



Neural representation of social concepts: a coordinate-based meta-analysis of fMRI studies

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Abstract

The possible uniqueness of social stimuli constitutes a key topic for cognitive neuroscience. Growing evidence highlights graded contributions to their semantic processing by the anterior temporal lobe (ATL), where the omni-category response displayed by its ventrolateral sector might reflect the integration of information relayed from other regions. Among these, the superior polar ATL was specifically associated with representing social concepts. However, most previous studies neglected the close relationship between social and emotional semantic features, which might confound interpreting the degree of overlap vs. specificity of social and emotional conceptual processing. We addressed this issue via two activation-likelihood-estimation meta-analyses of neuroimaging studies reporting brain structures associated with processing social or emotional concepts. Alongside a common involvement of the ventromedial prefrontal cortex, we found social and emotional concepts to be specifically associated with lateral temporal areas (including the superior polar ATL) and the amygdala, respectively. These results support the specialization of distinct sectors of the fronto-temporo-limbic circuitry for processing social vs. emotional concepts, and the integration of their output in medial prefrontal regions underlying the regulation of social behavior. These results pave the way for further studies addressing the neural bases of conceptual knowledge, its impairment after fronto-temporal brain damage, and the effect of rehabilitative interventions targeting its main functional modules.

Keywords Social concept · Emotional concept · Activation likelihood estimation · Anterior temporal lobe · Amygdala

Introduction

Some recent advancements in the neuroscience of conceptual knowledge reflect a wider paradigm change in cognitive neuroscience, from a modular view centered on cortical

specialization to distributed models of neuro-cognitive functioning integrating across input modalities, stimuli content, and underlying processes (Taylor et al. 2011). A lively debate revolves around the putative neural specialization for the *processing of social information* (Insel and Fernald 2004) at increasing levels of complexity from selective stimuli such as faces to transmodal information detached from sensory experiences, i.e. a more generic “social knowledge” (Rice et al. 2018). The latter potentially includes any kind of information concerning both social entities and behaviors as well as the words referring to them, encapsulated in *social concepts* used to convey meanings in communicative exchanges and to interpret others’ behaviors (Olson et al. 2013). Whether affective information constitutes a core component of social concepts, or rather underpins an independent type of *emotional concepts* associated to specific neural correlates, is debated (Vigliocco et al. 2014; Zahn et al. 2007). Increasing data highlight the involvement of the anterior temporal lobe (ATL) in representing social (Olson et al. 2013), and possibly affective (Olson et al. 2007), concepts, but different interpretations of such role have been proposed.

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The ATL has been considered an amodal convergence zone (Damasio et al. 2004; Tranel et al. 1997), or “hub”, supporting conceptual representations regardless of modality and semantic category (Patterson et al. 2007). However, the notion of a general-purpose semantic processor associating different aspects of conceptual knowledge has been challenged by considerable evidence of its prominent engagement in socio-affective processing (Ross and Olson 2010). The association between ATL damage and altered social semantic processing (Chan et al. 2009; Snowden et al. 2004, 2012; Thompson et al. 2004) led to suggest that this region might rather constitute a social-specific semantic hub (Wang et al. 2017, 2019), with its limbic and polar sectors possibly integrating affective and valence-related information (Rice et al. 2015). A distributed model of semantic knowledge indeed suggests that coherent conceptual representations are generated by “hub” transmodal regions merging modality- and content-specific contributions from other network nodes based on their connectivity patterns (Binney et al. 2016; Lambon-Ralph 2014).

Multifaceted evidence suggests that the ATL plays such a hub role in representing social concepts (Rice et al. 2018). The convergence of sensory pathways into the temporal pole (Olson et al. 2007), possibly supporting its role in multimodal perceptual analyses (Binney et al. 2012), fits with the effect of ATL damage on socio-affective processing (Kumfor et al. 2017) and social behavior (Mychack et al. 2001). Moreover, neuroimaging studies in healthy individuals have shown the distinct roles played by the ventrolateral ATL sector, associated with omni-category responses to different concept types, and its superior polar sector (sATL), showing a preferential response to social concepts (Binney et al. 2016). While this process also involves the main nodes of the mentalizing network, i.e. ventro- and dorso-medial prefrontal cortex (vmPFC and dmPFC), posterior cingulate cortex (PCC) and temporo-parietal junction (TPJ) (Frith and Frith 2006), sATL activity tracks the richness of conceptual knowledge (Zahn et al. 2007). Overall, increasing evidence suggests that the network traditionally associated with the broad notion of “mentalizing” can be parcellated into more specific and informative functions (Moll et al. 2005a, b; Zahn et al. 2020), including social conceptual processing within the ATL (Binney and Ramsey 2020; Ross and Olson 2010).

The available evidence on this topic might be confounded, however, by the close relationship between social and affective features (Wang et al. 2019), both of which have been associated with the fronto-limbic circuitry. Whether the ATL codes the affective features of social concepts, or rather integrates into coherent concepts emotional information processed in other structures such as amygdala or vmPFC (Kim et al. 2011), is still unclear. Preliminary neuroimaging findings suggested that the lateral ATL is not activated when processing emotional words (Beauregard 2007; Cato et al. 2004),

nor its activity is modulated by emotional valence (Zahn et al. 2007). More recent evidence confirms the sATL involvement in social semantics, but with an additional modulation by emotional valence in the temporal poles (Wang et al. 2019). This evidence suggests that the neural representations of social and emotional concepts are not completely overlapping, and that the coding of social concepts might integrate affective features represented either in the ATL itself, or elsewhere. Testing these hypotheses requires to assess the neural bases of either concept types, regardless of the constraints inherent in specific studies. This goal can be pursued with coordinate-based meta-analyses, a quantitative unbiased approach which allows identifying the areas that are consistently activated in a particular class of paradigms (Laird et al. 2005; Turkeltaub et al. 2002).

We thus performed a coordinate-based meta-analysis to unveil the neural bases of social concepts, over and beyond the role of their affective facets that were separately addressed in a second meta-analysis on non-social emotional concepts. We predicted the engagement of ATL and amygdala when coding social and emotional concepts, respectively. We additionally assessed their overlap in the mPFC, in which the integrated processing of both concept types might support the regulation of social interactions (Binney and Ramsey 2020).

Materials and methods

See further details in [Supplementary Methods](#).

Study design

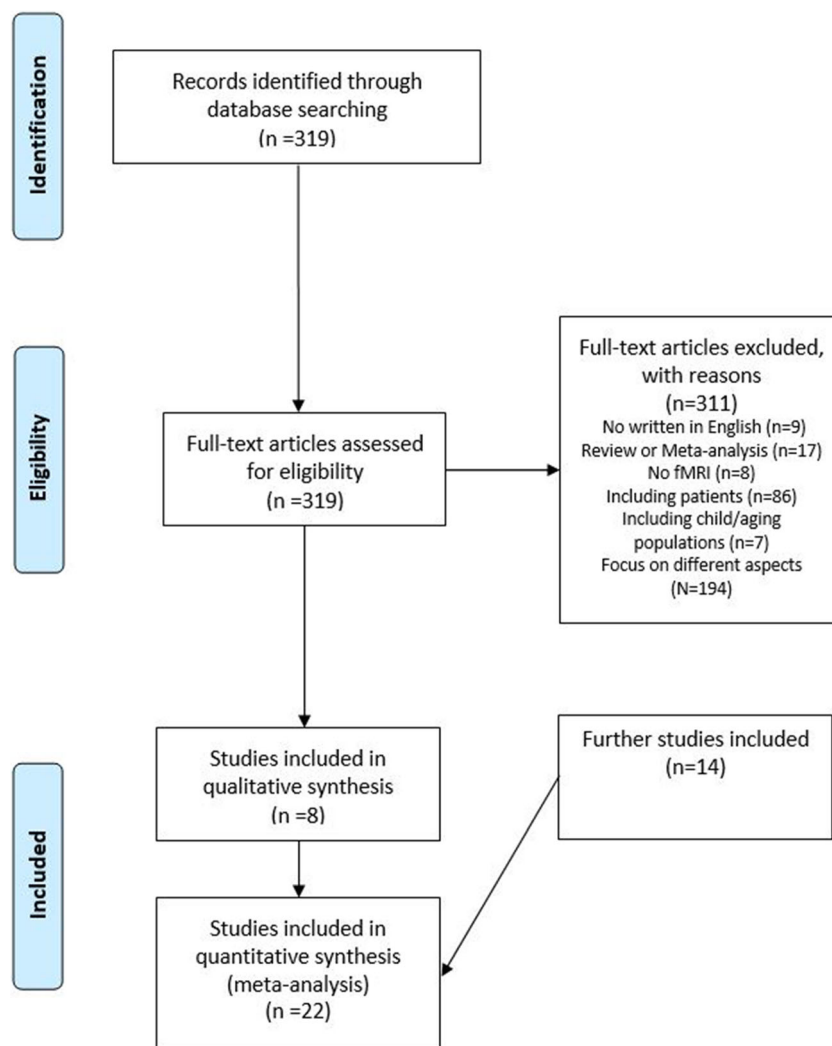
Based on the current prescriptions for ALE meta-analyses (Eickhoff et al. 2016), we aimed at including at least 17 experiments (contrasts) in each dataset, to achieve sufficient power for moderate effects and ensure that results would not be driven by single experiments.

Social concepts

We first surveyed the relevant literature by searching for “social concept fMRI” on Pubmed (<https://www.ncbi.nlm.nih.gov/pubmed/>), and by constraining this search to studies on human subjects published in the last 15 years (see Fig. 1 for a detailed flowchart of literature search and selection). From a pool of 319 studies, we retained only those fulfilling the following selection criteria:

- 1) published studies written in English;
- 2) empirical fMRI studies, while excluding review articles, behavioral studies and those employing other techniques, to ensure comparable spatio-temporal resolution;
- 3) studies including non-clinical and drug-free participants, to prevent possible differences in brain activity associated

Fig. 1 Flowchart of literature search and selection. The figure depicts the PRISMA flowchart describing the main stages of search and selection of relevant published papers on the neural processing of social or emotional concepts



with neuro-psychiatric diseases or pharmacological manipulations;

- 4) studies with adult subjects (age range: 18–60 years);
- 5) studies reporting whole-brain activation coordinates, rather than results limited to regions of interest (ROIs); moreover, we ensured that no partial brain coverage was reported in the Methods section of the retrieved papers.
- 6) studies investigating brain activity related to the processing of social concepts, meant as linguistic stimuli (words or sentences) whose referents are meaningful in the context of sociality and/or interpersonal interactions (Lin et al. 2015; Wang et al. 2019). Following Desai et al. (2018), to control for orthographic and phonological processes we included only studies using verbal stimuli (written words or sentences), while excluding those involving nonverbal materials such as pictures. Namely, we selected contrasts requiring participants to attend to verbal stimuli aimed to elicit a representation of social interaction by contrasting this kind of stimulus with concepts devoid of social facets. This selection retained studies contrasting

social and non-social emotions, while we excluded studies in which social concepts were contrasted with low-level baseline conditions such as rest or visual fixation.

We included studies fulfilling the above criteria regardless of: (a) stimulus valence; (b) experimental paradigm. This procedure led to include in the meta-analysis 22 previously published studies (Table S1), resulting from 23 experiments (individual comparisons reported) with 538 subjects and 302 foci. The inclusion of multiple contrasts/experiments from the same set of subjects can generate dependence across experiment maps and thus decrease the validity of meta-analytic results. To prevent this issue, we adjusted for within-group effects by pooling the coordinates from all the relevant contrasts of a paper into one experiment (Turkeltaub et al. 2002).

Emotional concepts

We searched for the coordinates associated with the neural processing of emotional concepts by applying additional

inclusion criteria to the studies reported in meta-analyses by Desai et al. (2018) and Brooks et al. (2017). We then expanded our search for other relevant studies by carefully examining both the studies quoting, and those quoted by, those two meta-analyses.

We selected only studies reporting brain activations associated with the processing of *emotional concepts* compared with stimuli without emotional characterization (i.e. neutral stimuli), while excluding comparisons with rest, fixation, or similar low-level conditions. We included only studies using verbal stimuli (written sentences or words). Since we aimed to assess both the specific and overlapping neural representations of social and emotional concepts, we excluded from this ALE analysis the studies using mainly emotional stimuli with social connotation.

We included studies fulfilling these criteria regardless of stimulus valence and experimental task, to ensure the generalizability of results. This procedure led to include in this ALE meta-analysis 27 previously published studies (Table S2), resulting from 27 experiments (individual comparisons reported) with 453 subjects and 287 foci.

Activation likelihood estimation (ALE)

We used the GingerALE software, based on Eickhoff et al. (2009; 2012; see [Supplementary Methods](#)), to identify consistently activated regions associated with processing either social or emotional concepts, as well as those specifically or commonly associated with these types of stimuli via direct comparisons and a conjunction analysis, respectively. The statistical maps were thresholded at $p < 0.05$, corrected for cluster-level family-wise error (FWE) with voxel-level forming threshold at $p < 0.001$ uncorrected (Eickhoff et al. 2016; Muller et al. 2018).

Results

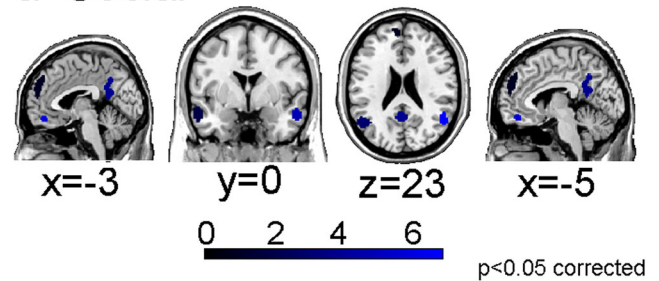
Neural representation of social concepts

The neural processing of social concepts recruited the dmPFC and vmPFC, PCC and precuneus, alongside both the posterior and anterior sectors of the lateral temporal cortex. In the former case, activations encompassed the middle temporal gyrus (MTG), superior temporal sulcus (STS) and TPJ bilaterally (Fig. 2; Table 1). Anterior temporal activations involved the inferior and middle temporal gyri bilaterally, extending into the superior temporal sulcus.

Neural representation of emotional concepts

Processing emotional concepts was associated with consistent activity in the vmPFC, alongside the left amygdala and pSTS/TPJ (Fig. 2; Table 2).

a Social



b Emotional

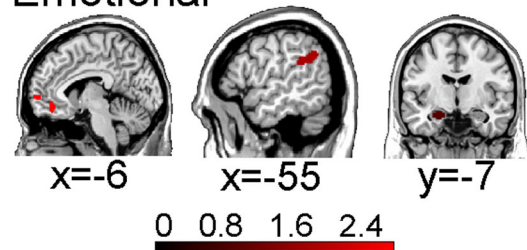


Fig. 2 The neural processing of social and emotional concepts. The figure reports the brain structures consistently associated with the processing of social (top, blue) and emotional (bottom, red) concepts. All the reported activations survived a statistical threshold of $p < 0.05$ corrected for multiple comparisons

Neural representation of social vs. emotional concepts

A conjunction analysis across social and emotional concepts highlighted a significant common activation in the vmPFC (Fig. 3; Table 3). Processing social, compared with emotional, concepts was associated with stronger activity in dmPFC, vmPFC and precuneus, alongside both posterior (MTG, pSTS and TPJ) and anterolateral temporal cortex, bilaterally (Fig. 3; Table 3). In the ATL, the social-related activity involved the inferior-middle temporal gyri bilaterally, extending into the superior temporal sulcus. The reverse comparison highlighted the left amygdala (Fig. 3; Table 3).

Discussion

We confirmed that processing social, compared with emotional, concepts is more strongly associated with a set of regions which have been collectively ascribed to the mentalizing network, i.e. dmPFC, ATL, pSTS/TPJ and posterior cingulate cortex/precuneus (Ross and Olson 2010; Arioli et al. 2018b). Emotional concepts selectively recruited the left amygdala, while the vmPFC was associated with both concept types. These findings provide novel insights into the contribution of content-specific semantic encoding to superordinate processes such as mentalizing and social cognition (Binney and Ramsey 2020).

Table 1 Neural bases of processing social concepts

Cluster #	Volume (mm ³)	x	y	z	ALE score	Label
1	3944	-8	54	32	0.033	Left Superior Frontal Gyrus
		-4	56	16	0.013	Left Medial Frontal Gyrus
2	3104	-58	-6	-26	0.029	Left Middle Temporal Gyrus
		-58	-2	-18	0.026	Left Middle Temporal Gyrus
		-62	-12	-14	0.020	Left Middle Temporal Gyrus
3	2936	-50	-62	20	0.029	Left Middle Temporal Gyrus
		-46	-68	30	0.020	Left Middle Temporal Gyrus
4	2544	-2	-54	22	0.022	Left Posterior Cingulate.
		-6	-52	16	0.019	Left Posterior Cingulate
		-4	-54	36	0.016	Left Precuneus
5	1672	56	0	-20	0.027	Right Middle Temporal Gyrus
6	1552	2	44	-14	0.027	Right Anterior Cingulate
7	1536	52	-60	22	0.029	Right Superior Temporal Gyrus

From left to right, the table reports the size (in mm³), stereotaxic coordinates of local maxima, ALE scores and anatomical labelling of the clusters which were consistently associated with processing social concepts

In keeping with several studies comparing social and non-social semantic processing, the superior polar ATL was specifically associated with social concepts (Fig. 2) (Binney et al. 2016; Lin et al. 2019, 2020; Skipper et al. 2011; Wang et al. 2019). This region is considered one of several “convergence zones” of a distributed network, centered in the ATL, in which the progressive integration of multiple features carried by upstream nodes generates coherent semantic representations (Olson et al. 2007; Rice et al. 2018; Visser et al. 2010). In particular, it has been suggested that the sATL role in social conceptual processing might reflect its sensitivity to the combination of social and either sensori-motor (Lin et al. 2019) or affective (Binney et al. 2015; Troche et al. 2014) information. Regardless of its specific interpretation, the functional role of the sATL is considered to reflect its connectivity within a larger network of areas, including frontal and limbic regions via the uncinate fasciculus (Bajada et al. 2017).

Indeed, processing social concepts was also associated with the mPFC, PCC and pSTS/TPJ, all of which are

intrinsically connected to the ATL (Yeo et al. 2011; Wang et al. 2019). All these regions have been previously associated with tasks requiring the attribution of mental states (Brunet et al. 2000), particularly when they involve social interactions (Lahnakoski et al. 2012; Walter et al. 2004) and the associated affective responses (Harris et al. 2007). Unlike the sATL, however, none of these regions show a direct relationship with the depth of semantic retrieval (Zahn et al. 2007). This widespread pattern of activity is thus suggestive of multifaceted contributions to the construction of social meaning, which might in turn support mentalizing (Ross and Olson 2010). Processing social groups is more likely to promote the retrieval of personal knowledge and autobiographical memories compared with individuals (Holland et al. 2011), which might explain the involvement of precuneus (Johnson et al. 2006). In turn, the latter is strongly connected with the mPFC (Cavanna and Trimble 2006), whose activity reflects distinct variables of social processing such as the number of stimuli in one’s social network (Lewis et al. 2012). The larger complexity of social

Table 2 Neural bases of processing emotional concepts

Cluster #	Volume (mm ³)	x	y	z	ALE score	Label
1	2272	-20	-6	-20	0.017	Left amygdala
		-28	0	-20	0.017	Left amygdala
		-28	6	-14	0.014	Left amygdala
2	1392	-58	-42	24	0.020	Left superior temporal gyrus
		-58	-52	28	0.019	Left supramarginal gyrus
3	736	-2	62	0	0.022	Medial frontal gyrus
4	704	-8	42	-14	0.018	Medial frontal gyrus

From left to right, the table reports the size (in mm³), stereotaxic coordinates of local maxima, ALE scores and anatomical labelling of the clusters which were consistently associated with processing emotional concepts

a Social and Emotional

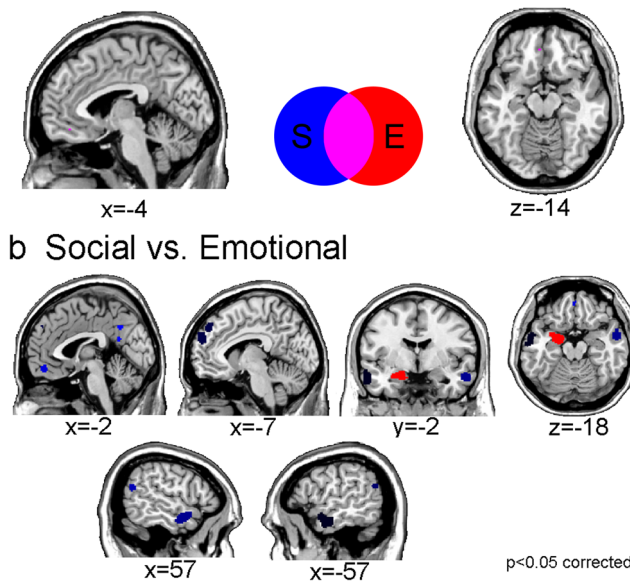


Fig. 3 Common and specific brain activity for processing social and emotional concepts. The figure reports the structures showing significant common (top, pink) and specific (bottom) brain activations associated with processing social and emotional concepts. All the reported activations survived a statistical threshold of $p < 0.05$ corrected for multiple comparisons

groups, compared with single individuals, might thus represent another factor promoting a stronger interplay between regions underlying social semantics and in-depth inferences on social actors' intentional states, such as the dmPFC (Meyer and Lieberman 2012; Mitchell et al. 2005; Sliwa and Freiwald 2017; Van der Cruyssen et al. 2015). This region plays a key role in decoding intentions in terms of internal mental states - e.g. thoughts, desires, and beliefs - when visuomotor cues are unavailable or insufficient (Arioli et al. 2018a, Arioli and Canessa 2019; Canessa et al. 2011; Van Overwalle and Baetens 2009) and proportionally to the abstractness of information processing (Baetens et al. 2014). Overall, this evidence highlights the possible contribution of social semantics to mentalizing, in terms of social conceptual representations detached from perceptual aspects (Trope and Liberman 2010; Wang et al. 2019).

A closer connection with the sensory dimension of social processing might involve the vmPFC (Roy et al. 2012), which was recruited by both emotional and social concepts. This region underpins evaluative processes modulating both social understanding and decision-making (Hiser and Koenigs 2018). One such process concerns flexible evaluations of social cues and behaviors, in conjunction with some of the aforementioned regions including dmPFC and precuneus. Such a domain-general function of vmPFC reflect its involvement in several tasks revolving around affective processing, e.g. emotion recognition (Drolet et al. 2012), learning (Nashiro et al.

2012), interference (Fales et al. 2008, 2009) and regulation (Morawetz et al. 2017), often in association with social stimuli (Immordino-Yang and Singh 2013). The vmPFC activation for both concept types might thus underpin the integration of emotion-related information into the neural representations of social concepts, likely enriched by signals on its valence, provided by the amygdala.

Indeed, in keeping with neuroimaging (Bickart et al. 2011) and lesional (Bickart et al. 2014) evidence of its role in affective processing, the amygdala was the only structure showing a selective response to emotional concepts. This structure has been mostly associated with processing nonverbal stimuli such as emotional faces (Duerden et al. 2013; Lindquist et al. 2016; Sergerie et al. 2008; Wager et al. 2003), while the effects of emotional valence on word processing are less consistent (Citron 2012) and often associated to the temporal pole (Ethofer et al. 2006; Kuchinke et al. 2005). Among the ATL semantic nodes, however, the temporal pole shows the strongest intrinsic connectivity with the amygdala (Wang et al. 2019). In line with distributed accounts of semantic cognition, the selective amygdala activation for emotional concepts is thus consistent with the segregated processing of social and emotional features into distinct ATL sectors (Wang et al. 2019), and their subsequent integration in semantic hubs. Moreover, the left-hemispheric lateralization of amygdala activation fits with previous evidence of an automatic processing of emotional words in the left hemisphere, providing fast access to semantically-associated stimuli (Abbassi et al. 2015; Herbert et al. 2011a, b; Moseley et al. 2012; Ponz et al. 2014). Its engagement might reflect a domain-general function such as stimuli evaluation based on their salience and behavioral relevance in terms of affiliation/aversion (Bickart et al. 2014; Canessa et al. 2013). This consideration highlights a potential limitation of this study, due to the heterogeneity of the stimuli used in previous studies on emotional concepts (generally focusing on high arousal and negative emotions) vs. social concepts (typically controlling for valence but not arousal). The evidence of stronger amygdala response to emotional than social concepts might thus reflect an inherent bias, which future studies should address, towards the use of negative emotional stimuli.

Other limitations of this work, mainly due to the number of relevant studies, concern the lack of evidence on multiple factors which might drive brain responses to social concepts, such as the fine-grain in the definition of "social knowledge", the level of linguistic processing (e.g. discourse, sentence, word), and/or the task employed to activate conceptual representations. Moreover, a cluster-based inference might favor large regions that are least likely to host content-specific representations. Finally, future studies might refine our findings by addressing subtler distinctions between the neural processing of exclusively-social, socio-emotional and exclusively-emotional concepts.

Table 3 Common and specific neural bases of processing social and emotional concepts

Social & Emotional						
Cluster #	Volume (mm ³)	x	y	z	Label	ALE score
1	8	-4	42	-14	Ventromedial prefrontal cortex	0.012
Social > Emotional						
Cluster #	Volume (mm ³)	x	y	z	Label	
1	2560	-62	-6	-23	Left Middle Temporal Gyrus	
		-62	-8	-19	Left Inferior Temporal Gyrus	
		-6	48	42	Left Superior Frontal Gyrus	
2	2384	-12	58	24	Left Superior Frontal Gyrus	
		-41	-66	27	Left Middle Temporal Gyrus	
		-47	-66	31	Left Middle Temporal Gyrus	
3	2088	-56	-60	20	Left Superior Temporal Gyrus	
		55	3	-20	Right Superior Temporal Gyrus	
		58	-6	-24	Right Middle Temporal Gyrus	
4	1608	48	-54	14	Right Middle Temporal Gyrus	
		54	-54	15	Right Superior Temporal Gyrus	
		53	-61	18	Right Middle Temporal Gyrus	
5	1112	-2	52	-14	Left Medial Frontal Gyrus	
		6	-58	26	Right Posterior Cingulate	
6	544	-4	-56	18	Left Posterior Cingulate	
		-2	-56	38	Left Precuneus	
7	368	0	-56	34	Left Cingulate Gyrus	
Emotional > Social						
Cluster #	Volume (mm ³)	x	y	z	Label	
1	1912	-24	-8	-16	Left Amygdala	
		-24	-7	-19	Left Amygdala	
		-19	-2	-15	Left Amygdala	

Common and specific brain regions associated with processing social and emotional concepts

From left to right, the table reports the size (in mm³), stereotaxic coordinates of local maxima, ALE scores and anatomical labelling of the clusters which were commonly (top) and specifically (middle, bottom) associated with a neural representation of social and emotional concepts

Conclusions

We provided novel meta-analytic evidence on both specific and overlapping neural bases of processing social and emotional concepts. Although the limited fine-grain of our findings prevents a parcellation of the “hub and spoke” functional modules (Binney et al. 2016), these results show that the neural correlates of processing social and affective semantic features are at least partially segregated in the lateral and medial ATL sectors, respectively. Once integrated into convergence zones, such as vmPFC, these features might underpin higher-order conceptual representations any kind of information concerning both social entities and behaviors as well as the words referring to them supporting communicative exchanges, as well as the evaluation and planning of social behaviors (Binney and Ramsey 2020). Observing distinct brain structures associated with processing either social or emotional concepts, or both, might suggest novel tools for assessing

pathological conditions characterized by different degrees of semantic, socio-emotional or behavioral impairments, such as the variants of fronto-temporal dementia (Chan et al. 2009). These results highlight the potential translational implications of social neuroscience (Arioli et al. 2018a), and pave the way for future studies addressing the neural bases of conceptual knowledge, its impairment after ATL damage, and the effect of rehabilitative interventions targeting its functional modules.

Author contributions Author contributions included conception and study design (all authors), data collection (MA), statistical analysis (MA), interpretation of results (all authors), drafting the manuscript work (MA, NC) or revising it critically for important intellectual content (all authors), and approval of final version to be published and agreement to be accountable for the integrity and accuracy of all aspects of the work (all authors).

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Compliance with ethical standards

Conflict of interest None of the authors have a conflict of interest to declare.

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