesis (Shamay-Tsoory and Abu-Akel, 2016). The *social saliency* hypothesis suggests that the brains of mammals evolved mechanisms [e.g., neuromodulatory molecules such as oxytocin and dopamine (Shamay-Tsoory and Abu-Akel, 2016); specific medial prefrontal cortex neurons (Bicks et al., 2015)] that represent the value of social cues and orient behavioral responses towards those cues. However, little research has examined the extent to which social saliency interacts with valence to influence large-scale brain activity in humans.

In the present meta-analysis, we systematically examine how the human neural reference space for valence varies as a product of the sociality of stimuli. We do so by meta-analyzing 493 neuroimaging studies of social and non-social affective content (614 experimental contrasts; 7,801 participants) published from 1992-2019. Building off past meta-analyses, we expect that the neural reference space for valence will consistently engage brain regions involved in visceromotor control, representation of bodily states, heightened sensory processing and representation and access to semantic knowledge (see Table 1, left column). However, many of these brain regions also play a role in social information processing, as revealed by human lesion studies, non-human animal studies and human neuroimaging studies of social behavior (see Table 1, right column). For instance, the social neuroscience literature reveals that the ventral striatum and

orbitofrontal cortex (OFC) are associated with social reward (Knutson and Cooper, 2005; McClure et al., 2004), whereas the amygdala, insula, and dorsal anterior cingulate (dACC) are associated with social rejection and punishment (Burklund et al., 2007; Masten et al., 2009). The fusiform gyrus and the occipito-temporal junction/extrastriate cortex have been related to face perception (Freeman et al., 2010; Grill-Spector et al., 2004; Kanwisher et al., 1997) and the posterior superior temporal gyrus (pSTG) and angular gyrus to perception of biological movement (Grossman et al., 2000). The medial prefrontal cortex (mPFC) (including both the dorsal and ventral medial prefrontal cortex (dmPFC, vmPFC), anterior cingulate cortex (ACC), and paracingulate cortex have been attributed to social cognition and mentalizing (Mar, 2011), or the ability to predict the abstract mental states of others (Andrews-Hanna et al., 2014; Campanella et al., 2014; Frith and Frith, 2003; Gallagher and Frith, 2003; Mars et al., 2012; Van Overwalle, 2009; Zaki et al., 2009). Mentalizing is also associated with temporal cortex including middle temporal cortex, superior temporal cortex and the temporoparietal junction (TPJ) (Koster-Hale et al., 2017).

Table 1. Brain regions associated with social and affective processing

Areas	Hypothesized Affective Function	Hypothesized Social Function
Fusiform gyrus and the occipito-temporal junction/extrastriate cortex	Responds to valence (Lang et al., 1998; Lindquist et al., 2016), and arousal (Hofmann et al., 2009; Lang et al., 1998; Mourao-Miranda et al., 2003)	Involved in face perception (Gobbini and Haxby, 2007; Kanwisher et al., 1997; Kanwisher and Yovel, 2006).
Posterior superior temporal gyrus (pSTG) and angular gyrus	Responds to valence (Lindquist et al., 2016; Narumoto et al., 2001), and arousal (Narumoto et al., 2001).	Involved in perceptions of biological motion and dynamic facial expressions (Grossman et al., 2000; Said et al., 2010)
Temporo-parietal junction (TPJ)	Responds to valence (Lindquist et al., 2016), and arousal (Kahnt and Tobler, 2013)	Mental state attribution (Van Overwalle and Baetens, 2009; Young et al., 2010)

Posterior cingulate cortex (PCC)	Affect (Kober et al., 2008), and reward processing (McCoy et al., 2003)	Social cognition and the ability to infer the mental states of others (Mar, 2011)
Dorsomedial prefrontal cortex (dmPFC)	Responds to valence (Lindquist et al., 2016), attention to one's affective state (Barrett and Satpute, 2013; Etkin et al., 2011), and attention to physiological arousal (Pollatos et al., 2007)	Social cognition and the ability to infer the mental states of others (Wagner et al., 2016)
Dorsal anterior cingulate cortex (dACC)	Responds to valence (Lindquist et al., 2016; Shackman et al., 2011; Weiss et al., 2018), arousal (Ebitz and Platt, 2015), and motivated behavior (Hayden and Platt, 2010)	Social cognition and the ability to infer the mental states of others (Singer et al., 2004), Social exclusion (Eisenberger, 2012; Eisenberger et al., 2003)
Ventromedial prefrontal cortex (vmPFC) extending into orbitofrontal cortex (OFC)	Responds to valence (Lindquist et al., 2016; Wilson-Mendenhall et al., 2013a), reward (Haber and Knutson, 2010), visceromotor regulation (Roy et al., 2012; Thayer et al., 2012; Zhang et al., 2014)	Social cognition and the ability to infer the mental states of others (Heberlein et al., 2008; Shamay-Tsoory et al., 2003), face perception (Freeman et al., 2010), accessing social conceptual knowledge (Knutson et al., 2007; Milne and Grafman, 2001; Stolier and Freeman, 2016) , engaging in socially appropriate behavior (Anderson et al., 1999; Beer et al., 2006), response to socially salient and novel social stimuli (Bicks et al., 2015)

Inferior frontal gyrus	Responds to valence (Lindquist et al., 2016), retrieval of emotion concepts (Brooks et al., 2016), and implicit emotion regulation (Lieberman, 2007; Torre and Lieberman, 2018)	Mirroring others' behavior (Kilner et al., 2009)
Temporal pole	Responds to valence (Lindquist et al., 2016), and emotion knowledge (Lindquist et al., 2014)	Social knowledge (Olson et al., 2007; Wang et al., 2017)
Anterior insula	Responds to valence (Lindquist et al., 2016), and arousal (Critchley et al., 2002), and representation of visceral state of the body in conscious awareness (Craig, 2009; Khalsa et al., 2009; Kleckner et al., 2017)	Mirroring others' behaviors (Wicker et al., 2003), empathy (Masten et al., 2011; Zaki et al., 2009)
Amygdala	Salience, motivational relevance (Cunningham and Zelazo, 2007), valence (Lindquist et al., 2016), and arousal (Lindquist and Barrett, 2012; Wilson-Mendenhall et al., 2013a)	Involved in face perception (Adolphs, 2009, 2010b; Todorov and Engell, 2008; Wang et al., 2014) (Engell et al., 2007; Mende-Siedlecki et al., 2013a)
Ventral striatum	Motivated behavior (Kelley, 2004; Robbins and Everitt, 1996)	Viewing attractive faces (O'Doherty et al., 2003)
Thalamus	Responds to valence (Lindquist et al., 2016), and monetary reward (Rademacher et al., 2010)	Social reward (Izuma et al., 2008)
Putamen	Visceromotor control (Alexander et al., 1991)	Social reward (Wake and Izuma, 2017)

Hippocampus	Responds to valence (Kumaran et al., 2016) and visceromotor regulation (Jacobson and Sapolsky, 1991) (Engin and Treit, 2007; Satpute et al., 2012)	Social memory (Smith et al., 2016) and social hierarchy learning (Kumaran et al., 2016; Kumaran et al., 2012; Schafer and Schiller, 2018)
Hypothalamus	Involved in visceromotor regulation (Sewards and Sewards, 2003)	Social reward (McHenry et al., 2017)
Periaqueductal gray (PAG)	Involved in visceromotor regulation (Bandler and Shipley, 1994; Behbehani, 1995; Carrive et al., 1989; Lovick, 1992), and behavioral adaptations (Buhle et al., 2013; Panksepp, 2004; Satpute et al., 2013a, b)	

In the present meta-analysis, we unite these two literatures by predicting that the degree of sociality of affective information will modulate activity within the broader neural reference space for valence. We hypothesize that increasing sociality during affective information processing requires recruitment of brain regions involved in prediction and abstraction, regardless of valence. Thus, we predict that social processing will be more likely to recruit brain regions involved in representing semantic knowledge, prior experiences, and abstract information such as the content of someone else's mental states. Such brain regions include heteromodal association regions such as dmPFC, PCC and lateral temporal cortex, as well as regions such as the inferior frontal gyrus, which help retrieve and select amongst this information (Binder et al., 2009; Corlett et al., 2022; Dvash and Shamay-Tsoory, 2014; Wilson-Mendenhall et al., 2013b). In contrast, we predict that non-social affective stimuli will involve these heteromodal regions to a lesser extent than social affective stimuli.

Meta-analytic mapping of social-affective brain function

We meta-analyzed 614 contrasts across 493 social and non-social and affective neuroimaging studies to reveal neural activity patterns that are consistent across the literature in social v. non-social affective processing. Studies in our database were

published from 1992-2019 and included 7,801 participants (see Table S1; Figure S1 and Methods Section for database details). As in our past work (Lindquist et al. 2012; 2016), we included only contrasts that compared against a neutral baseline and coded each contrast according to the social and affective qualities of stimuli presented to participants. Sociality was coded as a gradient ranging from experimental contrasts that showed all social stimuli, to some social stimuli, to no social stimuli. Affect was defined here as whether stimuli were pleasant or unpleasant in valence. We predicted that both social and non-social stimuli would yield activity patterns in limbic visceromotor regions, including the striatum, amygdala, hypothalamus, ACC and insula, that have been linked to affective responding in previous studies in the affective neuroscience literature (see Table 1). However, we predicted that the presence of social information would additionally yield more activations in non-limbic association cortices previously associated with processes such as prediction and abstraction, due to the more ambiguous and complex role social information has on affective responding.

We employed two types of meta-analytic methods to address these hypotheses. First, we used the Multi-level Peak Kernel Density Analysis (MKDA) to 1) statistically compare brain regions in which activity is more frequent in social v. non-social affective paradigms, and 2) descriptively identify the neural activity that is consistently present during social and non-social affective paradigms.

Next, we followed up our descriptive MKDA findings using the generative Bayesian Point Spatial Process (BSPP) Model (Kang et al., 2011b). The BSPP is a Bayesian method to predict the location of brain regions that are likely to be active during any given category (e.g., negative, social contrasts) based on reported peak activations, study-level variation, and measurement-level spatial noise in the literature. The advantage of the BSPP is that it can also be used as a classifier in "reverse inference" mode to assess whether brain activation is diagnostic of a certain psychological construct (e.g., sociality). We used reverse inference mode to see if it was possible to classify dimensions of sociality and valence. We first tested whether sociality and valence could themselves be classified in broad-scale brain patterns since past findings are inconsistent on this point (Chavez and Heatherton, 2015; Lindquist et al., 2016; Munuera et al., 2018). We then examined whether classification success of valence differed at different levels of

sociality. We predicted that classification success for valence would depend on sociality, such that classifying the valence of brain states would be less successful when stimuli were highly social, since these types of stimuli would invoke more reliance on brain regions involved in abstraction and might have less clear implications for visceromotor regulation, regardless of valence. In contrast, we predicted that the valence of brain states would be more easily classified when stimuli were non-social, insofar as responses to non-social threats and rewards may evoke less ambiguous predictions and visceromotor action when compared to social threats and rewards.

Methods

Data collection

We used PubMed to collect neuroimaging studies published between January 1992 and December 2019 following methods described in (Kober et al., 2008) and (Lindquist et al., 2016). Studies were included in the database if they applied affect-eliciting paradigms (using images, film clips, imagery, music, odors, etc.), with or without social content. For the present meta-analysis, we also selectively sampled studies of positive, non-social stimuli such as food since this quadrant of our proposed social-affective bi-dimensional space was relatively sparse in our prior database (Lindquist et al., 2016) of affective responding.

Six hundred and fourteen contrasts across 493 studies were included in the database, with a total number of 7,801 participants. Each contrast was coded on two primary dimensions of interest: affect (positive content; negative content) and sociality (all social content; some social content; non-social content) by two distinct coders with 100% agreement. The “all social” code referred to contrasts in which all the stimuli shown were social (e.g., all stimuli were facial or bodily expressions of emotion). The “some social” code referred to contrasts in which some stimuli were social, whereas some were not (e.g., an assortment of IAPS images that may varyingly present humans, animals and scenes) if the contrast collapsed across those image types (i.e., if the resulting brain activation could be said to be in part due to processing of social information). Contrasts that included stimuli in which the information presented was not exclusively social (contained pictures

of people in addition to other objects) or in which people relived autobiographical memories were also coded as "some social." Non-social contrasts did not contain any social content (e.g., images of spiders and snakes; images of food). The rational for separating these conditions is to demonstrate the neural responses to the social stimulus "per se" (i.e., the face), from the parts that are involved in processing more ecological social stimuli. See Supplementary Figure S3 for a binary social and non-social mapping in positive and negative valence.

As in our prior work (Lindquist et al., 2016), contrasts were also coded for methodological characteristics such as the modality used (e.g., vision, audition, recall), stimuli used (e.g., faces, scenes, sounds, etc.), and the type of contrast performed (e.g., positive v. negative, positive v. neutral). The codebook is available at https://osf.io/uzmxf/ and Table S1 summarizes our inclusion criteria. See supplementary Table S2 and supplementary Figure S1 for the relative proportion of contrasts by valence, sociality and modality, and Table S3 for the proportion of ROIs per the total number of contrasts within that condition. Moreover, Figure S2 summarizes the consistent neural activations along the dimensions of sociality and valence only in visual paradigms, demonstrating that the effects reported remain. Note that the MKDA and BSPP methods control for the base rate of contrasts entering the analysis such that a relatively greater proportion of one contrast type does not unduly influence the results.

Data analysis

Multilevel Peak Kernel Density Analysis (MKDA)

To identify consistent neural activity during social and non-social affective paradigms, we grouped the database into six categories along the dimensions of sociality and affect (Figure 3). Reported peak coordinates from studies contrast maps in each category were submitted to a coordinate-based meta-analysis using the Multilevel Peak Kernel Density Analysis (MKDA) (Wager et al., 2007). The MKDA begins by convolving reported peak activations from each study-level experimental contrast with a spherical kernel (i.e., a sphere with a radius of r = 12mm) and creating an "indicator map" of where reported activation occurred for each study-level contrast in the database. An indicator map was

generated for each study-level contrast in the database by setting voxels within the 12 mm spheres to a value of 1. To control for the quality of data entering the analysis, the contrast maps were then weighted by the square root of the sample size for each study and the quality of their statistics (see (Wager et al., 2007). To determine if a given voxel has consistent activation that is greater than would be expected by chance, the MKDA then compares the proportion of indicator maps with activation at each voxel to a null distribution by conducting Monte Carlo simulations (5,000 iterations) for each meta-analytic comparison. Monte Carlo simulations preserved the number of contrasts and coordinates within contrasts but randomly assigning the coordinate locations to any location in grey matter regions of the brain. Finally, a statistical map describing voxels with activation that is more consistent across study-level contrasts than would be expected by chance is produced and is thresholded using a height-based threshold and a cluster-based threshold that indicates a whole-brain family-wise error rate (FWER), with statistical correction of $p < .001$. For additional detail regarding the MKDA methodology see (Lindquist and Barrett, 2012; Lindquist et al., 2016; Wager et al., 2007). Meta-analytic statistical maps are available at https://osf.io/uzmxf/.

Bayesian Spatial Point Process Model (BSPP)

Reported peak coordinates from studies were submitted to the Bayesian Spatial Point Process Model (Kang et al., 2011b). The BSPP begins by estimating "population centers" of activity from the distribution of reported peak coordinates. The BSPP model compliments the MKDA in two ways. First, unlike the MKDA and other descriptive approaches [i.e., Activation Likelihood Estimation approaches (Laird et al., 2015)] the BSPP does not assume a spatial kernel size for convolution of reported peak coordinates (Salimi-Khorshidi et al., 2009), which may mask functional differences between adjacent brain regions. Rather than using a spatial kernel on peak coordinates, the BSPP model estimates clusters from the distributions of peak coordinates. For each cluster identified, the algorithm provides both the "population center" of peak coordinates and the spatial boundary of that center with confidence intervals on the basis of the spatial distribution of reported peaks. The BSPP can then perform a "forward inference" analysis to identify

where the locations of population centers for one category (e.g., negative, social contrasts) is greater than would be expected by chance.

Once the distribution of population centers is computed on the basis of reported contrasts, the BSPP can then use this information to compute the posterior probability of categories of interest (e.g., negative social v. negative non-social) given a set of brain coordinates ("reverse inference"). In this sense, the BSPP is also a classifier analysis, which provides information about whether individual contrast maps are reliable and also whether the pattern of activity in individual study maps provides information about the conditions. A detailed mathematical description of the BSPP is provided in prior work (Kang et al., 2011b). Hypothesis testing was conducted using chi-square tests for examining dependency between valence and social levels. Specifically, as an extension of the BSPP (Kang et al., 2011a), a hierarchical BSPP model is constructed for meta-analysis of the multi-type neuroimaging data and the posterior predictive probability is computed for classification of a new contrast given the foci (Kang et al., 2014). We examine the classification accuracy via a leave-one-out cross validation (LOOCV) procedure. Specifically, with a data set of n contrasts, for each contrast, the data is split into a training set of (n-1) contrasts and a test set of only one contrast. The hierarchical BSPP model is fitted on the training set and makes classifications for the only contrast in the test set. For the technical details of the BSPP classifications, see (Kang et al., 2014). We implemented the BSPP model for the following categories: (i) *valence only* (ii) *social only* (iii) *valence x social*.

We adopted the Chi-squared proportional test (Newcombe, 1998) to test whether the estimated LOOCV classification accuracy was significantly larger than chance (which was 0.5 for positive v. negative valence classifications and .33 for all social stimuli, some social stimuli, and non-social classifications). In addition, we computed sensitivity and specificity of classifications based on the counts of study contrasts that were correctly and incorrectly classified by the BSPP. Specifically, sensitivity was computed as:

$$Sensitivity = \frac{n\ True\ Positives}{n\ True\ Positives + n\ False\ Negatives}$$

Specificity was computed as:

$$Specificity = \frac{n\ True\ Negatives}{n\ True\ Negatives + n\ False\ Positives}$$

Results

Comparing social and non-social affective processing

We first used the MKDA to reveal which brain regions are statistically more likely to activate during social as opposed to non-social affective stimuli, regardless of valence. We compared studies that exclusively presented positive and negative social stimuli with those that exclusively presented positive and negative non-social stimuli (see Figure 1; Table 2). Social affective stimuli show significantly increased activations in the bilateral amygdalae, left anterior insula and the bilateral fusiform/extrastriate cortices compared to non-social stimuli. In contrast, non-social affective stimuli show significantly increased activations in the ventral anterior-mid insula, right NAcc, and ACC (see Figure 2; Table 3).

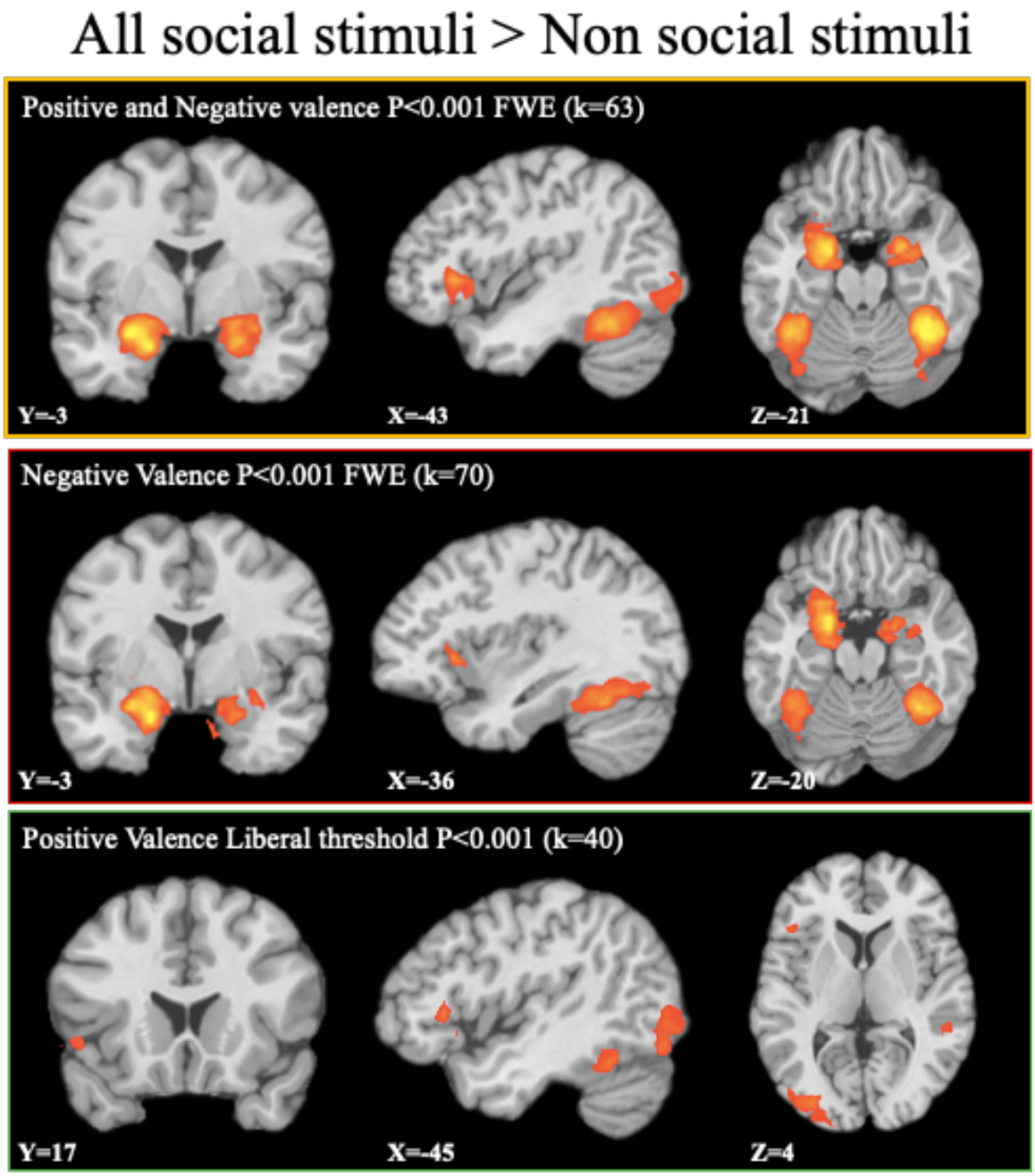

Figure 1. Meta-analysis of neuroimaging studies of affective stimuli in the contrast *All social stimuli* > *No social Stimuli* ($p < 0.001$, FWE-corrected) in positive and negative valence studies (top panel), negative valence studies (middle panel), and positive valence studies (lower panel).

1 **Table 2. Consistent neural activations for All social stimuli > No social Stimuli**

All social stimuli>No social stimuli	x	y	z	k (voxels)
Positive & Negative Valence				
Right Fusiform Gyrus	37	-54	-15	774
Left Fusiform Gyrus	-43	-54	-14	513
Left Amygdala	-25	-7	-7	292
Right Amygdala	25	-6	-11	143
Right Extrastriate Cortex	58	-44	13	102
Left Anterior Insula	-48	20	5	92
Negative				
Left Amygdala	-25	-7	-7	408
Right Fusiform Gyrus	37	-54	-15	291
Left Fusiform Gyrus	-37	-53	-17	228
Right Amygdala	19	-9	-8	113
Right Occipito-Temporal Junction	51	-73	1	109
Left Anterior Insula	-40	18	5	32
Positive				
Right Occipital Gyrus	42	-72	-9	398

Inferior Occipital Gyrus	-39	-78	-9	199
Left Fusiform Gyrus	-39	-51	-24	85
Right Superior Temporal Gyrus	60	-51	12	74
Right Fusiform Gyrus	39	-48	-15	73
Left Anterior Insula/Left Inferior Frontal Gyrus	-45	24	0	45

All findings ($p < 0.001$, FWE-corrected) in positive and negative valence studies, negative valence studies, and positive valence studies. X, Y, Z represent MNI coordinates. K represents the number of voxels in the cluster.

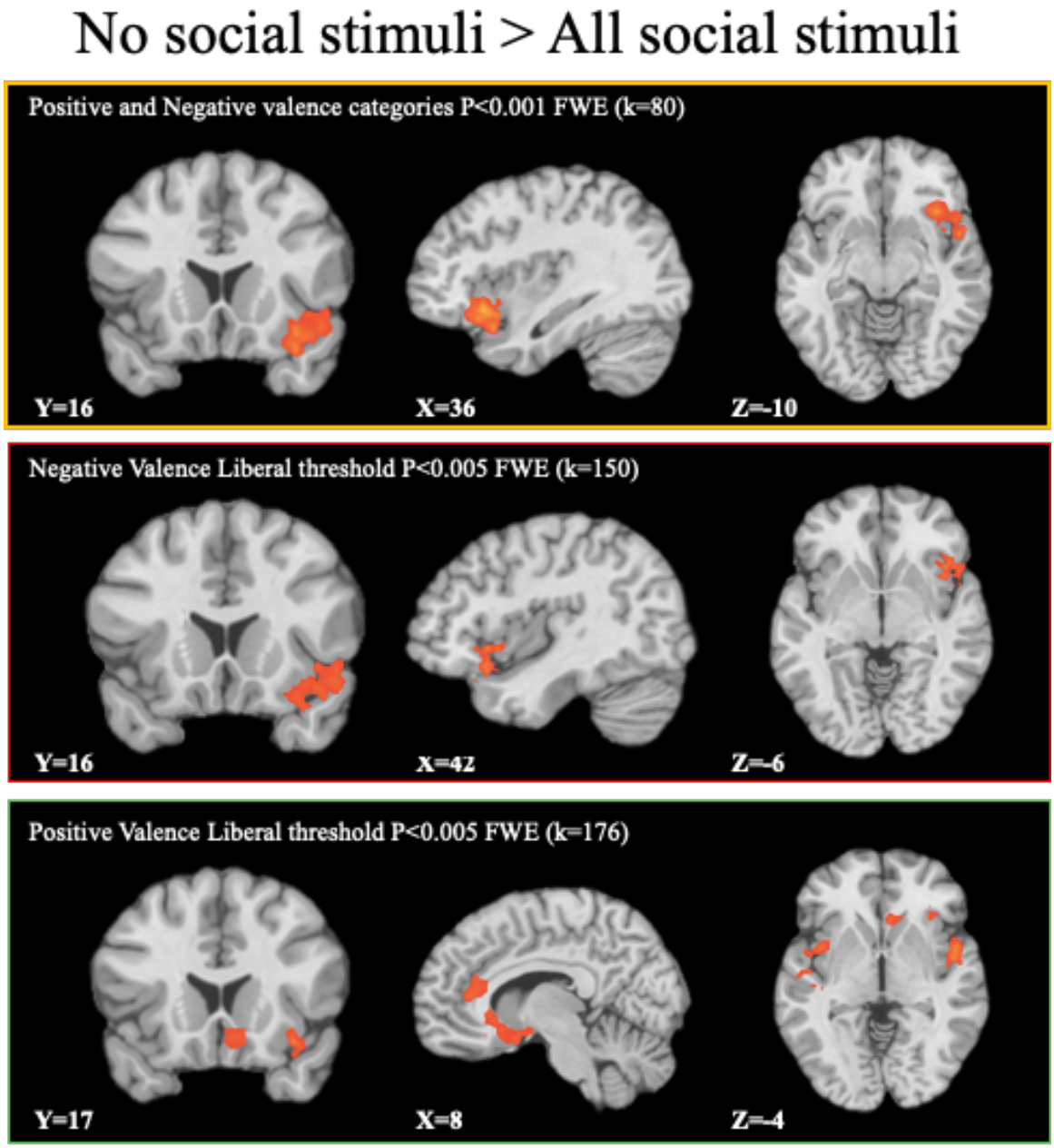

Figure 2. Meta-analysis of neuroimaging studies of affective stimuli in the contrast *No social stimuli* > *All social Stimuli* ($p < 0.001$, FWE-corrected) in positive and negative valence studies (top panel), negative valence studies (middle panel), and positive valence studies (lower panel).

Table 3. Consistent neural activations in the contrast *No social stimuli > All social Stimuli*

No social stimuli > All social stimuli	x	y	z	k (voxels)
Positive and negative valence				
Right Ventral Anterior-Mid Insula	36	21	-12	239
Negative Valence				
Right Ventral Anterior-Mid Insula	42	12	-6	239
Positive Valence				
Right Mid Insula	42	3	-12	269
Right Anterior Cingulate	0	3	6	250
Right ventral Striatum	6	9	-18	91
Left Mid Insula	-39	6	0	67
Right Anterior Insula	42	24	-15	49
Right Caudate	-15	9	-6	45
Left Posterior Insula	-42	-18	9	38

All findings ($p < 0.001$, FWE-corrected) in positive and negative valence studies, negative valence studies, and positive valence studies. X, Y, Z represent MNI coordinates. K represents the number of voxels in the cluster.

Mapping neural activations along the dimensions of sociality and valence

Next, we computed MKDA maps for each condition of interest along the dimensions of sociality and affect (see Figure 3). The amygdalae, NAcc and insula were active to all affective stimuli, whether social or non-social. As stimuli became increasingly social, regardless of valence, we saw increased activity within cortical aspects of the default and salience networks including the anterior and posterior cingulate cortices, mPFC, as well as premotor areas, and ventral visual cortex (Figure 3; Table 4).

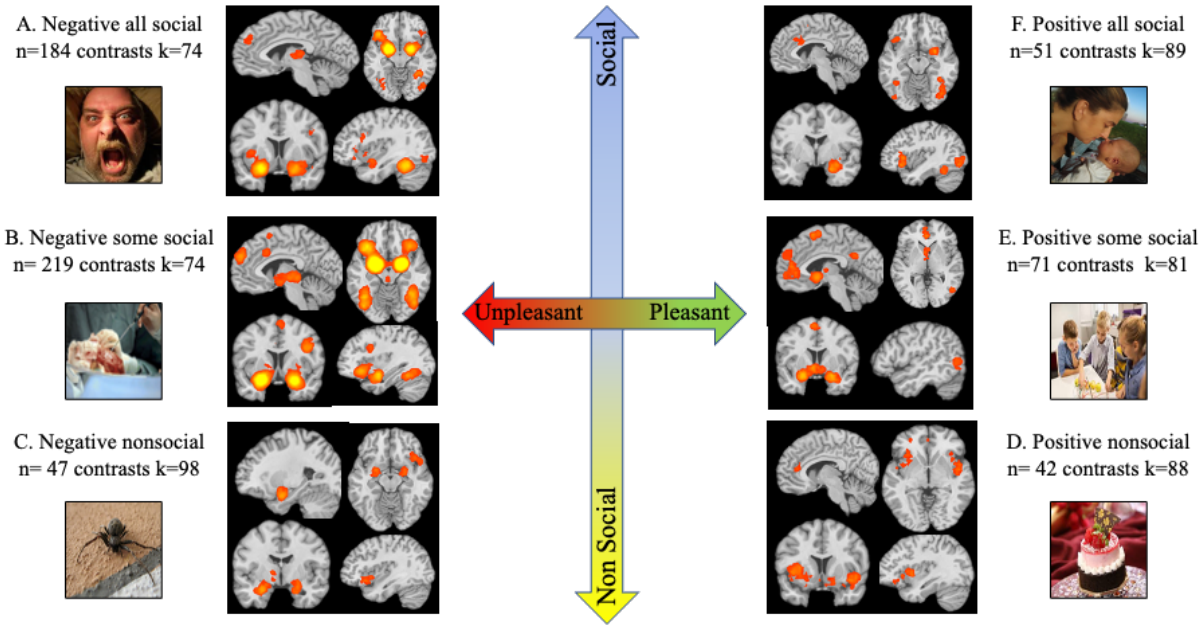

Figure 3: Consistent neural activations along the dimensions of sociality and valence (p<0.001, FWE-corrected). Negative contrasts (A, B, C) used stimuli rated as inducing negative affect (e.g., unpleasantness, negativity, anger, fear, disgust, contempt, sadness, etc.) by independent raters (i.e., in standardized stimulus sets) and/or by the participants in each study. Positive contrasts (D, E, F) used stimuli used stimuli that were rated as inducing positive affect (e.g., pleasantness, positivity, happiness, joy, pride, etc.) by independent raters (i.e., in standardized stimulus sets) and/or by the participants in each study. *All social* contrasts (A, F) contained exclusively social stimuli (e.g., human faces). *Some social* contrasts (B, E) contained a blend of social and non-social stimuli (e.g., an IAPS picture depicting a scenario) or contrasts in which the sociality of stimuli was implied (e.g., a human hand). *Non-social contrasts* (C, D) contained exclusively non-social stimuli (e.g., food, music, scenes). Map slices: A. Negative all social: x=-5, z=-12, y=7, x=38; B.

Negative some social: x=-5, z=-14, y=5, x=34; C. Negative non-social: x=-25, z=-14, y=-6, x=38; D. Positive non-social: x=7, z=-5, y=8 (liberal threshold p<0.005), x=-36; E. Positive some social: x=-4, z=0, y=3, x=50; F. Positive all social: x=-5, z=-14y=-3, x=-40.

Table 4. Consistent neural activations along the dimensions of sociality and affect

Meta-Analytic Map	**x**	**y**	**z**	**k**	**Proportion of contrasts**
Negative All Social p<0.001 FWE K=74					
Left Amygdala	-21	-3	-18	1273	32%
Right Amygdala	21	-6	-21	886	27%
Right Fusiform Gyrus	36	-54	-21	345	16%
Left Fusiform Gyrus	-39	-54	-21	295	13%
Right Extrastriate Cortex	48	-72	-3	248	11%
Right Anterior Insula	45	27	0	163	13%
Left Anterior Insula	-39	27	-12	155	15%
Left Thalamus	-9	-21	3	151	9%
Right Middle Temporal Gyrus	57	-33	0	139	11%
Left Middle Temporal Gyrus	-57	-51	9	95	11%
Right Inferior Frontal Gyrus	39	15	21	85	17%
Left Paracingulate Cortex	-9	51	30	75	9%
Left Inferior Frontal Gyrus	-48	27	15	64	9%
Right Mid Insula	33	12	0	18	9%
Negative Some Social p<0.001 FWE k=74					
Left Amygdala	-21	-3	-18	3733	39%
Left Fusiform Gyrus	-39	-60	-15	920	18%
Right Extrastriate Cortex	48	-69	0	840	19%
Right Amygdala	24	-3	-18	648	35%
Left Anterior Insula	-36	24	-12	565	22%
Left Extrastriate Cortex	-42	-72	0	384	18%
Right Ventral Anterior Insula	36	24	-9	290	15%

Right Fusiform Gyrus	42	-57	-18	275	11%
Left Paracingulate Cortex	-3	54	30	229	12%
Left Thalamus	-3	-24	-6	178	13%
Right Inferior Frontal Gyrus	51	33	9	149	14%
Supplementary Motor Cortex	6	15	57	146	13%
Left Inferior Frontal Gyrus	-48	12	27	127	11%
Dorsal Cingulate Cortex	0	18	30	99	11%
Right Thalamus	6	-27	-6	94	13%
***p<0.001 FWE k=29 voxels*:**					
Right Putamen	27	9	3	29	9%
Negative None Social p<0.001 FWE K=98					
Left Amygdala	-24	-3	-21	238	20%
Right Anterior Insula	45	21	-6	210	20%
Right Amygdala	21	-9	-24	157	18%
p<0.001 FWE k=26 voxels:					
Left Thalamus	-12	-3	3	26	15%
Positive None Social p<0.001 FWE k=88					
Right Anterior Insula	36	21	-12	346	22%
Left Mid Insula	-39	6	0	269	22%
Left Anterior Cingulate	0	39	6	109	19%
Lower threshold, k<57 voxels:					
Right Posterior Insula	48	-3	-3	57	22%
Right Nucleus Accumbens	18	9	-15	55	15%
Left Anterior Insula	-36	21	-3	36	20%
Right Orbitofrontal Cortex	36	33	-12	33	18%
Left Amygdala	-21	3	-15	21	20%
Left Orbitofrontal Cortex	-24	36	-15	15	16%

Positive Some Social p<0.001 FWE k=81					
Left Amygdala	-21	-6	-18	990	32%
Anterior Cingulate Cortex	0	39	0	388	20%
Right Amygdala	24	0	-18	223	25%
Right Nucleus Accumbens	3	3	-6	125	17%
Supplementary Motor Area	0	12	57	121	20%
Left Nucleus Accumbens	-6	6	-9	120	22%
Posterior Cingulate Cortex	0	-54	24	94	17%
Right Extra Striate Cortex	51	-69	9	93	15%
Paracingulate Cortex	0	57	21	75	13%

Positive All Social p<0.001 FWE k=85					
Right Amygdala	30	0	-15	203	26%
Left Anterior Insula	-39	24	-9	275	24%
Left Fusiform	-36	-51	-18	88	17%
Left Extrastriate Cortex	-39	-78	-9	151	21%
Dorsal Anterior Cingulate Cortex	-3	12	27	141	16%
Right Extrastriate Cortex	42	-72	-9	86	25%
Right Fusiform Gyrus	39	-57	-21	54	17%

All findings (p<0.001, FWE-corrected). X, Y, Z represent MNI coordinates. K represents the number of voxels in the cluster. Proportion of contrasts represent the percentage of contrasts that activate the cluster's peak.

The analyses are conducted across a wide range of modalities. While affective studies mainly apply visual stimuli, experiments using other modalities are also applied. Details on the number and ratio of the different modalities in each domain is specified on Supplementary Table S2. Notably, the positive non-social category had fewer visual contrasts, and more olfactory/taste/tactile contrasts compared to the other categories, which can bias the interpretation of specific activations in this category. Yet, insular activations remain significant in positive non-social category when only including visual contrasts, supporting its role in positive non-social processing (see Supplementary Figure

S2 for meta-analytical maps in all valence and social categories with only contrasts that applied visual stimuli is presented).

Identifying commonalities between social and affective categories

To spatially inspect commonality between social and affective categories, we next overlaid positive and negative activations for social and non-social MKDA maps (Figure 4). Both positive and negative social stimuli yielded activations in the bilateral amygdala, SMA, paracingulate cortex and extrastriate cortex (Figure 4A). We found valence differentiation in the striatum during social stimuli, as positive social stimuli activated the NAcc, and negative social stimuli activated the putamen (Figure 4A). At the cortical level, the anterior ventral insula and dACC were activated in negative social paradigms, and the vmPFC, ACC and PCC activated in positive social paradigms (Figure 4A). There was less spatial commonality in the regions associated with positive and negative non-social stimuli (Figure 4B). Negative non-social stimuli were associated with activation in the amygdala, thalamus and anterior insula. Positive non-social stimuli were associated with the NAcc, orbitofrontal cortex and throughout the insula- anterior, mid and posterior (Figure 4B). The complete list of activations is specified in Table 4.

We also examined the spatial commonality of social and non-social activations for positive and negative stimuli. Among negative stimuli (Figure 4C), social stimuli consistently involved the dACC, paracingulate cortex, SMA inferior frontal gyrus and fusiform (Figure 4C). Social and non-social negative stimuli commonly involved the bilateral amygdalae and anterior insula, however in the insula non-social stimuli activated more posterior voxels in the anterior insula spatially compared with social (Figure 4C). Among positive stimuli (Figure 4D), both social and non-social stimuli activated the basal forebrain. Social positive stimuli activated midline cortical regions, such as the mPFC and PCC, as well as the ventral striatum and amygdala (Figure 4D). Moreover, sensory-motor regions, including the SMA, extrastriate cortex, and the fusiform were active in social positive stimuli (Figure 4D). The posterior and mid-insula were

frequently active for non-social positive stimuli (Figure 4D). For statistical comparison between social and non-social positive and negative maps see Figures 1 and 2.

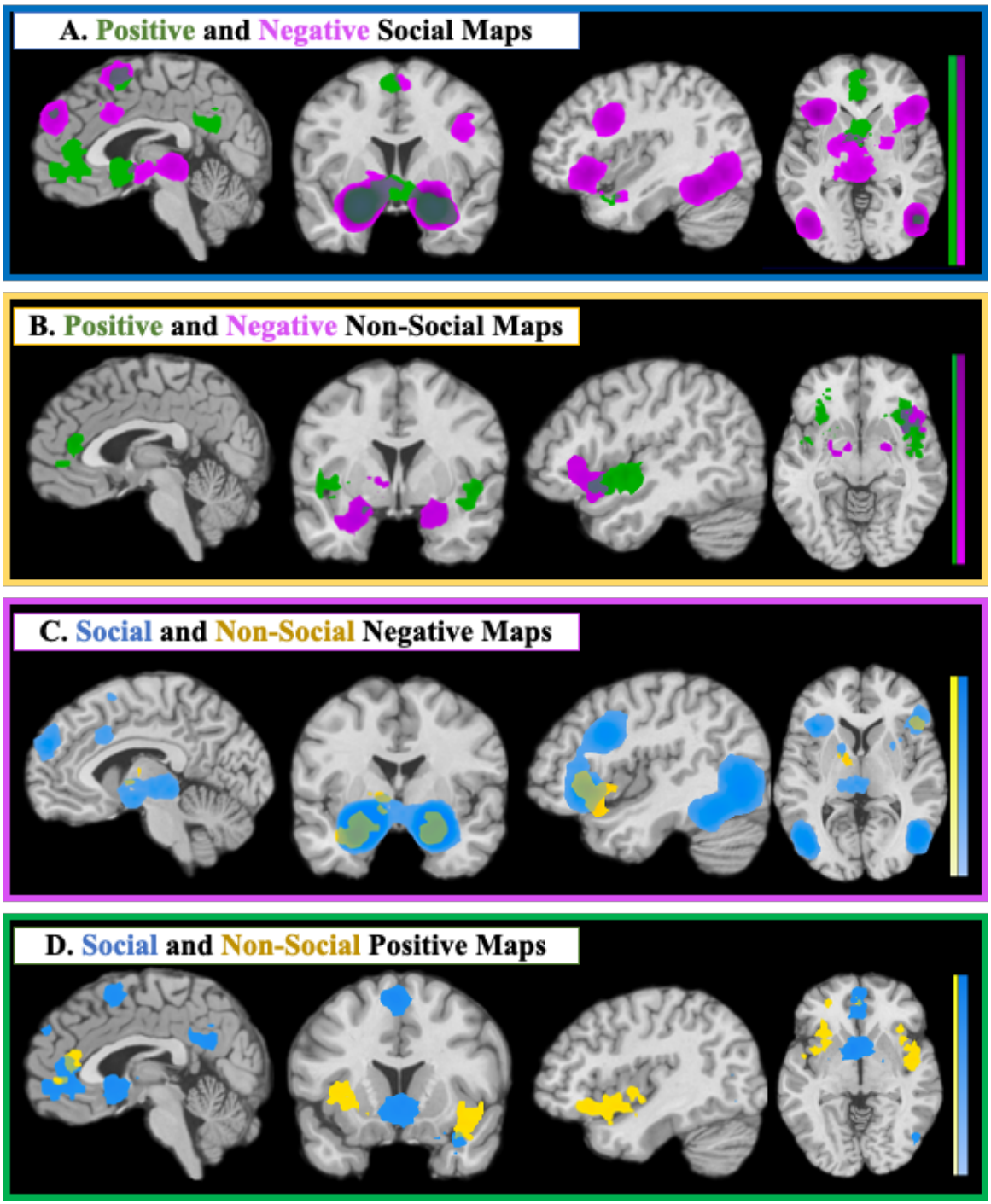

Figure 4. Differences and similarities among the different domains, overlay of MKDA maps ($p<0.001$, FWE-corrected). (A) Meta-analysis of neuroimaging studies of social studies, separating positive (green) and negative (purple) valence contrasts. Map slice:

x=3, y=2, x=39, z=-2; (B) Meta-analysis of neuroimaging studies of non-social studies, separating positive (green) and negative (purple) valence contrasts. Map slice: x=3, y=0, x=47, z=-9; (C) Meta-analysis of neuroimaging studies of negative affect separating social (blue) and non-social (yellow) contrasts. Map slice: x=-6, y=-3, x=44, z=3; (D) Meta-analysis of neuroimaging studies of positive affect separating social (blue) and non-social (yellow) contrasts. Map slice: x=3, y=12, x=41, z=-5.

Testing the neural specificity of social and affective processing

We next used BSPP to test whether individual contrast maps could be classified depending on social or non-social content, valence, or the combination of the two. When collapsing across the valence dimension, the classifier was unable to differentiate social processing from non-social processing, i.e., brain states related to viewing all social, some social, and non-social stimuli (χ^2 = 2.625, p = 0.622). See Table 5 for confusion matrices and classification sensitivity and specificity.

Table 5. Confusion matrices for classification of contrasts by sociality and valence

Classification by sociality

	True category			
Predicted category	**All**	**Some**	**None**	**Sensitivity/specificity**
All	56	74	81	.19/.82
Some	103	132	191	.35/.62
None	129	176	219	.45/.54

Classification by valence

	True category		
Predicted category	**Negative**	**Positive**	**Sensitivity/specificity**
Negative	357	307	.64/.27
Positive	199	112	.27/.64

Cells represent the number of contrasts accurately classified (shaded cells on the diagonal) and misclassified (unshaded cells, off-diagonal).

When collapsing across the social dimension, the classifier performed significantly better than chance (χ^2 = 8.618, p = 0.003), however, this was primarily driven by a greater tendency to classify contrasts as negative (Table 5). Yet, this was not true for highly social stimuli, as seen in the differential effects of classifying valence at different levels of sociality (Table 6). When stimuli were all social, the classifier was unable to predict the valence of brain activity (χ^2 = 1.089, p = 0.297), suggesting that the brain responds similarly to positive and negative highly social stimuli (i.e., "all social"). However, when stimuli contained relatively fewer social stimuli (i.e., "some social") (χ^2 = 14.822, p < .001), or non-social stimuli (χ^2 = 28.081, p < .00001), it was increasingly able to differentiate positive from negative valence.

Table 6. Confusion matrices for classification of contrasts by valence at different levels of sociality

Classification for valence in all social stimuli

	True category		
Predicted category	**Negative**	**Positive**	**Sensitivity/specificity**
Negative	187	87	.75/.19
Positive	63	21	.19/.75

Classification for valence in some social stimuli

	True category		
Predicted category	**Negative**	**Positive**	**Sensitivity/specificity**
Negative	199	108	.81/.37
Positive	48	63	.37/.81

Classification for valence in non-social stimuli

	True category		
Predicted category	**Negative**	**Positive**	**Sensitivity/specificity**
Negative	51	21	.61/.79
Positive	33	78	.79/.61

Cells represent the number of contrasts accurately classified (shaded cells on the diagonal) and misclassified (unshaded cells, off-diagonal).

Discussion

Our findings demonstrate across 614 neuroimaging contrasts that both social and non-social affective information is processed by core regions distributed across the whole brain, including the NAcc, amygdala, ACC, anterior insula and mPFC. These limbic regions are collectively associated with engaging visceromotor control (Atzil and Barrett, 2017; Kleckner et al., 2017). In contrast, additional cortical regions were relatively more likely to be recruited when stimuli included social information. Specifically, contrasts

containing relatively more social stimuli reliably activate limbic and heteromodal cortical regions that have been previously associated with prediction of sensory, visceral, and motor outcomes, such as the PCC and mPFC (Barrett and Simmons, 2015). The PCC and mPFC have been furthermore linked to making predictions about other people's abstract mental states, or mentalizing (Heberlein et al., 2008; Mar, 2011; Shamay-Tsoory et al., 2003; Wagner et al., 2016). These findings potentially represent higher-order governing of visceromotor control in the context of social information and perhaps reflects the complexity inherent to responding adaptively to social affective information (Barrett and Simmons, 2015; Chanes and Barrett, 2016; Djerassi et al., 2021). Indeed, compared to non-social affective stimuli (e.g., spiders or food rewards), the visceromotor predictions necessary to respond to social affective stimuli (e.g., a person making a threatening face, a group of smiling individuals) may be less concrete and requires more abstraction and mental simulation.

Linking findings to predictive processing and allostasis

The consistent involvement of regions spanning visceromotor limbic cortex, primary interoceptive cortex, and heteromodal association areas across both social and non-social affective processing is aligned with newer *predictive models* (Katsumi et al., 2021a; Katsumi et al., 2021b) of the brain, which presume that the brain uses past experiences and knowledge represented in heterometal association cortices in a Bayesian fashion to predict future sensations. It is thought that such predictions are more adaptive than responding reactively, which is computationally inefficient and too slow to guide adaptive action (Friston, 2010; Katsumi et al., 2022; McEwen, 1998; Sterling, 2012). Insofar as our findings implicate regions specifically involved in visceromotor control and interoception, they are also consistent with neuroscientific models of *allostasis*, which more specifically link predictive processing to the management of organisms' metabolic demands, action regulation, and survival (Barrett, 2017b; Kleckner et al., 2017; McEwen, 2000; Sterling, 2012). According to models of allostasis, the brain's primary function is to regulate the metabolic demands of the entire organism and ensure survival by constantly integrating information from the body and the environment to predict and prepare for upcoming physiological regulation demands before they happen (Barrett,

2017b; Kleckner et al., 2017; McEwen, 2000; Sterling, 2012). In this view, neural activations involved in social and affective processing maintain allostasis by representing an internal model of the impact that stimuli in the outside world are likely to have on the body (Barrett, 2017a). When motor action is predicted, regions associated with visceromotor control such as the ACC and the ventral portion of the anterior insula send projections to the peripheral body via a system of subcortical regions that control the autonomic and endocrine systems such as the hypothalamus, central nucleus of the amygdala, and PAG (Barrett, 2017a; Kleckner et al., 2017).

Recently, an "allostatic-interoceptive network" has been identified in the human brain on the basis of tract-tracing studies of regional connectivity in non-human animals, laminar gradients of prediction and prediction error processing in the non-human brain, and resting state functional connectivity patterns in the human brain (Barrett, 2017a; Kleckner et al., 2017). Many of the visceromotor limbic regions, primary interoceptive regions, and heteromodal association cortex we observed across social and non-social affective contrasts in the present meta-analysis are part of that network. Of course, we did not directly measure allostasis in this study, and future work must ultimately examine how social and non-social affective stimuli differentially implicate metabolic regulation. Nonetheless, an allostatic framing may be able to explain some of our more interesting findings.

Saliency and social saliency

Despite relative differences in the activation of such cortical regions, our Bayesian classification analyses could not detect a categorical distinction between social and non-social affective brain processing. That is, there was not a distinctive neural pattern of activations that could be reliably categorized as "social processing". This effect was likely driven by highly social stimuli, which had the lowest sensitivity of all the social categories we tested. Interestingly, although the classifier was able to differentiate positive and negative stimuli in general, it was also unable to do so at high levels of sociality. Critically, negative and positive social paradigms both recruited the amygdala

to a similar degree, which is a hub within a broader network linking the anterior insula, dACC, striatum, and medial prefrontal cortex (Bickart et al., 2014).

We cannot rule out the possibility that these findings are a merely a product of the methods used— "social" stimuli such as disembodied faces are ambiguous without context (Hassin et al., 2013) and likely require greater predictive efforts on the part of the brain to decode, whereas non-social images of food or spiders may still be meaningful without their context. Moreover, low-level characteristics of the stimuli, such as spatial frequency or visual complexity could potentially explain this differential effect, in the sense that positive and negative social stimuli might be visually more like each other than positive and negative non-social stimuli. The present meta-analysis could not empirically address these alternative interpretations. Nonetheless, these possibilities still suggests that social stimuli rely more on contextualized predictions, and thus may recruit greater resources to predict and generate behavior. Moreover, the finding that neural activations during highly social positive and negative stimuli were undifferentiable is ultimately consistent with previous work demonstrating a general social saliency effect within neuromodulatory mechanisms of social behavior. Both oxytocin and dopamine also show a general "social saliency" effect by regulating behavior in the context of both affiliation and aversion (Shamay-Tsoory and Abu-Akel, 2016).

In contrast to social stimuli, we found more differentiation and less commonality within the networks for positive and negative non-social stimuli. The non-social negative stimuli recruited regions more typically associated with saliency and orientation of attention (e.g., amygdala and anterior insula) (Campbell, 2007; Krueger and Hoffman, 2016), while positive non-social stimuli recruited regions within a network more typically associated with behavioral response to reward (e.g., basal forebrain) (Elliott et al., 2000; Kelley, 2004; Robbins and Everitt, 1996).

Considering allostatic models of brain function, these findings may collectively suggest that the types of predictions necessary for non-social affective stimuli are somewhat distinct from those necessary for social affective stimuli. The brain may make behavioral predictions more efficiently in the presence of non-social stimuli; in contrast, social stimuli may be more ambiguous because they involve abstractions of others'

mental states and behaviors and are highly situated in context. For example, in the presence of spiders, snakes, and snarling dogs, predictions may involve relatively less abstract mental simulation, representation of prior experiences, and abstract reasoning about the context and instead may involve relatively concrete visceromotor predictions (e.g., avoidance behavior). Yet in the presence of social stimuli such as scowling or frowning faces, predictions may rely on abstract mental simulation, representation of prior experiences, and abstract reasoning about the meaning of the facial behavior in the present context. As such, adaptive responses may involve more highly differentiated visceromotor predictions (e.g., avoidance behavior in one context, approach in another). Of note, such cortical recruitment may not merely relate to the "sociality" of the stimulus per se, but may be a product of the complexity of social information. Future research should examine whether such activation varies as a feature of the ambiguity of a stimulus' allostatic consequences, regardless of its sociality.

Our findings may also weigh in on the role of particular brain structures. For instance, there is debate regarding the role of the striatum in processing the overall salience versus the specific valence of stimuli. For example, it has been demonstrated that responses within the striatum (particularly the ventral striatum) depend on the salience of the stimuli (Zink et al., 2006). Building on this work, other groups have suggested that the ventral striatum encodes both salience and valence (Cooper and Knutson, 2008; Jensen et al., 2007; Litt et al., 2010). And finally, other meta-analyses have shown that distinct portions of the striatum encode each salience and valence (Bartra et al., 2013). Here we demonstrate that across the literature, the right ventral striatum responds differentially to valence in non-social stimuli, but bilateral ventral striatum similarly responds to positive and negative social stimuli, which both have high saliency to social organisms (Atzil et al., 2018; Shamay-Tsoory and Abu-Akel, 2016). Together, our approach enables a bi-dimensional mapping of striatal function across categories of valence and sociality. These findings may contribute to debate about striatum function by suggesting that the striatum codes for allostatic value rather than valence and saliency per-se.

Contributions and Limitations

It should be noted that although our meta-analysis is the largest to our knowledge to examine the brain basis of social and affective neural processing, others have examined the interplay of sociality and valence. Chavez and Heatherton (2015) used an automated meta-analytic tool to compare studies that investigated "social" phenomena and "valence" within the mPFC and amygdala (Chavez and Heatherton, 2015). In a follow-up neuroimaging study, they examined the representational similarity between multivoxel patterns in the mPFC when participants viewed images that varied in sociality and valence (Chavez and Heatherton, 2015). They found that the brain's response to social positive stimuli was the most distinct from the brain's response to non-social negative and non-social neutral stimuli. However, like our meta-analysis, within social v. non-social stimuli, the brain's response to negative and positive stimuli was not differentiated. Another recent meta-analysis evaluated the meta-analytic activations and co-activations of brain regions in social neuroimaging experiments and report that social brain function relies on domain-general circuits that include sensory, limbic and associative cortices (Alcala-Lopez et al., 2018). While this paper analyzed across different domains in social neuroscience, they did not evaluate non-social paradigms. Our findings thus build upon prior work by demonstrating a broader set of regions that respond to social affective stimuli, and contrasting them with non-social affective stimuli.

One limitation of the present work is that we do not explicitly model the arousal dimension of affect alongside valence and sociality. Arousal is the subjective dimension most commonly associated with visceromotor activation during allostasis regulation (Carter et al., 2009; McEwen, 1998; McEwen and Wingfield, 2003; Sterling, 1988) but is often uncontrolled in individual studies in the literature [i.e., in stimulus sets commonly used in the studies within our meta-analytic database, valence and arousal dimensions are correlated; see (Lindquist et al., 2016)]. Future research and specific hypotheses about the nature of arousal in social and affective experience are needed; it may be the case that "saliency" corresponds to an arousal dimension insofar as visceromotor control activates the autonomic nervous system (Kleckner et al., 2017). Another limitation is that the present database exclusively examined social and non-social affective stimuli but did not draw from the infinitely large set of stimuli that are "non-affective" for both practical and philosophical reasons. In this sense, we only examined how the brain differentially

represents clearly valenced stimuli that are social versus non-social. It would be interesting in future research to examine how the regions we observed during social and non-social affective tasks regions are related to brain regions that represent social, neutral stimuli (e.g., images of expressionless faces). However, we would argue on both empirical and philosophical grounds that non-affective social stimuli may not exist. Even structurally neutral faces are subjectively experienced as valenced (Mende-Siedlecki et al., 2013b; Todorov and Engell, 2008) and activate structures such as the amygdala involved in salience processing and visceromotor control (Weierich et al., 2010). Nonetheless, we did not include neutral social stimuli in the present meta-analysis since this would have necessitated also including neutral non-social stimuli, and the range of non-affective, non-social stimuli used in neuroimaging studies is potentially limitless (e.g., ranging from abstract shapes to Gabor patches to visual scenes).

It could be argued that we could have examined neural responses to neutral social stimuli by including neutral v. affective contrasts (e.g., neutral v. positive social stimuli or neutral v. positive non-social stimuli) in our meta-analysis. We opted not to because these types of contrasts (i.e., often considered "deactivations" in studies focused on affect) are inconsistently reported throughout the literature (see (Lindquist et al., 2012) for a discussion). Thus, more individual studies (e.g., (Chavez and Heatherton, 2015) should titrate the value of stimuli (ranging from highly positive to more neutral to highly negative), rather than categorically ranking their "affective" or "social" content.

Last, the increased activations in visual regions in social compared to non-social studies can be related to the mode of experiments, as while affective neuroimaging studies tend to use mainly visual stimuli, some non-social studies use more olfactory/taste/tactile stimuli. We include tabulations of the modality used to induce affect across contrast type in Table S4 and also reproduced findings within the most frequent modality (vision) in Figure S2. Many of the core differences between contrast types are replicated in these sensitivity analyses.

Conclusion

Decades of neuroscience research and roughly 30 years of neuroimaging research have sought to understand the set of brain regions consistently associated with pleasant and unpleasant affect in humans. This is the first work to our knowledge to examine how activation in those brain regions varies as a product of the sociality of the stimulus. Our findings map the neural commonalities and differences along dimensions of valence and sociality, linking both to neural mechanisms of visceromotor control. This neural level of analysis begins to inform us about mechanisms of affective processing across a variety of experiences that are relevant to the human condition (aversion v. appetitive motivation; social avoidance v. affiliation).

Table S1. Inclusion and exclusion criteria for the neuroimaging papers included in the present analysis

Inclusion criteria	Exclusion criteria
Paper was published after January 1990 and before January 2020	Paper was published after December 2019
Paper uses PET or fMRI	Paper does not use PET or fMRI
Paper conducts contrasts using subtraction analyses	Paper conducts regressions, correlations, connectivity analyses, multivoxel pattern analysis, or other method that does not rely on subtraction
Paper reports peak activations for contrasts conducted	Paper does not report peak activations for contrasts conducted
Contrasts test the neural basis of affective experience (i.e., the feeling of discrete emotions such as anger, fear, disgust, happiness, contempt, etc. or feelings of pleasure or displeasure that are induced by pictures, music, recall, films, odors; or when participants judge the meaning of emotional words)	Contrasts test the neural basis of pain, fear conditioning, explicit memory, priming, learning, error processing, hunger/thirst, sexual arousal, emotion regulation (suppression or re-appraisal), anticipation of emotion (but not experience), comparison is between specific geno/phenotypes, comparison is between arbitrarily created groups (e.g., chocolate cravers v. not)
--or--	
Contrasts test the neural basis of affective perception (i.e., the perception of discrete emotions such as anger, fear, disgust, happiness, contempt, etc. or pleasure or displeasure in conspecifics faces, voices, or bodies)	
Contrasts subtract a neutral condition (reference) from the condition of interest (target)	Contrasts subtract an emotional condition (reference) from the condition of interest (target)
Participants in the sample are healthy adults	Participant in the sample are patients, children, or elderly adults

Table S2. Count of study-level contrasts by valence and sociality included in the analyses

Contrasts	Positive Valence	Negative Valence	Total
All Social	51	184	235
Some Social	71	219	290
Non-Social	42	47	89
Total	164	450	614

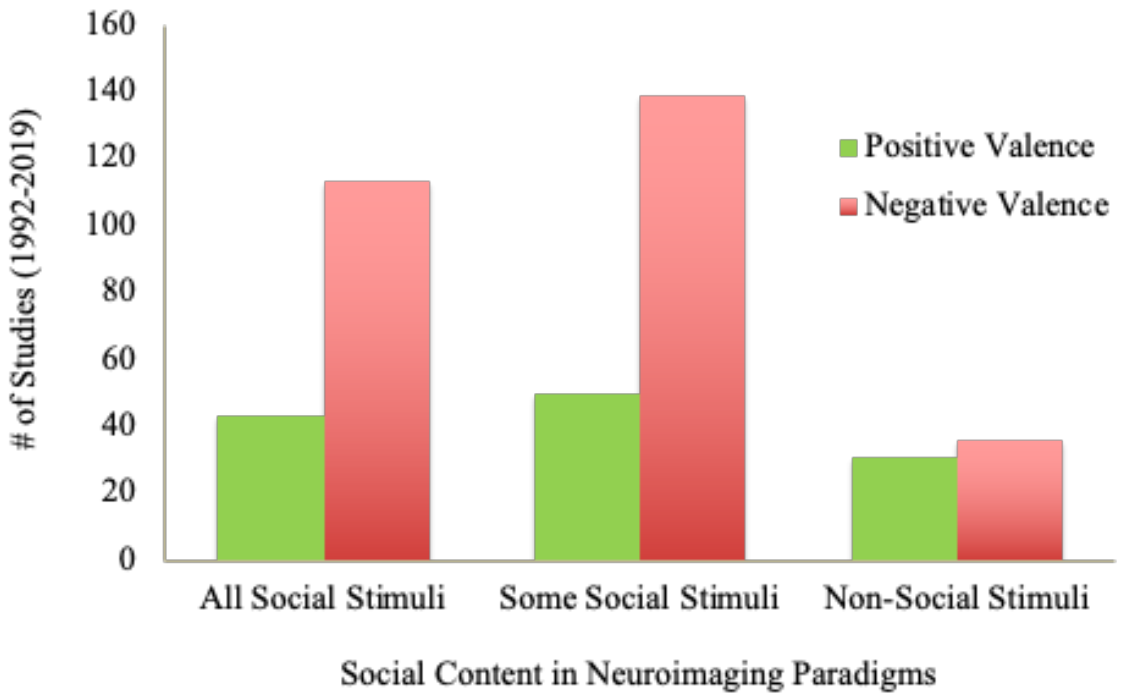

Figure S1. Count of studies in each category of the database. All studies were published between January 1992 and December 2019, and collected following methods described in (Kober et al., 2008; Lindquist et al., 2016).

Table S3. The ratio of statistically-thresholded ROIs in each domain

Domain	How many ROIs	How many contrasts	Ratio
Negative All Social p<0.001 FWE K=74	14	184	0.07608696
Negative Some Social p<0.001 FWE k=74	15	219	0.06849315
Negative None Social p<0.001 FWE K=98	3	47	0.06382979
Positive None Social p<0.001 FWE k=88	3	42	0.07142857
Positive Some Social p<0.001 FWE k=81	9	71	0.12676056
Positive All Social p<0.001 FWE k=85	7	51	0.1372549

Table S4. Count and percentage of different modalities used in the literature across valence and social dimensions.

Social Stimuli	Number of Contrasts	Vision	Audition	Taste	Olfaction	Tactile	Visual and Auditory	Olfaction and Taste	Auditory and Olfaction	Recall/Imagery	Mimicry
Positive All Social	51	41	4	0	0	0	2	0	0	0	0
Positive Some Social	71	51	1	0	1	0	7	0	0	0	0
Positive Non-Social	42	9	7	12	4	5	0	2	1	0	1
Negative All Social	184	147	16	0	2	0	9	0	0	0	0
Negative Some Social	219	171	3	1	1	0	6	0	0	0	0
Negative Non-Social	47	28	5	4	4	1	0	0	1	0	1

Social Stimuli	Number of Contrasts	% Vision	% Audition	% Taste	% Olfaction	% Tactile	% Visual and Auditory	% Olfaction and Taste	% Auditory and Olfaction	% Recall/Imagery	% Mimicry
Positive All Social	51	80.39	7.84	0.00	0.00	0.00	3.92	0.00	0.00	0.00	0.00
Positive Some Social	71	71.83	1.41	0.00	1.41	0.00	9.86	0.00	0.00	0.00	0.00
Positive Non-Social	42	21.43	16.67	28.57	9.52	11.90	0.00	4.76	2.38	0.00	2.38

Negative All Social	184	79.89	8.70	0.00	1.09	0.00	4.89	0.00	0.00	0.00	0.00
Negative Some Social	219	78.08	1.37	0.46	0.46	0.00	2.74	0.00	0.00	0.00	0.00
Negative Non-Social	47	59.57	10.64	8.51	8.51	2.13	0.00	0.00	2.13	0.00	2.13

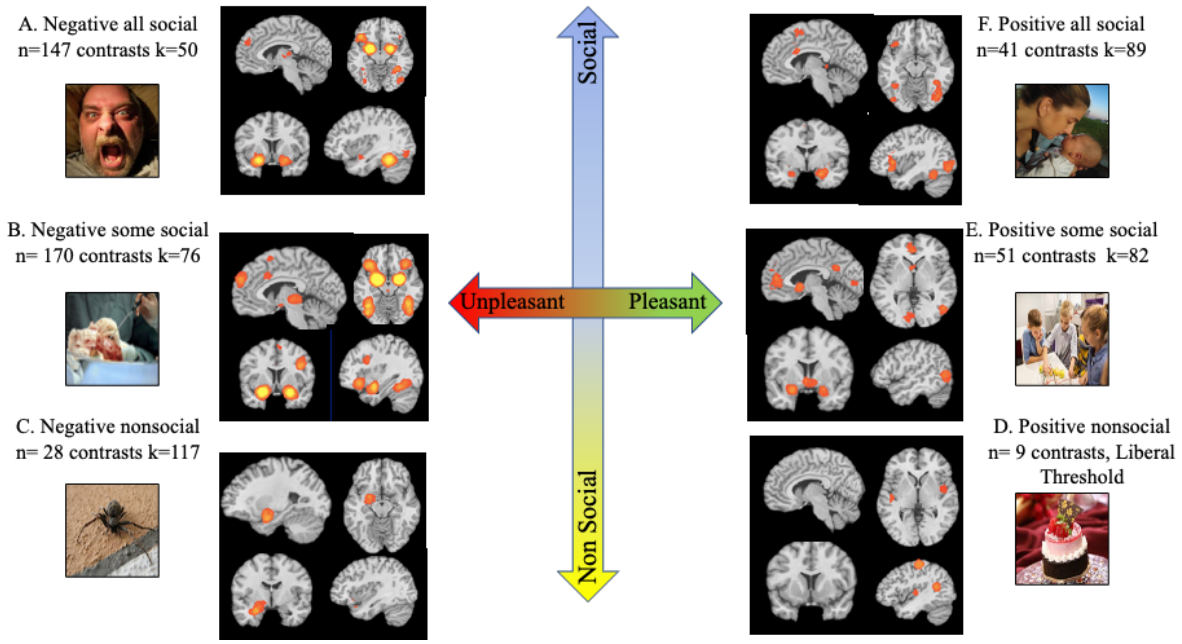

Figure S2: Only Visual Modality. Consistent neural activations along the dimensions of sociality and valence (p<0.001, FWE-corrected). Negative contrasts (A, B, C) used stimuli used stimuli that were rated as inducing negative affect (e.g., unpleasantness, negativity, anger, fear, disgust, contempt, sadness, etc.) by independent raters (i.e., in standardized stimulus sets) and/or by the participants in each study. Positive contrasts (D, E, F) used stimuli used stimuli that were rated as inducing positive affect (e.g., pleasantness, positivity, happiness, joy, pride, etc.) by independent raters (i.e., in standardized stimulus sets) and/or by the participants in each study. *All social* contrasts (A, F) contained exclusively social stimuli (e.g., human faces). *Some social* contrasts (B, E) contained a blend of social and

non-social stimuli (e.g., an IAPS picture depicting a scenario) or contrasts in which the sociality of stimuli was implied (e.g., a human hand). *Non-social contrasts* (C, D) contained exclusively non-social stimuli (e.g., food, music, scenes). Map slices: A. Negative all social: x=-5, z=-12, y=7, x=38; B. Negative some social: x=-5, z=-14, y=5, x=34; C. Negative non-social: x=-25, z=-14, y=-6; x=38 (liberal threshold p<0.005); D. Positive non-social: x=7, z=-5, y=8 (liberal threshold p<0.005), x=-36; E. Positive some social: x=-4, z=0, y=3, x=50; F. Positive all social: x=-5, z=0, y=-3, x=-42 (all maps are at liberal threshold p<0.005).

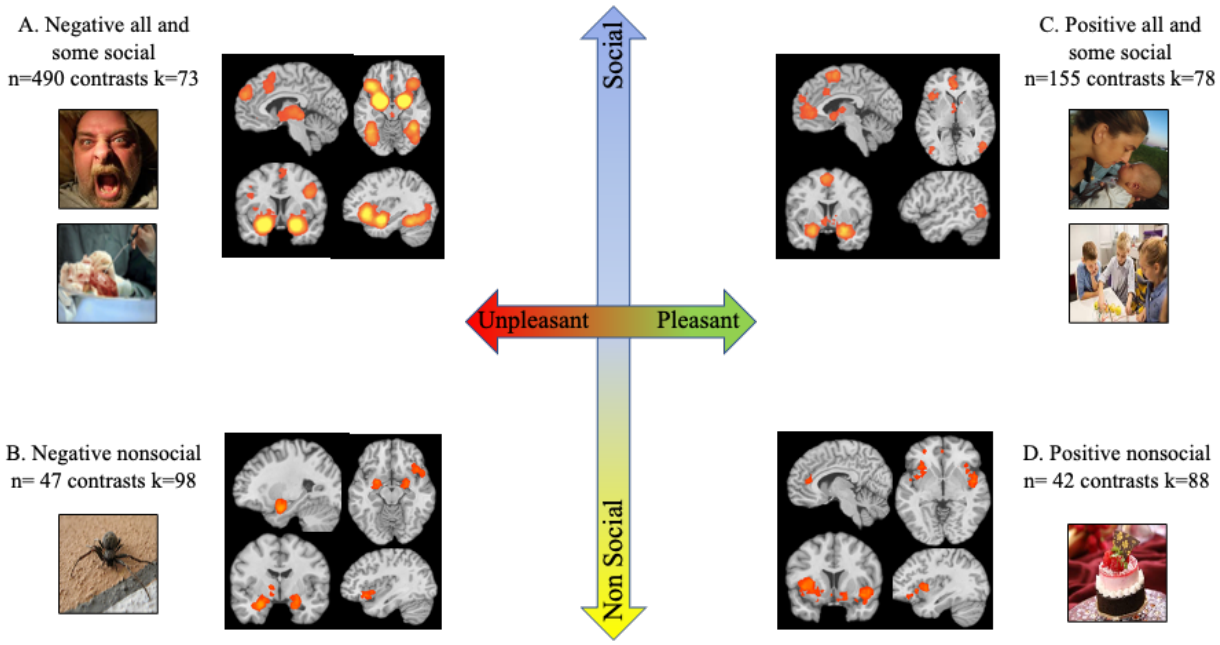

Figure S3: Consistent neural activations social, non-social, positive and negative contrasts (*p*<0.001, FWE-corrected). Negative contrasts (A, B) used negative stimuli. Positive contrasts (C, D) used positive stimuli. *Social* contrasts (A, C) contained social stimuli (e.g., human faces or IAPS picture depicting a scenario with social information). *Non-social contrasts* (B, D) contained exclusively non-social stimuli (e.g., food, music, scenes). Map slices: A. Negative social: x=-5, z=-14, y=5, x=34; C. Negative non-social: x=-25, z=-14, y=-6; x=38; D. Positive non-social: x=7, z=-5, y=8 (liberal threshold p<0.005), x=-36; E. Positive social: x=-5, z=0, y=-3, x=-42.

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