PHILOSOPHICAL TRANSACTIONS B

rstb.royalsocietypublishing.org

Review

Cite this article: Desai RH, Reilly M, van Dam W. 2018 The multifaceted abstract brain. *Phil. Trans. R. Soc. B* **373**: 20170122. http://dx.doi.org/10.1098/rstb.2017.0122

Accepted: 11 May 2018

One contribution of 23 to a theme issue 'Varieties of abstract concepts: development, use and representation in the brain'.

Subject Areas:
cognition

Keywords:
semantics, abstract concepts, embodiment, events, emotions, numbers

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Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4105346.

THE ROYAL SOCIETY PUBLISHING

The multifaceted abstract brain

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Abstract concepts play a central role in human behaviour and constitute a critical component of the human conceptual system. Here, we investigate the neural basis of four types of abstract concepts, examining their similarities and differences through neuroimaging meta-analyses. We examine numerical and emotional concepts, and two higher-order abstract processes, morality judgements and theory of mind. Three main findings emerge. First, representation of abstract concepts is more widespread than is often assumed. Second, representations of different types of abstract concepts differ in important respects. Each of the domains examined here was associated with some unique areas. Third, some areas were commonly activated across domains and included inferior parietal, posterior cingulate and medial prefrontal cortex. We interpret these regions in terms of their role in episodic recall, event representation and social–emotional processing. We suggest that different types of abstract concepts can be represented and grounded through differing contributions from event-based, interoceptive, introspective and sensory-motor representations. The results underscore the richness and diversity of abstract concepts, argue against single-mechanism accounts for representation of all types of abstract concepts and suggest mechanisms for their direct and indirect grounding.

This article is part of the theme issue 'Varieties of abstract concepts: development, use and representation in the brain'.

1. Introduction

In investigations of the semantic system, two broad categories of concepts have been used. Concrete concepts, such as *tree*, *hammer* or *lion*, have attracted a lion's share of research on the neural basis of the semantic system. These concepts have an identifiable, bounded referent that can be experienced with the five senses. They also tend to fall into taxonomic, hierarchical categories, such as animals, tools and living things, owing to clusters of co-occurring features ('has legs' and 'has eyes'), and are intuitively easier to reason about. A large body of evidence now indicates that such concepts are based, at least partially, in action and perception systems of the brain, a view referred to as embodiment, or more generally, grounded cognition [1–5]. Abstract concepts, such as *democracy*, *philosophy* or *evaluation*, on the other hand, are messier and are more difficult to characterize and categorize. They evoke complex and rich experiences involving episodes and situations, emotions, relations, introspection and interoception,[1] but lack a clear sensory-motor experience. However, such concepts are very frequently encountered in language and represent one of the most sophisticated and important abilities of the human mind. Based on some behavioural findings, such as the fact that people list fewer features for abstract than concrete words, and require higher response times for abstract words, it is suggested that abstract concepts are more impoverished and 'less semantic'. But it is not clear that there is anything impoverished about many abstract concepts such as *justice* or *opinion*. Semantic richness may be largely a matter of the methods used to measure it, which may be more or less suitable for certain types of concepts. The apparent semantic poverty of abstract concepts may be an artefact of methods suited to evaluating concrete concepts [6,7].

While abstract concepts have been studied for at least three decades, neuropsychological investigations of patients with conditions such as aphasia and semantic dementia typically define 'semantics' entirely in terms of concrete concepts, often only concrete objects. This is driven, in part, by the popularity of tasks such as picture naming and picture association in standardized test batteries, which are suited to concrete concepts. This tendency also trickles down to neuroimaging studies. Even today, it is not uncommon to see studies that use a few concrete object categories such as animals and tools as stimuli, and assume that the results speak to the entire semantic system. The bias against abstract concepts starts with the definition itself, in that they are defined negatively by what they lack rather than by what they contain. They are essentially 'everything that is not concrete'. This is a bit like dividing buildings into 'dwellings' and 'non-dwellings'. This can be useful especially if we are mainly interested in dwellings, but it shortchanges the diversity of non-dwellings that can vary from hospitals to museums to shopping centres. The most important feature of a movie theatre is not that people do not live there.

Over the last decade, there has been a growing realization of the importance and diversity of abstract concepts. Intense debate has been generated relating to the representation of abstract concepts, driven mainly by the observation that they do not seem suitable for grounding in action and perception systems. This has resulted in a number of valuable theoretical proposals which range in their degree of embodiment and a number of distinct mechanisms that are required to account for concrete and abstract concepts [8]. In general, these theories treat abstract concepts as a single entity to be explained by a particular mechanism. To be sure, concrete and abstract concepts do not form a clean dichotomy, but vary on a continuum that is commonly implemented using the continuous measure of concreteness rating (and the closely related measure of imageability). Researchers have typically used the high end of the continuum for the concrete category, and mid- to low range concepts are classified under 'abstract'.

Neuroimaging and neuropsychological research has consistently suggested that abstract and concrete concepts differ. The particular brain regions involved and the reasons for these differences remain controversial, but the existence of differences is consistent. Neuropsychological double dissociations have pointed to reliance of concrete concepts on featural or taxonomic, and that of abstract concepts on associative or thematic information [7,9–13] (see [8] for a discussion). With regard to neuroanatomy, a meta-analysis of 19 studies [14] found that two regions were consistently activated for abstract over concrete words or sentences: the left anterior temporal lobe (ATL) and the inferior frontal gyrus (IFG). This contrasts with the findings for concrete concepts, which revealed a more extensive network that includes bilateral angular gyrus (AG), posterior lateral, medial and ventral temporal lobe, and posterior cingulate (pCi) and precuneus [14,15].

These findings are consistent with both of the classical theories of abstract/concrete concept representation. According to the Context Availability Theory [16–18], abstract words are more reliant on the context in which they occur. Abstract word processing requires greater activation of, and integration with, the context. This is consistent with the left IFG activation, which is associated with strategic semantic access and integration. The Dual Coding Theory [19,20] posits that only concrete concepts have a direct connection to image-based or visual representations, while abstract concepts are represented only through verbal associations. Activation of a number of areas associated with higher-order visual processing, such as the parahippocampal gyrus, fusiform gyrus and middle occipital gyrus (MOG), as well as greater bilateral activation, supports this view. Left lateralized activation for abstract concepts, including the traditional language processing area of IFG, also supports the notion of importance of verbal associations for abstract concepts.

According to the meta-analyses, abstract concepts would appear to have a significantly smaller footprint than concrete concepts, involving only the left IFG and lateral ATL, whereas concrete concepts reveal a much more extensive territory. This apparent small footprint of abstract concepts may be misleading for multiple reasons. First, note that these activations only reveal areas activated to a greater extent for abstract concepts relative to concrete ones. They do not include areas that may be equally activated by both types of concepts, or those that are activated by abstract concepts, but even more so by concrete concepts. Secondly, meta-analyses are designed to detect consistent activation across studies that identify neural correlates of a particular psychological process. Activations found in a smaller proportion of included studies are assumed to be unreliable or false positives, likely resulting from statistical accidents or a flaw in the experiment such as a confound. However, this is not necessarily the case. Variable results between different experiments can exist if categories with different underlying representations are lumped together. For example, concepts that refer to mental processes (*thought* and *consideration*), those that refer to social structures and constructs (*democracy* and *conspiracy*) and those that have a strong emotional component (*praise* and *anger*) could potentially have different neural representations. Legitimate variability resulting from these differences is eliminated in a meta-analysis.

Apart from the heterogeneity, there is an additional methodological issue that adds variability to concepts that are classified as 'abstract' in different studies, and hence in the results of these studies. As Pollock [21] has recently pointed out, concepts with intermediate concreteness ratings tend to have high standard deviations. They are not truly rated as 'intermediate' by many raters, but as clearly concrete by some and clearly abstract by others. Abstract stimuli used in many studies contain words with intermediate and high standard deviation ratings, and hence, their abstractness is in question. Concrete concepts selected in many studies tend to have low standard deviations and tightly cluster near the high end of the concreteness scale. Using parametric variation in concreteness (e.g. [22]) can mitigate this, but the high variability related to intermediate ratings is still problematic. This can potentially explain some of the discrepancy in neuroimaging and behavioural results, such as the advantage of concrete over abstract words, or the importance of taxonomic versus thematic information for concrete and abstract words, respectively.

Here, we meta-analyse neuroimaging studies from four categories of abstract concepts, with two aims. The first is to examine the similarities and differences between the neural correlates of types of abstract concepts, to test whether different subcategories differ substantially, or whether a single representation format for not-concrete words is likely.

A related second aim is to examine the possibility that at least some types of abstract concepts can be grounded in brain circuits subserving other functions, such as emotional or spatial processing, and event representations. We review emotional and numerical concepts expressed symbolically and two 'higher-order' processes that reflect abstract thought: morality judgements and theory of mind (ToM). Apart from the salience and controversial nature of these domains, they are chosen because of the substantial body of neuroimaging work on these domains that can be used to draw inferences across a variety of stimuli and tasks.

2. Numerical concepts

Numerical magnitude can be conveyed through symbolic (e.g. Arabic numerals or written number words) or non-symbolic stimuli (e.g. dot patterns), and has been pointed out as a key example of abstract semantics. The question of how abstract numerical magnitude information can be represented, or grounded in sensory-motor systems, therefore forms one of the key challenges for any theory of cognition. Previous evidence has suggested that semantic information of the domain of numerical cognition can be grounded through its systematic association with left-to-right coordinates of space [23,24]. Numerous studies have indeed demonstrated that numerical cognition shares computational processes with spatial processing. Dehaene *et al.* [23] demonstrated that subjects were faster in making parity judgements to small numbers when responding with their left hand, while judgements to large numbers were faster in the case of a right-hand response. Such a demonstration of a common representational format underlying numerical magnitude information and the spatial characteristics of a response was termed the SNARC effect (Spatial–Numerical Association of Response Codes) and has been taken as evidence for a spatial nature of numerical magnitude representations analogue to the location on a 'mental number line'. In line with the observation that the SNARC effect is typically not observed earlier than in 9-year-old children and becomes stronger from childhood to elderly age [25,26], it has been suggested that it reflects the long-term practice of using spatial information in processing numerical magnitude [27,28] and establishment of a reading–writing system [29]. The exact nature of the spatial information recruited during numerical magnitude processing seems to be modulated by cross-cultural differences in the direction of the writing system [30–32]. Furthermore, it has been shown that the SNARC effect is modulated by finger counting habits and hand preference [33,34]. This finding might reflect the fact that the direction of the spatial–numerical association given by a writing system seems to be an important determinant in shaping finger counting habits [35]. Moreover, an influence of finger counting habits and hand preference might signify the coexistence of multiple number–space mappings that are based on either extra-personal physical space or finger counting habits. Findings from studies that tried to disentangle these influences are mixed, with some studies reporting a stronger influence of body-based than space-based representations [36,37], while other studies found the reverse pattern [38,39]. Altogether, findings have shown that numerical magnitude information shares computational processes with spatial representations that are based on either personal or extra-personal number–space mappings.

In line with the idea that numerical cognition overlaps with computational processes that underlie spatial processing and/or finger counting actions, spatial processing areas in the posterior parietal cortex play a role in the processing of numerical magnitude information across a wide range of tasks like mental calculation, approximation and number comparison [40,41] and across cultures [42]. Similarly, patient studies show that lesions to the parietal cortex are associated with deficits in numerical processing ranging from magnitude comprehension to number subtraction or bisection [43], and repetitive transcranial magnetic stimulation (rTMS) over posterior parietal regions has been shown to reduce the SNARC effect in a parity judgement task [44]. To investigate if the abstract domain of numbers is grounded in brain areas involved in spatial processing, we conducted an activation likelihood estimation (ALE) meta-analysis on peak coordinates reported in neuroimaging studies on number processing.

(a) Methods

First, we describe general methods that were used for meta-analyses in all domains. Peer-reviewed articles were obtained from literature search or existing meta-analyses, to which additional inclusion criteria were applied. Specific contrasts were included if they contained a whole-brain neuroimaging analysis and contrasts with linguistic baseline conditions (with the exception of numbers, where non-linguistic baselines such as scrambled letters are commonly used). This excluded contrasts that used 'rest', fixation or a similar low-level condition. Comparisons with nonverbal materials such as pictures were also excluded, as they do not control for orthographic and phonological processes. Coordinates for all the included contrasts across the different domains were extracted and, where necessary, converted from Montreal Neurological Institute (MNI) to Talairach space using the icbm2tal transformation tool provided in GingerALE 2.3.6 [45,46]. In the ALE analysis using GingerALE, we used a corrected cluster-level $p < 0.05$, 1000 permutations, uncorrected $p < 0.005$. A region of interest (ROI) analysis was also included to examine the left ATL and left AG, two areas that often emerge during semantic processing, which were also corrected using the same parameters.

Studies included for the numerical concepts domain were selected on the basis of meta-analyses by Arsalidou & Taylor [47] and Sokolowski *et al.* [48]. From the 146 studies included across these two meta-analyses, we only included studies that investigated numerical magnitude processing by means of symbolic stimuli (i.e. Arabic numerals like '1, 5' or written number words like 'three, nine', in either the visual or auditory modality) and that did not involve any calculation of some sort (e.g. multiplication or addition). Contrasts that involved judging numerosity or counting (e.g. five circles versus seven circles) were removed. Furthermore, we excluded positron emission tomography (PET) studies, studies that used children as subjects, studies that did not include a control for general executive processing (e.g. number comparison versus rest), studies that used tasks that heavily relied on other cognitive processes (e.g. delayed-number matching) and studies that only used contrasts that focus on higher-order numerical processing (e.g. positive versus negative integers, congruent versus incongruent, comparing different number ratios). After screening all studies, 23 separate contrasts remained, with a total of 126 foci from 375 participants (figure 1; electronic supplementary material, table S1).

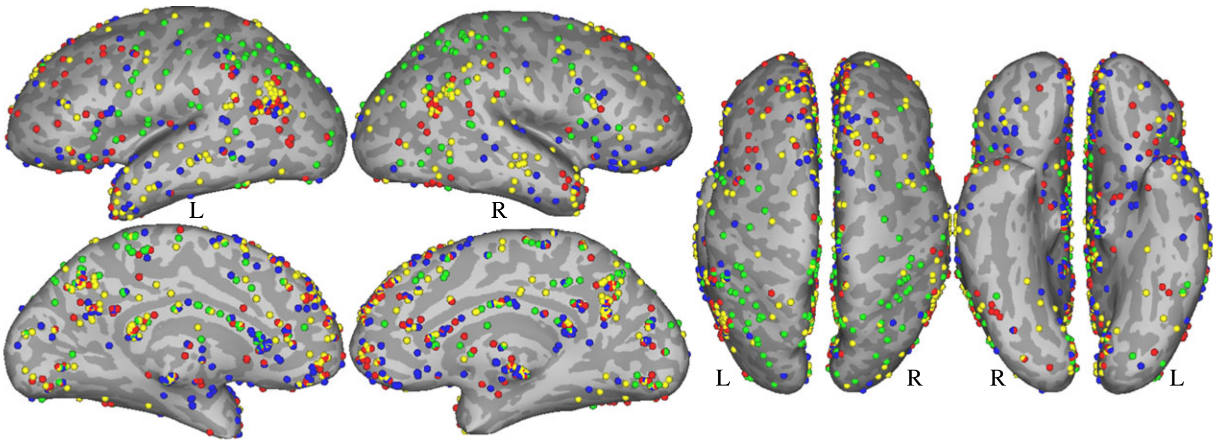

Figure 1. Peaks from all contrasts used in the meta-analyses. Green—numbers, blue—emotion, red—morality, yellow—theory of mind.

Table 1. Clusters for the numerical cognition meta-analysis. Coordinates are reported in Talairach space and refer to the location of the maximum observed ALE value. clust., cluster number; hem., hemisphere; BA, approximate Brodmann area; ALE, activation likelihood estimate; vol., volume.

clust.	hem.	brain area	BA	*x*	*y*	*z*	ALE	vol. (mm^3)
1	R	inferior parietal lobule	40	36	−44	40	0.024	5792
		middle temporal gyrus	39	30	−60	30	0.014	
		superior parietal lobule	7	24	−64	42	0.014	
				28	−52	44	0.013	
				36	−64	48	0.009	
2	L	inferior parietal lobule	40	−42	−44	38	0.020	3824
				−48	−38	48	0.013	
				−34	−40	44	0.013	
3	L	superior parietal lobule	7	−24	−58	42	0.015	2632
				−24	−54	44	0.015	
		precuneus	19	−30	−66	36	0.013	
			31	−26	−76	24	0.008	

(b) Results

Three significant clusters of activation, with a total of 12 peaks, were found for numerical cognition (table 1 and figure 2). These fell in the right anterior intraparietal sulcus (IPS), extending into the posterior IPS and the superior parietal lobule (SPL), and the left anterior IPS, extending into the inferior parietal lobule (IPL) and the left posterior IPS.

(c) Discussion

The IPS has been consistently linked to spatial processing and attention as well as visually guided grasping [49–54]. It is part of the classic where/how dorsal visual pathway [53,55], although the binary distinction between dorsal/ventral pathways has been challenged [56], with evidence that the dorsal pathway may also contain object representations that subserve actions. Regarding number processing, Eger *et al.* [57] showed that, in a task that did not require the explicit activation of magnitude information, processing of numeric symbols across the visual and auditory modality elicited activation in a bilateral region of the horizontal section of IPS (hIPS). In addition, imaging studies have provided evidence that the hIPS plays a role in the coding of non-symbolic numerical magnitude [58] and shows a distance-dependent recovery of activation for newly presented numbers irrespective of the symbolic or non-symbolic nature of the stimulus material [59]. The finding of an involvement of the hIPS in the processing of numerical magnitude information has been replicated across a wide range of tasks such as number comparison, mental calculation and approximation [40,41,60] (although we eliminated calculation tasks here) and has been replicated across cultures [42]. Patient studies have demonstrated that parietal lesions are associated with deficits in numerical processing ranging from magnitude comprehension to number subtraction or bisection [43]. These results have led to the proposal that the hIPS contains a representation of numerical magnitude that is independent of the modality of presentation (i.e. visual or auditory, [57,61]). The finding of an important role of the hIPS in the processing of numbers is in line with the idea that numerical magnitude is grounded in brain regions that code for extra-personal spatial representations.

Alternatively, or in addition to spatial representations, these results may reflect the activation of body-based

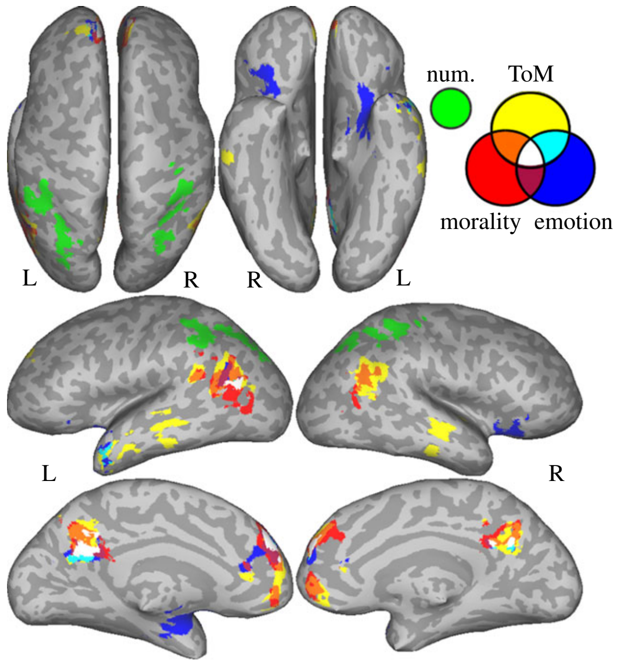

Figure 2. Results of the meta-analysis showing significant ALE values within each domain, and overlap.

representations acquired through finger counting habits. It is difficult to distinguish between these two proposals on the basis of these neuroimaging findings, given that the hIPS has traditionally also been strongly linked with the control of hand and finger movements [62–65]. A number of studies have provided evidence for a role of finger and hand movement representations in the grounding of numerical knowledge by showing that numerical magnitude processing not only involves parietal regions but also extends to the primary motor cortex [41,60,66,67] and increases corticospinal excitability of hand muscles [68]. Several peaks were observed in the current analysis in the motor cortex, but did not survive the meta-analysis owing to their distributed nature.

IPS involvement, especially in the right hemisphere, could reflect the activation of a generalized magnitude system, as proposed by A Theory of Magnitude (ATOM) [69,70]. ATOM suggests a single system responsible for many types of magnitude estimations, including those for time, space and number, with the right parietal lobe as the key component. Neuroanatomy suggests that such common representations are grounded in action–perception systems. To argue that these magnitude representations are abstract, positive evidence would need to be provided to the effect that they do not contain any spatial or action components.

The lack of frontal activation in the current meta-analysis might reflect the fact that we only selected studies that used 'simple' number tasks like numerical comparison, whereas studies of numerical cognition typically include a wide array of tasks that involve additional arithmetic processing [47]. Similarly, while AG was seen in the three other domains meta-analysed below, its absence from the current domain is noteworthy, given its strong association with numerical cognition [71]. This can also be explained by the fact that AG is most commonly seen in tasks that involve calculation. During calculation, it is involved with recall of memorized mathematical facts (such as $3 \times 4 = 12$) [72] and transfer of facts between calculations [73]. Involvement of AG is likely minimized here owing to the inclusion criteria that eliminated calculation tasks.

In addition to confirming the role of IPS in number processing, these results demonstrate that it also holds for purely symbolic stimuli, and without the use of higher-order tasks. The bilateral extent of IPS, SPL and IPL activation for number processing suggests grounding of numerical concepts in the processing of physical space and the spatial/non-spatial characteristics of hand movements. However, it should be noted that the precise nature of conceptual grounding of numerical magnitude information seems to vary extensively between individuals and cultures [30,31,35], reflecting interindividual and task-specific differences in the disposition to map numbers to different body parts, to personal versus extra-personal space or even to non-spatial force parameters [74]. These interindividual differences in number–space mappings can likely be explained by factors such as handedness, counting habits and writing system direction [33–35]. For example, some cultures use counting systems that use specific body parts in sequence, like counting on fingers but also using elbows, knees and eyes [75, p. 242]. These systems can top out at 12, or go as high as 74, and can even cycle through these two or three times to obtain even higher values. Such systems can be neurobiologically grounded in cortical representations of body parts that go well beyond fingers.[2]

3. Emotion concepts

From the perspective of semantic information, emotion refers to the emotional or affective experience elicited by the use of a word. Based on the circumplex model [76,77], two dimensions are often used to describe emotion semantics: arousal describes the amount of emotional 'energy' or the level of engagement of the organism, and valence describes the hedonic tone of the emotional state, ranging from positive to negative. Although more highly valenced stimuli are also frequently more highly arousing [78], this pattern is stronger for negative than for positive words [79]. Other dimensions have also been proposed to describe emotional stimuli. For example, a word can be classified according to whether it is 'biological', that is, if its emotional content is relevant to evolutionary success [80]. However, arousal and valence are the most commonly studied in psycholinguistic evaluations of emotion.

Emotional arousal and valence are often cited as playing a critical role in the difference between abstract semantics and concrete semantics [7,81,82]. Abstract words, in general, tend to be more emotionally valenced than concrete words [83] and, within the domain of abstract words, highly arousing words elicit different behaviours from emotionally neutral words; the distribution of lexical decision reaction times is narrower and earlier for emotional words [84]. There is even evidence for a specific role of emotion in processing abstract concepts that is absent in concrete concepts: behavioural performance [85,86] and deterioration of semantic memory in Alzheimer's dementia patients [87] show effects of emotional content within abstract words but not within concrete words. This suggests that the emotional information associated with abstract words is uniquely critical to how their meanings are stored in the brain. We performed a meta-analysis of neuroimaging studies that examined affect through verbal materials.

Table 2. Clusters for the emotional cognition meta-analysis. *Area that was significant only in the ROI analysis.

clust.	hem.	brain area	BA	x	y	z	ALE	vol. (mm³)
1	L	dorsomedial prefrontal cortex	9	−6	48	34	0.020	4608
				−4	48	26	0.017	
				8	50	16	0.014	
		anterior cingulate	32	−4	38	18	0.014	
		middle frontal gyrus	9	−14	38	28	0.012	
2	L	amygdala		−26	−4	−12	0.020	2752
		hippocampus		−28	−14	−14	0.015	
3	L	precuneus		−4	−56	24	0.027	2448
4	R	IFG/orbitofrontal gyrus	47	32	20	−12	0.020	1808
				38	26	−2	0.011	
5	L	anterior temporal lobe*		−47	−6	−23		
				−53	−7	−5		
6	L	angular gyrus/TPJ*		−49	−61	18		

(a) Methods

Studies or contrasts were selected that investigated emotion by means of verbal stimuli only, excluding studies that used materials such as pictures, videos or music, either as the condition of interest or as the control condition. The dimension of valence has been experimentally isolated from emotional arousal by a few neuroimaging studies, but it is often confounded with emotional arousal. In the current analysis, the majority of studies that purport to study valence contrasted either positively or negatively valenced words with emotionally neutral words. The neutral word baseline is also low-arousal relative to either positive or negative words; hence, it is difficult to distinguish arousal from valence across these studies. Thus, the peaks included in the current analysis are restricted to experiments that contrast emotional arousal, even if some may also be contrasting valence. We included foci from experiments that contrasted emotionally valenced words with neutral words, or an explicitly valenced semantic task with a non-emotional semantic task. Thirty-three separate experiments were included, with a total of 205 foci (figure 1) from 560 participants (electronic supplementary material, table S2).

(b) Results

Four significant clusters of activation, with a total of 10 peaks, were found in the ALE meta-analysis for the emotion domain (table 2 and figure 2). Activations fell in the bilateral dorsomedial prefrontal cortex (dmPFC) and anterior insula, the left anterior cingulate, medial superior frontal gyrus (SFG), amygdala, hippocampus and precuneus as well as the right orbitofrontal cortex (OFC) extending into the pars orbitalis.

(c) Discussion

Of the areas that emerged in the ALE meta-analysis, the amygdala is the most specific to emotion processing relative to other forms of abstract semantics. Neuroimaging studies consistently report the amygdala as being sensitive to emotional arousal across many types of stimuli (for review, see [88]). It emerges in both contrasts comparing negative words with neutral words [89–91] and those comparing positive words with neutral words [92,93]. Traditionally, amygdala is considered to be part of the subcortical pathway that is dedicated to processing emotions, especially fear. This view has been challenged [94], and instead, it is suggested that it is part of a broader network that evaluates the emotional significance of (especially visual) stimuli and also the possible responses to it [95,96]. While amygdala has an important role in emotion processing under this model, it suggests that cortical areas such as the OFC and anterior cingulate cortex (ACC) have a greater role in evaluating emotional significance than is traditionally assumed [96].

The OFC is also unique to emotional content in the current meta-analysis. The OFC is often associated with decision-making and predicting rewards (for review, see [97]), and in the left hemisphere, this may include emotional decision-making, specifically ‘counterfactual emotions’, e.g. regret following emotional decisions [98]. A recent meta-analysis of emotion semantics found left OFC activation for verbal emotion stimuli compared with nonverbal emotion [99]. Although the literature included in the current analysis does reveal some peaks in the left OFC [93,100], only the right OFC emerges as significant for emotion semantics. This area emerges in the few studies that specifically test emotional valence and/or attempt to decorrelate or control for the effects of emotional arousal [101–103]. The right OFC plays a role in social cognition; patients with social anxiety disorder have impaired functional connectivity between the right OFC and amygdala, suggesting that both areas are important for successful emotional and social processing [104]. Even in healthy adults, grey matter volume in the bilateral OFC correlates negatively with symptoms of emotional dysregulation, supporting the theory that both hemispheres of the OFC are important to emotional processing [105]. OFC specifically has a role in computation of valence. Rapid electrophysiological responses (100–150 ms) to discrimination of valence of a visual stimulus are observed in OFC [106]. An fMRI study [107] used representational similarity analysis to show that both positive and negative valence stimuli, across sensory modality, showed distinct patterns in bilateral OFC. Furthermore, subjective valence ratings could be classified based on activation similarity patterns in OFC and generalized across subjects.

The region of ACC activated by emotion concepts, pregenual ACC, is considered to be part of the emotion processing network for both linguistic and non-linguistic stimuli [108–110], and is specifically associated with valence [111]. It is connected to amygdala [112] and to autonomic nuclei associated with visceromotor control in monkeys [113]. More recently, the role of ACC in emotion processing is thought to involve modulating the activity of amygdala [109,114].

In contrast to the emotion-specific activation patterns in the amygdala, OFC and anterior insula, a wide region of medial frontal areas, as well as the pCi and precuneus, were commonly activated across abstract semantic domains. Apart from general semantics, these regions are also associated with emotion processing from multivariate classification studies [115]. For example, using movies and mental imagery, Saarimaki *et al*. [116] found distinct signatures of six basic emotions in dmPFC, ventromedial prefrontal cortex (vmPFC), ACC and precuneus/pCi, in addition to amygdala and OFC, in a multivoxel analysis. Classification generalized between movies and imagery methods. We suggest that the medial frontal regions and precuneus/pCi are unlikely to be specialized for emotion processing, although they may be upregulated by emotional content. Domains with extensive activation in these regions (emotion, ToM and moral judgements) take place during social interactions or elicit memories of interactions in the form of episodes or events. The fact that emotional movies and mental imagery activate these regions, and the activity generalizes across the modalities, supports this view. A meta-analysis comparing social cognition, emotional processing and introspection found overlapping areas between emotional and social cognition that included the orbitofrontal and medial frontal cortex [117]. The ROI analysis also revealed some activation for the left AG during emotion processing, which overlaps with the larger temporo-parietal junction (TPJ) clusters for morality and ToM, and is discussed later.

The left ATL also emerged in the ROI analysis. Among its many associated functions, such as general semantics, sentence processing, short-term memory, social cognition and processing unique entities, the ATL has previously been implicated in emotional arousal [118,119] and valence [90,120] as well as social processing such as detection of familiar faces [121]. Research on non-human primate lesions suggests that the ATL's role in social processing may, at least in part, rely on its role in emotional processing [122,123]. There is also evidence that the ATL is involved in emotional processing even when controlling for the presence of social cognition [124,125]. The connectivity of the temporal pole is similar to that of amygdala, and damage to the pole causes Klüver–Bucy syndrome. Some symptoms of this syndrome include social withdrawal, blunted affect, tameness or diminished fear, which are produced by lesions to either temporal pole, OFC or amygdala [122,126].

In summary, emotion semantics consistently activated regions of the network implicated in the experience and processing of emotions. 'Core' regions of this network, amygdala and OFC, were activated uniquely for emotion words (with respect to the domains evaluated here). Other regions, such as the ACC, ATL, AG, precuneus/pCi and medial PFC (mPFC), overlapped with other domains and may be involved in episodic memory, social cognition and general semantics (see General discussion, §7). These results are consistent with Barrett's theory of constructed emotion [127,128]. Briefly, this view suggests that the brain runs an internal model based on past experiences to perform allostasis, which refers to the regulation of the body's internal environment by anticipating physiological needs. Interoception is the representation and utilization of these internal sensations. Past experiences are implemented as concepts, which are embodied representations that predict what is about to happen in the sensory environment. When the internal model creates an emotion concept, a situated conceptualization (or categorization) results in an instance of emotion. The activation of visceromotor regions involved in interoception (amygdala, anterior insula, OFC, ACC and mPFC) and those associated with representation of events and situations (AG, precuneus/pCi and ATL) is broadly consistent with this view (see also [129], where evidence for situated conceptualizations for emotions was found in a neuroimaging study using a task context where situations were described explicitly).

4. Morality

Morality has been defined as a set of guiding principles that includes standards of right and wrong conduct, or rules that guide us in our everyday choices and actions [130]. Moral judgements involve decisions about what we would do when faced with a moral dilemma, or evaluations of the decisions and actions of others in situations that involve moral principles like harm, justice and fairness. Deciding what to do when faced with a moral dilemma or deciding whether an action is right or wrong might involve slightly different processes [131], with the former relying on additional self-referential processes [132]. Theoretical accounts have argued for a role of abstract-inferential, self-referential and emotional processes in moral judgements. For example, studies suggest that moral cognition is influenced by the perceived intentionality of agents' actions [133–135]. To judge whether an agent's action is intentional requires the ability to infer other's desires, thoughts and behavioural dispositions [136,137] often captured by the term ToM. Support for the idea that abstract-inferential processes play a role in moral cognition comes from neuroimaging studies, showing that moral evaluations and decisions share common neural resources with brain areas engaged in ToM, including medial frontal and temporo-parietal brain regions [138]. Evidence for a role of emotional processes in making moral judgements comes from studies showing that experiencing empathy promotes moral behaviour towards other people [139], and morally inappropriate behaviour can be attributed to a deficiency in empathic skills [140,141]. In line with this proposal, neuroimaging and lesion studies have provided evidence that moral decision-making relies on the vmPFC [142,143]. It has been argued that the vmPFC plays a role in emotion regulation and that its involvement in studies on morality therefore reflects a role of emotional processes in making moral judgements [144]. To investigate neural regions underpinning moral cognition mediated verbally, and to examine their relationship to other abstract domains, we conducted an ALE meta-analysis using neuroimaging studies on moral decision-making.

Table 3. Clusters for the morality meta-analysis.

clust.	hem.	brain area	BA	x	y	z	ALE	vol. (mm^3)
1	L	dorsomedial prefrontal cortex	9	−2	50	26	0.024	6536
	R			2	46	30	0.024	
				−4	42	28	0.022	
2	L	temporo-parietal junction	22	−46	−58	16	0.034	5800
				−58	−50	16	0.016	
		middle occipital gyrus	19	−48	−68	6	0.016	
		inferior parietal lobule	39	−46	−66	28	0.013	
				−34	−58	22	0.010	
3	L	precuneus	7	−4	−54	28	0.024	4552
				−2	−60	34	0.021	
				0	−46	26	0.016	
4	R	ventromedial prefrontal cortex	10	4	52	2	0.020	2432
	L			−10	48	0	0.013	
5	R	temporo-parietal junction	39	48	−58	20	0.022	2168
		superior temporal sulcus		44	−60	8	0.017	

(a) Methods

Studies included for the morality domain were selected on the basis of a meta-analysis by Garrigan *et al*. [132]. From the 28 studies included in this meta-analysis, we selected studies that investigated morality by means of written sentences, statements and scenarios (excluding studies that used animated stimuli, pictures or vignettes). After screening, 20 separate experiments remained for inclusion, with a total of 182 foci from 395 participants (figure 1; electronic supplementary material, table S3).

(b) Results

Five significant clusters of activation, with a total of 15 peaks, were found across the morality studies. Activations fell in the bilateral dmPFC, vmPFC, AG, supramarginal gyrus (SMG) (or TPJ[3]; [145]), left MOG and precuneus/pCi (table 3 and figure 2).

(c) Discussion

The TPJ is activated by abstract-inferential processes that have been proposed to underlie ToM abilities like inferring other's desires, thoughts and beliefs [138,146–149]. Most theoretical accounts have argued for a role of both the left and right TPJ in ToM. However, contributions to ToM abilities seem to differ between hemispheres [150]. A study by Saxe & Wexler [150] showed that the right TPJ showed a response that was restricted to the attribution of mental states, while the left TPJ showed a response to the social background information of a protagonist that was not significantly different from the response during mental state attribution. Based on these findings, the authors suggested that the left TPJ is involved more broadly in the coding of socially relevant information of a protagonist, whereas the right TPJ is selectively involved in the attribution of mental states. Deciding what to do when faced with a moral dilemma or deciding whether someone's actions can be considered right or wrong requires a general coding of socially relevant information of a protagonist and more specifically the attribution of intentions to others' behaviour. Furthermore, the overlap in activation between morality and ToM tasks suggests that these abilities rely on similar abstract-inferential computational processes, which may involve general semantic knowledge and, more specifically, events and episodic information. TPJ/AG is also commonly found in studies of semantics involving individual concrete or abstract words, and is more strongly activated for concrete words [15], and likely has a more general role. The General discussion further addresses this point.

One region that was uniquely seen for the morality domain was the ventral-most aspect of TPJ bilaterally, extending into the occipito-temporal cortex. This region is similar to the ventral subdivision of AG identified by Seghier *et al*. [151]. It responds more strongly to picture semantics than to written words, and likely has a role in visual semantics, which is also the function associated with the lateral occipito-temporal cortex. Thus, its role is unlikely to be specific to morality and possibly reflects vivid visual imagery evoked by scenarios used in morality tasks.

Medial frontal areas, dmPFC and vmPFC, are commonly seen in social cognition, abstract-inferential processing and emotion regulation [109,152–156]. It has been suggested that the vmPFC tracks the value of rewards and valence of emotional stimuli [155,157,158], regulates emotions [144,155] and plays a role in mesolimbic reward systems [159,160]. Furthermore, it has been shown that lesions of the vmPFC are associated with deficits in empathic processing and ToM abilities [161]. Studies on moral cognition typically involve situations and moral dilemmas that involve principles like harm, justice and fairness. We suggest that the common activation of the vmPFC across studies on moral decision-making reflects a role of emotional processes in making moral judgements. The dmPFC plays a role in the processing of complex social judgements on visual face stimuli [162], abstract-inferential processes involved in ToM [154,163] and the generation and regulation of emotion [156]. In line with the idea that the dmPFC plays a role in emotion regulation, the dmPFC shows strong functional connectivity with subcortical regions involved in emotion processing [156], and the region homologous to the dmPFC in the macaque monkey has strong neuroanatomical projections to core limbic structures [164,165]. Advanced cognitive abilities such as social cognition also involve dmPFC [152,153]. Recent studies have provided evidence that the dmPFC is hierarchically higher and especially important for highly demanding and uniquely human social cognitive tasks [166,167]. Consistent activation of the dmPFC in studies on moral cognition, and its overlap with emotion, therefore likely reflects the demanding abstract-inferential processes involved in moral judgements, as well as a role of emotional processes in moral decision-making.

Like TPJ, the precuneus/pCi is frequently activated in studies of general semantics, emotions and higher-order processes such as morality. Some authors have interpreted it as being responsible for visual awareness, self-awareness and self-referential processing, or consciousness [168–170]. We suggest that its role is likely more general, and this is further addressed in the General discussion.

In summary, the present meta-analysis shows that moral decision-making based only on verbal stimuli involves a network of areas including medial frontal and temporo-parietal brain regions, and overlaps greatly with areas associated with general semantics, social and episodic memories, and emotion regulation. This suggests a process that is based in retrieval of socially relevant entities and events, as well as emotions.

5. Theory of mind

ToM, often referred to as 'mentalizing', is traditionally defined as the process of inferring the beliefs, thoughts or feelings of another person, especially when those beliefs differ from one's own beliefs [136]. In recent years, the term has been used to describe other situations involving the 'self' and 'other', including abstracted social behaviour (e.g. shapes performing social-like behaviours), trait judgements and strategic social games, among other tasks [171]. It is further complicated by the fact that ToM relies on thinking about another person, making it difficult to experimentally isolate from social cognition. Here, we focus on the original definition of ToM, inferring the beliefs of others, and specifically focus on the use of verbal stimuli, e.g. inferring one's beliefs from a written story about his/her circumstances and behaviours. This is often studied by contrasting responses to 'false belief' stories, in which a protagonist acts according to information that the reader knows to be false, against 'photo' descriptions, in which an outdated photograph is described with some information that the reader knows is no longer true [172]. Both conditions involve verbal descriptions of some false information, but only the false belief stories involve imagining the beliefs of another person.

As in other domains of abstract semantics, ToM tasks often rely on social cognition and/or emotion perception. There is debate as to how these domains are related. It is generally agreed that emotion perception is an affective process while ToM is a cognitive one; yet, ToM is often required to infer the emotional state of another person, and both processes could reasonably fall under the umbrella of social cognition [173]. Mitchell & Phillips describe several cognitive models comparing ToM and emotion processing. They may be separate mechanisms that differ in how much arousal is required (ToM is 'cold', emotions are 'hot'; [174]); they may be connected processes which are accessed serially, such that emotional processing precedes ToM [175], or they may have a superset–subset relationship, in which ToM is a complex process that includes emotion [176,177]. In all of these models, it is acknowledged that ToM is a more complex, high-level process than emotion processing.

(a) Methods

Only studies that investigated ToM by means of verbal stimuli were included for the ALE meta-analysis. We included foci from experiments that contrasted sentences or vignettes describing the mental states of others (typically beliefs) with a sentence or story about the protagonist's physical circumstances or a non-ToM scene; or that contrasted tasks which require inference about another's beliefs with tasks that require non-ToM comprehension. Twenty-eight separate contrasts were included (electronic supplementary material, table S3), with a total of 250 foci from 554 participants (figure 1).

(b) Results

Seven significant clusters of activation, with a total of 15 peaks, were found across the ToM studies. Activations fell in the bilateral medial frontal cortex (dmPFC and vmPFC), TPJ, middle superior temporal sulcus (STS), precuneus/pCi, left SFG, ACC, ATL and the right middle frontal gyrus (MFG) (table 4 and figure 2).

(c) Discussion

The areas seen in the domain of ToM have a great deal of overlap with the areas in the moral reasoning meta-analysis, with the addition of the ATL mid-STS. In a meta-analysis, Schurz *et al*. [178] showed that the TPJ and medial frontal cortex are the most task-indifferent regions that are involved in ToM, and they are also the most consistent areas to emerge during verbal narrative tasks. The STS has also been implicated in the 'ToM network', although this area is somewhat less consistent and may rely specifically on social animations [147] or inferring desires, rather than beliefs, of another person [179]. It also emerged in a semantic meta-analysis [15], where most studies did not involve inference about others' beliefs or desires. The description of these areas as a 'network' may not be entirely accurate, however; these areas play important roles in the cognitive processes involved in ToM, but their specific functions are likely distinct between regions.

The TPJ, overlapping with both morality and emotion domains, is consistently activated while imagining another's thoughts [146], emotional state [180] or beliefs [147]. The TPJ is also activated across a wide variety of ToM-related modalities and tasks, e.g. during entirely visual tasks that require taking the perspective of another [181] and the interpretation of jokes that require inference about others' beliefs [148,182]. The TPJ is also involved in making moral judgements of others based on their intentions [138,183], even in children [184], consistent with the TPJ's involvement in the morality analysis above. Like in studies of morality, there is some disagreement over whether there are separate lateralized roles for the right and left TPJ in ToM processing. For example,

Table 4. Clusters for the ToM meta-analysis.

clust.	hem.	brain area	BA	x	y	z	ALE	vol. (mm^3)
1		ventromedial prefrontal cortex	10	0	48	2	0.030	9304
	R	dorsomedial prefrontal cortex	9	2	50	34	0.030	
	L			−4	50	16	0.023	
	R	middle frontal gyrus	10	2	44	−8	0.017	
	L	superior frontal gyrus	9	−20	50	36	0.016	
		anterior cingulate	32	−2	36	10	0.013	
2	L	temporo-parietal junction	39	−50	−58	20	0.056	6112
3	L	precuneus	7	−2	−56	32	0.036	5944
				0	−58	24	0.025	
4	R	temporo-parietal junction	39	48	−54	24	0.048	5264
5	R	superior temporal sulcus	22	50	−18	−8	0.026	2928
6	L			−54	−24	−6	0.023	1760
7	L	anterior temporal lobe	21	−50	0	−22	0.017	1504
				−56	−6	−12	0.015	
				−42	2	−30	0.011	

the left TPJ is activated by false belief stories and also by 'false sign' stories that involve a protagonist being misled, but do not explicitly require consideration of the protagonist's beliefs [185,186]. The right TPJ, on the other hand, may be involved in detecting an incongruity between the protagonist's behaviour and his/her environment [185,186], or it may be a more domain-general monitor of working memory and attentional demands [187,188]. In either case, it is clear that both left and right TPJ play a role in both ToM and morality domains [189–191]. Its likely functions are more general, which are considered in the General discussion.

The medial frontal cortex is a very consistent area of activation during ToM studies [192,193] using both verbal and nonverbal tasks [194], but also like the TPJ, its role in cognition may not be specific to ToM, because it has also been implicated in other forms of social and emotional processing [122,192]. As discussed above, there are also differences between the specific roles of dmPFC and vmPFC [109,195,196] as well as medial and lateral subregions [179]. In the current analysis, the verbal ToM studies included peaks in all relevant subregions of the medial frontal cortex.

The ACC, in addition to ToM tasks, also emerges during tasks that require introspecting about one's own beliefs or judgements [176,197]. It is also involved in similar higher-order social and especially affective tasks, such as understanding jokes [148] and processing abstract or affective words [108,180], and was seen in our emotion meta-analysis, suggested to play a role in modulating activity in amygdala.

Finally, the ATL emerged during ToM processing, in conjunction with emotional processing in the left hemisphere. This is unsurprising, given that the ATL is involved in detecting the emotional states of others [198,199] or making moral judgements about others [200], which require ToM. This likely reflects the ATL's role in emotional and social processing, as discussed earlier.

Thus, the neural areas involved in ToM overlap substantially with those of other domains, in particular morality and emotional processing. Morality and ToM tasks often entail similar cognitive abilities, namely considering the mental and emotional states of others.

6. Domain-general abstract processing

Finally, an ALE meta-analysis was performed collapsing across peaks from all four domains. Six clusters of activation, with a total of 16 peaks, were found across all domains (104 experiments, 1884 participants and 763 foci). Activations fell in the bilateral TPJ, dmPFC, vmPFC, left MFG, SFG, precuneus/pCi, ATL and the right ACC (table 5 and figure 3, pink/purple).

These regions overlap with the semantic system identified in Binder *et al.* [15], which reflected predominantly concrete semantics.[4] To perform a direct comparison with the results of Binder *et al.*, and to better identify concrete semantics, we used peaks from that study after eliminating contrasts and tasks that targeted abstract or metaphoric content (e.g. affective judgement). This resulted in 981 peaks (of the original 1145). An ALE analysis using these peaks (using the same threshold used for other domains here) is depicted in figure 3 (blue/purple).

Considering the abstract map, the contrast between figures 1 and 3 (and the circumscribed left ATL/IFG activation in [14]) is striking: the former shows activations that are widely distributed and involves most regions other than primary sensory and ventral temporal regions, while figure 3 shows a relatively circumscribed set of regions. In one sense, the meta-analysis in figure 3 does not contain false negatives by definition, in that it is meant to detect consistent activation controlling for the total number of peaks. But in another sense, such an analysis can create false negatives if heterogeneous tasks and domains are included. A significant proportion of the cortex involved in abstract concept processing does not show up on the map, not necessarily because the peaks from individual studies are false positives or are unreliable, but because they reflect different underlying processes. Even within a single domain, such as emotions, the distribution of peaks is much more extensive than what is obtained in the emotion map in figure 2. In this sense,

Table 5. Areas activated in the meta-analysis across all domains.

clust.	hem.	brain area	BA	x	y	z	ALE	vol. (mm³)
1	R	dorsomedial prefrontal cortex	9	0	48	32	0.054	19 376
				0	50	26	0.051	
		ventromedial prefrontal cortex		0	48	2	0.045	
	L	middle frontal gyrus		−8	40	−6	0.025	
	R	anterior cingulate		4	34	14	0.020	
	L	superior frontal gyrus		−14	32	44	0.020	
2	L	temporo-parietal junction		−50	−58	18	0.088	8680
3	L	precuneus		−4	−56	24	0.065	8536
4	R	temporo-parietal junction	39	48	−56	24	0.071	5368
5	L	anterior temporal lobe		−50	4	−20	0.031	2736
				−42	10	−28	0.023	
				−44	2	−28	0.022	
6	L	inferior parietal lobule	40	−42	−44	38	0.022	2192
				−48	−40	48		
				−50	−40	44		
				−52	−44	32		

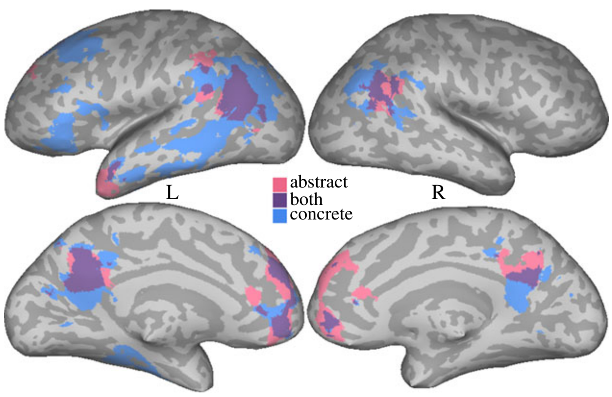

Figure 3. Results of the meta-analysis collapsing across all four abstract domains are shown in pink/purple. Activation from a meta-analysis of peaks from Binder *et al.* [15], after removing abstract peaks, is depicted in blue/purple, with purple showing the overlap between the two.

the conclusion that abstract processing relies on only a small set of regions is misleading. This highlights the importance of the specific stimuli chosen for an experiment, the task and the control conditions, which can lead to variability within and across domains. Any negative conclusions based on a meta-analysis (the lack of involvement of a region in a domain) should be treated with caution if there is a chance that the stimuli, tasks or controls reflect heterogeneous processes.

Regions overlapping between domain-general abstract processing and concrete concepts were bilateral TPJ, precuneus/pCi, dmPFC and vmPFC, with a left > right pattern, and are discussed below.

7. General discussion and conclusion

We examined the representation of concepts related to numerical, emotional, moral and ToM processing. Basic number concepts showed a signature in bilateral IPS that extended into SPL. This supports the idea of spatial and body/finger-based representation of numbers. Verbally mediated emotion concepts activated areas associated with emotion processing and regulation, including the left amygdala and the right OFC, supporting grounding of emotion concepts in emotional experience. Higher-order, inferential processes of morality and ToM show partial overlap with areas associated with emotion processing in medial PFC and ATL, and also show activation in general concrete semantic areas, namely AG, precuneus/pCi and ATL. Apart from partial grounding in emotions, this suggests access to episodic/semantic content, as opposed to a process that is fundamentally different from other types of semantics.

The meta-analysis across the four abstract conceptual domains revealed a map (figure 3) that shows significant overlap with a map based on concrete concepts and includes bilateral AG/TPJ, dmPFC, vmPFC, precuneus/pCi and the left ATL. (Numbers do not significantly contribute to these areas, but the other three domains do.) Using a large set of concepts that varied in their sensory-motor attributes, a recent study [201] identified several 'hub' areas that were commonly activated by all attributes, which included all of the areas seen here, with the notable exception of ATL. ATL has also been suggested to be a semantic hub region [202,203].

We suggest that the reason for the similarity of activation patterns between two seemingly very different types of semantics (concrete concepts versus emotions and abstract-inferential processing) can be explained by the role of social and episodic knowledge and the semantic content of the episodes. For precuneus/pCi, two functional subdivisions have been suggested, where the anterior section is involved in mental imagery, and the posterior region in episodic memory retrieval [170]. In a meta-analysis comparing episodic encoding and retrieval, precuneus/pCi was upregulated for retrieval compared with encoding [204]. A related function of this area is in egocentric versus allocentric spatial processing [205,206]. The overlap map revealed that the retrosplenial cortex was activated for concrete but not for abstract concepts, while a more dorsal section in the right precuneus showed the opposite pattern. While retrosplenial cortex plays multiple roles associated with episodic memory, it is especially important for spatial memory [207,208]. Activation of retrosplenial (along with parahippocampal) cortex for concrete but not for abstract concepts suggests a more direct reliance on spatial content for concrete concepts, while abstract concepts evoke episodic memories that are less spatial in nature.

AG has been proposed to be involved in a wide variety of functions (see [71] for a review). It features prominently in concrete concept processing and has been proposed to integrate sensory-motor features [5,15,201,209,210]. While bilateral AG is seen in concrete > abstract contrasts, it also responds to abstract concepts when compared with a non-semantic control condition [108,211]. Beyond integrating features of static concrete concepts, it is likely to have a special role in integrating information across time, in processing events and relations. The left AG has been associated with understanding stories [119,212], verb argument structures [213] and thematic relations [214,215]. Boylan *et al*. [216] tested the response of AG to several types of two-word combinations, and found that it tracked the presence of an event-denoting verb, supporting the view that AG responds to event structure. Along with precuneus/pCi, AG is also a central node in the default-mode network [217,218] in the resting state, which is rich in episodic, prospective, introspective and semantic content involving objects, relations, plans, emotions, people and events [5,163,219,220]. Recently, Thakral *et al*. [221] found that applying rTMS to the left AG reduced the amount of episodic details produced during simulation and memory tasks based on event words (but not during a free association task), providing evidence for its role in episodic simulation and episodic memory. The set of common regions identified here was also found during sustained episodic simulations [222]. Spunt *et al*. [22] found activation of the same network seen here, consisting of AG, ATL, precuneus/pCi and mPFC, when actions (riding a bike) were processed at high levels of abstraction (*Why ride a bike? To get exercise*) versus low levels of abstraction (*How to ride a bike? Grip handlebars*). The 'why' question brings episodic or situational context into play. Based on a review of such findings, Rugg & King [223] recently proposed that AG represents retrieved episodic information, supported by a more general role in representing multi-modal and multi-domain information. Along the same lines, Ramanan *et al*. [224] proposed that AG is the critical contributor to episodic reconstruction across past, future and atemporal contexts, and actively represents and integrates disparate sensory-perceptual details into a rich multi-modal 'contextual layer'. In summary, processes that are common across these abstract domains appear to be related to event and relation processing, episodic recall, imagery and emotion processing, and are also triggered by concrete concepts.

(a) Representing abstract concepts: a proposal and implications for theories

We suggest that event- or situation-based representations provide one mechanism for understanding and grounding of many types of abstract concepts. Exemplars and prototypes for concrete object categories (*apple*) are objects. Objects with a certain range of feature values (e.g. colours, patterns, shapes, sizes and tastes), or those with a family resemblance to other apples, constitute 'good' or acceptable instances of apples. For some abstract concepts, exemplars and prototypes are events, and family resemblance is computed over event structures. Concepts inhabit a space whose dimensions include event-based or situational information, interoception, introspection, and sensory-motor features that contribute to varying degrees. For example, we hypothesize that event-based representations are critical for conceptual processing related to morality and ToM, as well as for concepts related to social constructs (*justice* and *democracy*), which is supplemented by interoceptive affect. For emotion concepts, interoception plays a central role, supplemented by event representations. Introspection is most salient for concepts related to cognition (*thought* and *consideration*). Number concepts rely on body-part-based and spatial representations, with little contribution from events. There is no categorical distinction between concrete and abstract concepts, but the reliance on event-based, interoceptive, introspective and sensory-motor dimensions differs. Concrete object concepts, in general, rely more strongly on sensory-motor properties, but other dimensions can play a greater role for specific concepts (e.g. interoceptive affect can play a greater role for concrete object concepts with salient emotional features, such as *knife*; event information contributes to *picnic*), or due to task demands. An additional dimension that can contribute to some abstract concepts is metaphoric representation, which is not examined here. Abstract concepts can be understood by analogies to concrete domains [225–227], exemplified by metaphors such as *grasping an idea* or *moving up in the company*. Here, correspondence is established between understanding and physical grasp, and between power/authority and higher spatial location, respectively.

Space does not permit discussion of the behavioural findings here, but we note that consistent with the current proposal, a number of investigators have pointed out the importance of contextual, and especially relational or social, information for at least some types of abstract concepts, and provided behavioural evidence in healthy subjects [18,85,228–230]. Additionally, in the treatment of persons with aphasia, training on abstract concepts (*justice*) leads to generalization to related but untrained concrete concepts (*jury*), but not vice versa [231,232]. This is also consistent with event-based representations of these abstract concepts that activate concrete entities contained therein. The current study builds on this body of work and provides new evidence from neuroimaging that is not limited by behavioural tasks such as property generation, or explicit consideration of a situation.

While we have provided preliminary neuroimaging evidence in support of some of these hypotheses, a very limited set of abstract concepts was examined here, and it is clear that much work remains to be done to devise ways of partitioning abstract concepts, and to delineate the dimensions and their relative contributions to their representation. Nonetheless, these findings provide constraints on theories of concept representation. Both classical theories, Dual Coding and Context Availability, assume two differing mechanisms that apply to the entire categories of abstract and concrete concepts. This trend of a hybrid approach is also seen in recent theories. A single mechanism dedicated to abstract concept processing carries with it an implicit assumption that not being concrete is a good unifying principle. For example, some models combine embodied and distributional information that is used predominantly for concrete and abstract concepts, respectively [233–235]. Similar to the Dual Coding theory, Dove [236,237] proposed a view where abstract concepts rely on amodal symbols, which acquire meaning only from their relationship with other symbols. Accounts that propose a single and amodal mechanism for abstract concept representation are challenged by the current results, for the two reasons outlined above: (i) there are important differences in how different types of abstract concepts are represented; and (ii) the areas that are commonly activated across abstract domains overlap with those for *concrete* concepts, and those implicated in episodic memory, event processing, imagery and emotions. The current results fit most naturally within the framework of situated cognition (e.g. [238–241]) and can be interpreted as being most compatible with situated theories, such as Language and Situated Simulation [241] and the Words as Social Tools (WAT) [230,242] proposals. WAT emphasizes the importance of social information that is accessed through words. Activation of areas involved in event representation, episodic memory, emotions and concrete concepts is consistent with retrieval of social interaction memories that have all of these components. While there was no clear support for the other aspect of the theory which postulates linguistic, mouth-related and phonological basis for all types of abstract concepts, negative results are not necessarily conclusive, as emphasized earlier. The Affective Embodiment view [83,243] proposes that affective experience and emotional development are crucial for abstract concepts, and sensory-motor experience is important for concrete concepts. Emotions provide a bootstrapping mechanism for acquisition of abstract words. Although the 'core' regions associated with emotion processing, amygdala and OFC, were not activated by all abstract domains, the common activation of mPFC and ACC, involved in emotion processing and regulation, can be interpreted as being broadly consistent with this view, at least for the types of abstract concepts examined here.

Finally, it is worth keeping in mind that many, if not most, brain areas are highly multi-functional. Areas such as mPFC, OFC, insula and precuneus/pCi are activated in a staggering variety of studies and have numerous functional interpretations. The interpretations that we argue for are supported by a large body of literature, and not just by one or two isolated studies. Nonetheless, caution should be used deriving functional interpretations from these activations, with consideration given to alternative views and possibilities, especially with regard to complex processes such as introspection and interoception, as our understanding of the functions and connectivity of these regions increases.

(b) Conclusions

We have provided evidence that both differences and similarities exist in the representation of the four types of abstract concepts considered here. We show that the representation of abstract concepts is much more widespread in the brain than is often assumed. Emotional and number concepts can be grounded directly in emotional, spatial or action-related brain circuits. Higher-order abstract processes of morality and ToM can also be processed and grounded through events, episodic memories and simulations, which in turn rely on emotions, imagery and lower-order concepts. The differences suggest that the way in which various types of abstract concepts are represented can differ substantially. While 'abstract' is a useful label to situate oneself in the general area, faster progress can potentially be made if theory development focuses on varieties of abstract concepts and their characteristics, and explores possibly different formats and mechanisms. Promising initial steps in this direction have been taken by a number of investigators (e.g. [82,244–246]). Theory-driven, top-down approaches (e.g. starting by examining categories devised by linguists, available in a thesaurus) and data-driven bottom-up approaches are both promising ways of teasing apart potential categories of abstract concepts from complex high-dimensional neuroimaging or behavioural data. Based on the similarities in activation between the domains, we also propose that events or situations may constitute an important dimension in representing many types of abstract concepts. Categories of abstract concepts may differentially weight event-based, interoceptive, introspective and sensory-motor information.

Data accessibility. This article has no additional data.

Authors' contributions. R.H.D. conceived of the topics discussed in the paper. M.R. ran the meta-analyses, reviewed literature and collected peaks on emotions and ToM domains. W.v.D. reviewed literature and collected peaks on numbers and morality domains. All authors wrote the paper.

Competing interests. We have no competing interests.

Funding. This work was supported by the NIH/NIDCD grant R01 DC010783 to R.H.D.

Endnotes

[1]Here, *interoception* refers to the sensory perception of internal body states. *Introspection* is used to refer to reflection on one's mental processes, such as reasoning, thoughts, beliefs and will.

[2]We thank an anonymous reviewer for pointing out these counting systems.

[3]Here, we use the term 'TPJ' for consistency with the terminology typically adopted in morality and ToM studies. However, it is worth pointing out that this term is used to refer to a variable set of anatomical regions that includes AG, lateral occipital cortex, STS, SMG and pMTG. Often activations that are entirely contained in one of these regions are described as being in the TPJ, which seems unnecessarily vague and creates potential for incorrect reverse inference.

[4]To rule out activations due to executive processing demands, Binder *et al.* [15] eliminated contrasts that had greater difficulty for the condition of interest relative to that of the control condition. Because abstract conditions frequently have greater difficulty/reaction time, many such contrasts were excluded, resulting in an increase in bias towards concrete semantics, which stemmed from the fact that there were many more studies of concrete concepts to begin with.

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