

Review

Dual coding of knowledge in the human brain

Yanchao Bi^{1,2,3,*}

How does the human brain code knowledge about the world? While disciplines such as artificial intelligence represent world knowledge based on human language, neurocognitive models of knowledge have been dominated by sensory embodiment, in which knowledge is derived from sensory/motor experience and supported by high-level sensory/motor and association cortices. The neural correlates of an alternative disembodied symbolic system have previously been difficult to establish. A recent line of studies exploring knowledge about visual properties, such as color, in visually deprived individuals converge to provide positive, compelling evidence for non-sensory, language-derived knowledge representation in dorsal anterior temporal lobe and extended language network, in addition to the sensory-derived representations, leading to a sketch of a dual-coding knowledge neural framework.

(A human to an android): There was a thought experiment they gave us. It's called 'Mary in a Black and White room.' Mary is a scientist, and her special subject is color. She knows everything there is to know about it [...] But she lives in a black and white room. She was born there, raised there [...] One day... Mary walks out and she sees a blue sky. And at that moment she learns something that all her studies couldn't tell her. She learns what it feels to see color. The thought experiment was to show the students the difference between a computer and a human mind. The computer is Mary in the black and white room. The human is when she walks out. – Ex Machina (a Movie, 2014), citing [1].

Knowledge representation: sensorial versus symbolic notions granted by different disciplines

What does it mean, to know? Is knowing supported by symbolic relations versus knowing through **sensory experience** (see [Glossary](#)) the difference between (current) machines and humans, as suggested in the earlier movie dialogue?

The human brain stores vast amounts of knowledge about the world, such as the color of roses, the shape of the earth, the mechanisms of evolution, and the functions of a jury. Various sorts of knowledge guide a broad range of behaviors, from recognizing objects to understanding words, reasoning, and decision making. Understanding how world knowledge is represented is one of the oldest and most-debated questions in any discipline interested in the mind and brain. The discussions in every field, including philosophy, psychology, and cognitive science, center on two broad notions of representing knowledge: symbolic versus embodied (sensory/motor-experience-derived). The **symbolic representation**, granted by Mary in the black and white room in the thought experiment earlier [1], is the prevalent way to represent knowledge in artificial intelligence. Beyond computers, similar notions have also been assumed in various cognitive (e.g., dual coding by both verbal and nonverbal [2,3]) and philosophical theories (e.g., dualism [4]). Despite this popularity in some areas, neurocognitive (biological) models of knowledge implementation are more strongly influenced by the notion of 'sensory **embodiment**', which start with the assumptions that knowledge, at least about the physical world (e.g., the shape of an apple), is

Highlights

Neural systems have been assumed to represent knowledge through the embodiment of sensory experiences. This type of knowledge representation is considered fundamentally different from the artificial intelligence approach, which implements knowledge representation using the 'symbolic' approach.

Recent behavioral and neuroimaging studies of color knowledge (and other visual knowledge) with and without visual experience provide empirical evidence for the neural coding of non-sensory, language-derived knowledge, along with the sensory-derived representation, in different brain systems.

The proposed dual-coding neural framework motivated by these recent empirical findings offers nature's solution to the classical challenges of knowledge representation associated with either only the symbolic tradition in artificial intelligence or only the embodied approach in neuroscience.

¹State Key Laboratory of Cognitive Neuroscience and Learning & IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing, China

²Beijing Key Laboratory of Brain Imaging and Connectomics, Beijing Normal University, Beijing, China

³Chinese Institute for Brain Research, Beijing, China

*Correspondence: ybi@bnu.edu.cn (Y. Bi).



acquired through and grounded in the sensory experiences stored in the higher-order sensory/motor and association cortices [5–12]. In this review, I discuss recent compelling empirical evidence that identifies a **language-derived**, non-sensory form of object **knowledge representation**, in addition to a **sensory-derived knowledge representation**, leading to a dual-coding neural framework of human knowledge representation. To explain the rationales of these recent studies and help readers appreciate their implications for neurocognitive theories of knowledge, I first briefly present the current neurocognitive views of object knowledge representation.

Sensory-derived representations for object knowledge in current neurocognitive models

The ‘sensory embodiment’ notion in neurocognitive models of knowledge stems from a combination of considerations: biological entities acquire information through sensory/motor interaction with the world; the neural mechanisms of these sensory/motor systems have long been identified in the brain; and numerous neuroimaging studies during over two decades have shown that retrieving knowledge activates brain regions in the territory of the corresponding sensory/motor (primary and associative) cortices. For instance, retrieving color knowledge about objects (e.g., the color of roses) induces activation close to human V4, a region critical for color perception [13,14], and processing words whose meanings have strong associations with color tends to modulate activities in this territory [15]. Thus, current neurocognitive theories often assume, to various extents, that object knowledge, at least that can be perceived through sensory modalities, is grounded in and abstracted from sensory/motor experiences/systems and their connections through some set of combinational mechanisms [5–12]. It is axiomatic that humans can learn via **language experience** about things they have not personally experienced sensorily (e.g., someone can learn that ‘roses are red’ by reading/hearing language without seeing red roses), yet, quoting [16] ‘In common with other embodied cognition theories, however, our model maintains that all concepts are ultimately grounded in experience, whether directly or indirectly through language that refers to experience’.

While cognitive research has shown that representations abstracted away from specific sensory experience is a given for human knowledge (e.g., [17]), it has been difficult to isolate, articulate, and identify neural correlates supporting non-sensory-derived knowledge. This is because in a typically developed brain, various sensory experiences can be evoked by even abstract concepts (e.g., justice) or objects one cannot directly sensorily perceive (e.g., quark). In cases of deprivation of input from one sensory modality, such as in congenital blindness, most knowledge about the physical properties can still be gained and represented through other sensory modalities (e.g., the shape of an apple can be obtained through touch without vision). This difficulty in cognitively excluding sensory-derived representations leads to a further mapping difficulty between brain activity and cognition.

A clean test of how non-sensory knowledge is represented would involve testing what happens to information that can only be obtained through a particular modality when that sensory modality is absent. This is exactly why philosophers [1,18] have long been fascinated by color knowledge. Color sensation is exclusively visual, driven by the wavelength of light, and for humans there are no other senses to experience it. Colors to a congenitally blind individual mirror Mary in the black and white room. What, and how, do the brains of individuals without sight represent about colors (and other visual-exclusive knowledge)? Answers to these questions are a special opportunity to isolate non-sensory knowledge in the human brain. In the following sections, I will review recent empirical findings that provided such answers and which converge to provide compelling, positive evidence for the existence of non-sensory representations, even for highly sensory-related knowledge, along with a sensory-derived form of representation.

Glossary

Embodiment: the notion that cognition, including knowledge representations, depends deeply upon features of the physical body of an agent, including specific sensory channels and motor programs with which the agent interacts with the world.

Language-derived knowledge

representation: information representations that are derived from language inputs, where information is coded by complex relations among symbols that are independent from sensory experiences.

Language experience: language experience is to be treated differently to (nonverbal) sensory experience in this context. Although language is, perforce, perceived through sensory channels (e.g., auditory for spoken language, visual for written language and sign language, touch for Braille), it is special in its manner of coding information. Its modality-specific sensory form is unrelated to its information contents (meaning), that is, it is arbitrary [68].

‘Rose’ or “玫瑰” (/meigui/, rose in Chinese), being said loudly or faintly, written in blue font or green, does not affect the associated knowledge. This contrasts with (nonverbal) sensory-derived knowledge representations, where the knowledge is tightly coupled with or analogous to the actual sensory experience (see similar discussions in [69]).

Natural language processing (NLP):

the approach to process and analyze large amounts of natural language data with computers to extract regularities of structure or meaning.

Sensory-derived knowledge

representation: information representation derived from sensory experiences, that is, the content of the information is directly related to aspects of sensory experience (for humans: visual, auditory, haptic, olfactory, or taste). Language is not considered to be part of the sensory system.

Sensory experience:

sensory experience, as mostly used in the current context of information coding, refers to nonverbal seio9.64(a)0(l)n(o)-246.8(ta)28.7(tsu9.64

Knowledge about visual knowledge without vision: behavioral evidence

The first wave of studies empirically testing color knowledge in congenitally blind individuals started almost four decades ago. This first wave showed that congenitally blind people do have various types of knowledge about color and object color properties, as reviewed in [19]. Briefly, early work found that blind children use color adjectives and color names in their speech, know that color refers to perceptual qualities of objects that cannot be felt by touch, learn to name colors of common objects [20–22], group objects by colors in free-recall tasks [23], and recover the Newtonian color circle based on verbal color labels [24,25]. Given this work's relevance to the larger question about knowledge representation, color knowledge in the blind has recently been more rigorously investigated, with detailed benchmark comparisons, as reviewed in detail below.

word contents (meaning), with very few exceptions (e.g., onomatopoeia).

Symbolic representation: ways of representing information by symbols that can be manipulated on the basis of rules (e.g., a grammar for language).

Knowledge about color terms

For detailed comparison with sighted individuals, multiple types of color words (basic and descriptive color terms) have been tested using a similarity rating task with paired color terms and multiple blind (congenital and noncongenital) and control conditions [26]. The color space of the blind individuals is overall strikingly similar to that of the sighted individuals (Figure 1A), with some of the congenitally blind subjects indistinguishable from the sighted, and there was greater individual variation in the blind group. The high degree of correlation ($r = 0.93$) between the color term spaces of blind and sighted individuals has been replicated, however, this relationship was lower than results for action words ($r = 0.99$) [27]. Compared with the intriguing cross-modal associations that have been reported in sighted individuals (red is heavier than yellow), blind individuals as a group also have color-weight associations, but not as strongly as object-taste associations (boulder-sour, with association strength in the sighted individuals as benchmarks), suggesting that both sensory and language experience contributes to such cross-modal associations [28].

Knowledge about object color properties

Another line of research has tested what blind individuals know about object colors. Blind and sighted individuals' knowledge about colors of common fruits and vegetables was probed using multiple behavioral tasks [29]. The results again yielded a high degree of similarity between blind and sighted (Figure 1B) and a greater degree of individual variation in blind relative to sighted individuals. Furthermore, the correlation strengths between knowledge about color and other typical (nonvisual) sensory properties for fruits and vegetables (including shape, touch, taste), as well as general semantic relations (both continuously rated and categorically measured), were indistinguishable between the blind and sighted groups, indicating that the blind was not differently relying on associations with other sensory properties to derive color relations.

Knowledge about other visual-specific properties

Beyond color, investigation has been carried out on other visual-specific properties [30,31]. For vision and light verbs (e.g., peek versus feel/perceive; shimmer versus boom/roll), a group of congenitally blind individuals showed an indistinguishable knowledge space from sighted controls (by means of word similarity judgment). Multidimensional scaling analyses showed that blind individuals distinguish, like sighted individuals, verbs of light emission from verbs of sound emission (Figure 1C). This work suggests that not only color, but also other visually based concepts, can be acquired without typical visual input in congenital blindness.

Summary

Over a dozen behavioral studies spanning over four decades, across multiple paradigms (generation, sorting, rating, cross-modal association) and languages (English, Italian, Mandarin Chinese) paint a highly consistent picture of color and other visual knowledge in people with

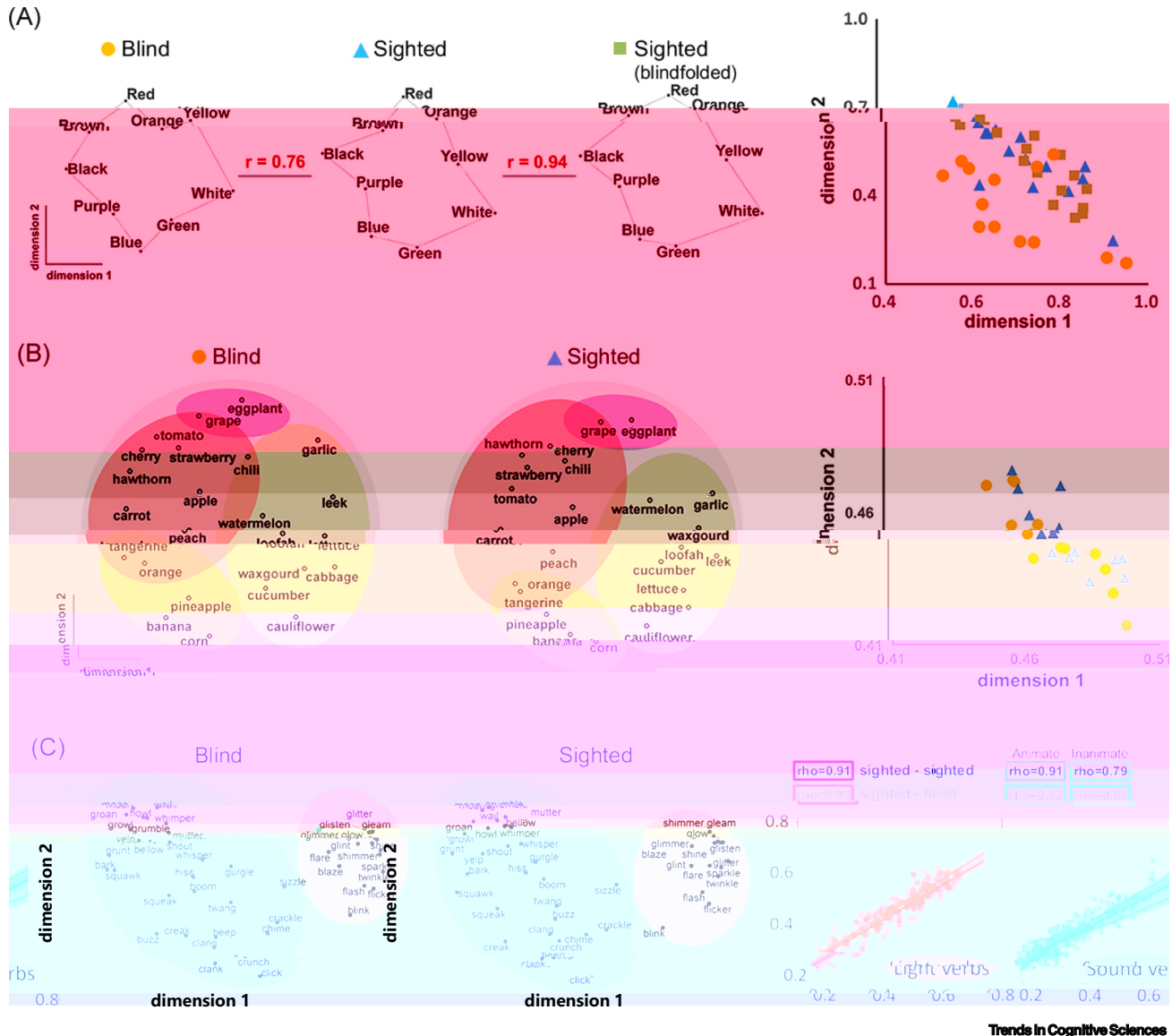


Figure 1. Behavioral profiles of visual knowledge with and without vision. (A) Color term spaces yielded from multidimensional scaling (MDS) on individual dissimilarity matrices from congenitally blind, sighted, and an independent group of blindfolded sighted control. Pearson correlations between group average matrices were shown in red characters (all $P < 0.001$). Each individual's weight along dimensions 1 and 2 for the color term spaces were displayed in the right plot. Reproduced from [26]. (B) Object color spaces obtained through MDS on individual object color similarity matrices from the congenitally/early blind and sighted groups and one subject space in which the coordinates of each point correspond to each blind (yellow disks) or sighted (blue triangles) individual subject's weights along dimensions 1 and 2 of the object color spaces. Reproduced from [29]. (C) Congenitally blind and sighted group MDS results for emission verbs were shown in left panel. Correlations of blind (light colors) and sighted (dark colors) groups to the sighted reference group for light emission verbs and sound emission verbs, computed on group's average normalized similarity ratings, were shown in the right panel. Animate agentive and nonagentive (inanimate object) sound verbs are shown separately in different shades of blue. Reproduced from [30].

complete visual deprivation. (i) Without actually sensorially experiencing color, humans can still acquire knowledge about color relational structures, in patterns that are highly similar to those of the sighted; (ii) at the group level, the similarity with sighted color knowledge tends to be lower than non-visual-specific properties (see also [32]); (iii) there is greater individual variation within the blind population relative to the sighted, with cases spanning from fully indistinguishable

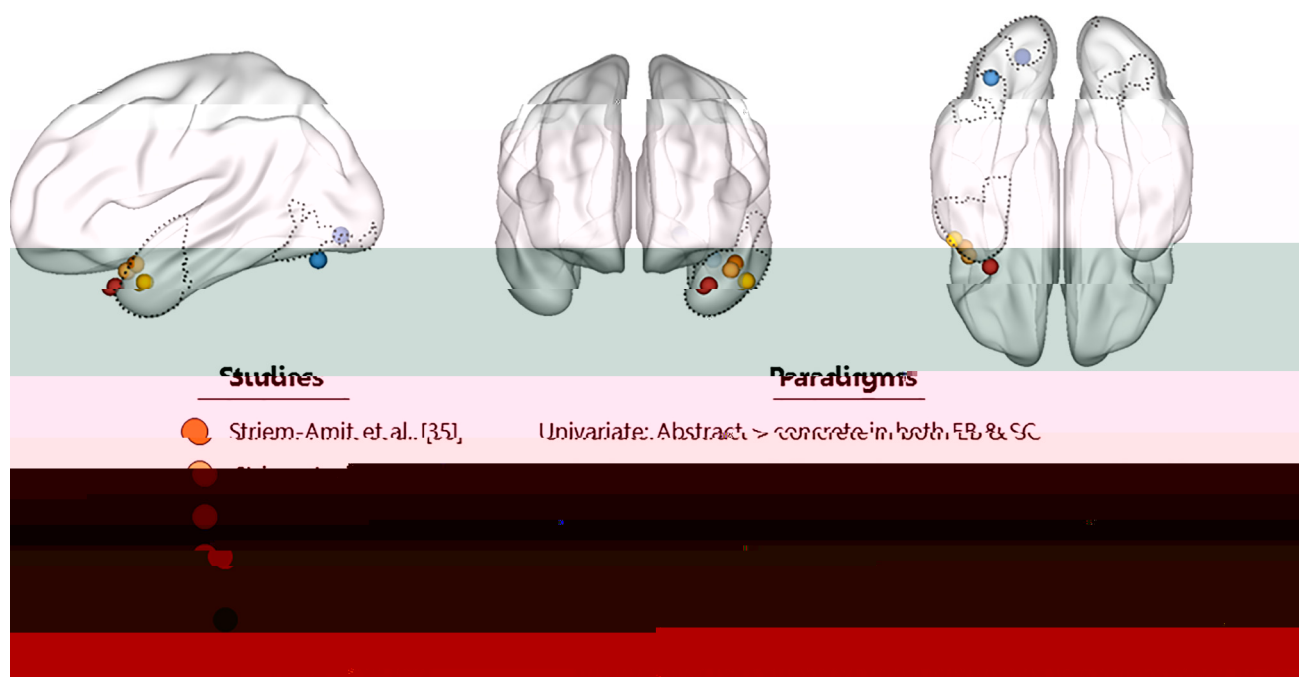
from the sighted to quite different, suggesting that additional sensory experience may reduce idiosyncrasy (see also [33]). The critical point these results make is that humans can form knowledge space about a particular sensory property in the complete absence of that sensory experience, in ways perfectly supporting behavioral probing through questions and answers via language, like in a Turing test scenario [34].

Knowledge about visual knowledge without vision: the brain basis

What is the brain basis of visual-concept knowledge acquired without vision? Recent fMRI studies of neural activity patterns in congenitally blind and sighted groups have provided important clues, as described below (Figure 2).

Knowledge about color terms and other visual concepts

Neural responses in sighted and congenitally blind individuals have been examined to words depicting visually dominant phenomena, including colors (e.g., 'red', 'rainbow', 'island'), words without specific sensory features (abstract concepts, e.g., 'freedom'), and words for non-visual sensorily accessible concepts (e.g., 'square', 'rain', 'cup') [35]. A cluster in dorsal anterior temporal lobe territory (ATL), including anterior superior temporal gyrus/sulcus (STG/STS) and temporal pole (TP), showed a significant word type by group interaction, with stronger activity to 'rainbow' (or 'red') compared with 'rain' (or 'square') in the blind group ('rainbow'/'red' is not sensorily accessible but 'rain'/'square' is), but no difference in the sighted group (all sensorily



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Figure 2. The brain basis for visual knowledge with and without vision. The peaks showing sensitivity to visual knowledge in congenitally blind and sighted groups in anterior temporal lobe (ATL) and color perception cortex across studies and paradigms, including univariate analyses, adaptation, and representation similarity analyses, are projected onto the same brain for visualization. The anterior dashed line was drawn based on the Harvard-Oxford atlas of ATL and included the temporal pole (8#), the anterior superior temporal gyrus (9#), the anterior middle temporal gyrus (11#), the anterior inferior temporal gyrus (14#), the anterior temporal fusiform cortex (37#), and the anterior parahippocampal gyrus (34#). The posterior dashed lines were drawn based on the neurosynth results in the ventral visual cortex using 'color' as a keyword: association test thresholded at a false discovery rate of 0.01. Reproduced from [27,29,35]. Abbreviations: EB, early blind; RSA, representational similarity analysis; SC, sighted control.

accessible; Figure 2 [35]). In another neuroimaging study using an adaptation paradigm, perceptual similarity judgments about paired color names produced repetition suppression effects in V4 for sighted individuals and STG (along with precentral cortex) for the blind group, with a peak in the anterior portion of STG [27] (Figure 2). These two studies convergently identified dorsal ATL to be sensitive to non-sensory-derived knowledge.

Knowledge about object color properties

The brain basis of object color knowledge [29] has been uncovered using representational similarity analysis (RSA) [36]. Participants listened to names of fruits and vegetables and retrieved their typical colors. The association between the neural representation similarity matrix (correlation pattern across items) and the object color behavioral judgments was computed and significant correlations were taken as evidence for neural representation of object color knowledge. Two types of regions were obtained (Figure 2): (i) in the sighted brain, but not the blind brain, a region in the posterior fusiform within the color-perception-sensitive territory (close to V4) yielded neural activity pattern associated with object color similarity; (ii) a region in the left dorsal ATL (anterior STG and TP), not sensitive to color perception in the sighted, supported object-color knowledge in both the blind and sighted groups, even after the effects of other sensory properties were controlled for. In the sighted, but not in the blind group, these two sets of brain regions are intrinsically, functionally connected [29]. Note that the study also reported that under a more lenient threshold, object-color representation in the ventral/medial ATL was observed in the sighted and not in the blind, showing convergence with the findings that these regions are related to sensory-derived color processing (e.g., [9,35]).

Summary

Although only a handful of studies have addressed this question, the neural representations for visual knowledge with and without vision appear to be clear. These studies across multiple paradigms (univariate activity contrasts, adaptation, RSA) and languages (Italian, Mandarin Chinese) converge to provide positive evidence for neural coding of non-sensory knowledge representation (for at least color and other visual concepts) in dorsal ATL in the human brain, while also confirming the sensory-derived representation in the visual cortex in the sighted. Importantly, RSA revealed that such coding of color knowledge in dorsal ATL occurs not only in the blind but also the sighted brain, indicating that even when sensory-derived properties are available there are both sensory-derived and non-sensory representations.

Broader types of imperceptible knowledge in dorsal ATL: abstract words

Are these findings reviewed earlier specific to color and the other specific visual concepts tested, or do they reflect a general mechanism of non-sensory knowledge coding in dorsal ATL? There

by the hypothesis that this region (and potentially its extended network) is sensitive to non-sensory, language-derived knowledge representations that are not specific to visual knowledge. Intriguingly, if the language-derived knowledge for both perceptible and abstract properties is represented in the dorsal ATL, why is there stronger activity for abstract properties? This pattern might be because abstract knowledge is more richly derived from language and/or because perceptible knowledge has a network with additional sensory-derived representations across the distributed brain regions and thus the activation strength may be diluted across the network.

A dual-coding knowledge neural representation framework

The empirical review earlier, primarily focusing on visual knowledge in the blind and jointly considering studies of other types of broad semantic knowledge, allows us to sketch a dual-coding knowledge neural representation framework (Figure 3, Key figure). The well-established sensory-derived (embodied) representation is again confirmed, for color stored close to V4 and for other types of properties more broadly in higher-order sensorimotor and related association cortices based on the previous literature. Another form of knowledge supports the similar color

Key figure

A cognitive neuroanatomical model of knowledge representation



cases. The neural distinction was only made possible based on the manipulation of subjects' sensory experience (or lack thereof) and the dissociation of the brain regions. Upon observing such dissociations, however, we are allowed to further hypothesize potential differences, in addition to the commonalities, regarding the information structure in these two systems.

On the one hand, language depicts only part of the sensory spectrum, differing across different sensory modalities and different languages. It has recently been shown that different languages have different verbal codability for various senses (color, shape, sound, taste, touch, and smell), with colors tending to be most strongly coded and smell to be least, despite humans having rich olfactory perception ([50], see discussions in [51]), highlighting the differences in information coding in the language- and sensory-derived systems (see also [32], but see [52]). A person or a computer deriving knowledge solely from language may then learn different types of sensory-derived knowledge not equally well.

On the other hand, language also offers mechanisms to construct meaning beyond those derived directly through sensory-motor experience. Because it is a rule-governed, symbolic system, free from sensory/motor constraints, language allows manipulation of existing symbol relations and

Box 2. Dual neural coding of number knowledge

The existence of embodied and disembodied forms of object knowledge representation has a parallel framework in the number system. Here, we outline these findings and consider the universality of such a symbolic structure in human cognition.

The number system: sensory-derived versus non-sensory symbolic representations

While it has been argued that number representation extrapolates from an analogous magnitude system derived from various sensory inputs (for a wider review of an embodied approach of number processing, see [85]), recent evidence suggests the existence of a different, symbolic system for integer numbers. This latter system is based on language, involving the acquisition of small exact number word meanings first and discovering the logic of verbal counting, without implication of representations of approximate numerical magnitudes (see review in [86]). In addition to the developmental and adult behavioral studies, the neural evidence was that the intraparietal sulcus represents both symbolic (words, digits) and non-symbolic (visual sets) number in the brain, without evidence of shared representation across these two formats [87].

Comparing language-derived knowledge about objects and about numbers

Is there a shared, domain-general symbolic system underlying object (and other semantic) knowledge and number knowledge? The answer is not straightforward. Ample studies comparing number versus more general semantic processing have shown different brain activity patterns: general semantics (comprehension object knowledge) activates distributed networks entailing ventral and lateral temporal, temporoparietal junction, and ventral frontal regions (mainly in the left hemisphere), and numbers bilateral prefrontal, intraparietal, and ventrolateral temporal regions [88]. The latter set of brain regions are engaged when mathematicians process mathematical statements [89]. However, in these previous studies, sensory- and language-derived knowledge representations (in either the general semantic or the number processes) were usually not distinguished. Thus, the observed differences might be attributable to expected differences in the sensory-derived systems, given how number derives from the magnitudes of sensory inputs and object semantics from other sensory properties (e.g., shape, color). We can only speculate based on the few studies where such distinctions are made: for object color knowledge the language-derived symbolic representation was identified to be dorsal ATL (as reviewed here); the number symbolic structures in intraparietal sulcus [87]. While these findings tentatively suggest distinct neural support for language-derived representations for general knowledge relative to number symbolic representations, future studies that more carefully compare these two systems are warranted.

(whole brain) activity patterns (count models and GloVe models [56–59]), language processing regions/networks (word2vec and LSA models [53,60]), and inferior temporal cortex (COALS and LSA models [61,62]). These results, while providing proof-of-concept evidence that the brain may represent information derived from language, need to be considered with caution when drawing conclusions about neural computational algorithms (e.g., [55,63]). Given the correlation between language- and sensory-derived structures (see earlier), and the correlation between different NLP models [55,64], specific targeted contrasts between different computational algorithms and different inputs (e.g., language versus sensory) are warranted to test the explanation and prediction of neural organization.

Implementation

What neural properties of the human ATL support a sensory-independent, language-derived knowledge system? The dorsal ATL cluster functionally identified in the blind color studies [27,29,35] representing non-sensory language-derived knowledge is in a subsection of ATL that shows different cytoarchitectural, functional response, and structural/functional connectivity patterns from the other ATL subsections, including an ATL subregion that is most different between humans and macaques, aligning with the hypothesis of a potentially human-specific language-derived representation (Box 3). Beyond dorsal ATL, network topological analyses on the broader semantic-processing network, constructed from resting-state connectivity mapping among regions that are consistently activated by semantic tasks [41], showed three subnetworks ([65]; see also [66]). Two correspond to the perisylvian language network and multisensory experiential network (default mode network), mirroring the separation of the language- and sensory-derived systems in the current dual-coding knowledge neural framework (the third is a frontal parietal control subnetwork). Interestingly, the three regions that were consistently more

Box 3. The neural architecture of ATL

Parcellation analyses based on cytoarchitecture, structural connectivity, functional connectivity, and functional coactivation patterns have converged in identifying different subregions within ATL. Worth highlighting is that the dorsal ATL cluster functionally identified in the blind color studies as representing non-sensory language-derived knowledge included a subregion of ATL that has been identified as ‘TG’ in cytoarchitecture studies of human ATL [90]. This subregion differs from the other ATL subregions that were the extension of auditory, visual modalities, and limbic systems. Convergent evidence has been obtained from later parcellation studies based on structural connectivity [91], functional connectivity [92], and functional activation patterns [93]. This dorsal ATL subregion (TG in [88,90]) is structurally connected with the orbital part of superior frontal gyrus and gyrus rectus (laterally) and ventral/medial temporal cortex (ventrally) [91], and intrinsically functionally connected with the language processing network ([29]; language network defined by language localizers, [37]) and the default-semantic network [92]. It tends to be activated along with distributed regions in frontal, temporal, and parietal regions in a wide range of tasks, including sensory, language, semantic/episodic memory, and social-emotion tasks [93], in line with its functional role in knowledge representation. Intriguingly, while the other subregions of ATL have homologous regions in the macaque brain, the TG region is ‘most difficult to be mapped in macaque brains’ [92], converging with its functional role as a language-derived symbolic knowledge system that might be human-specific.

strongly activated by abstract words than concrete words [38] (i.e., dorsal ATL highlighted in the current review, IFG, and pMTG) are part of the perisylvian language network and ATL and pMTG were also identified as connector hubs connecting the language network and the other two networks [65]. This suggests that they play a role in bridging language-derived systems with other aspects of semantic processing (sensory-derived representations and executive control) through brain connectivity.

Concluding remarks

Knowledge is at the heart of human cognition, constituting the basis for understanding all kinds of inputs, reasoning, and decision making. The last several decades of cognitive neuroscientific research converged on uncovering the embodied mechanisms of knowledge representation, identifying the neural correlates of knowledge derived from sensory experiences. The neural mechanisms that support abstract, flexible, knowledge beyond sensory access, like ‘magnetic field’, ‘evolution’, and ‘rationality’, have been elusive. By taking advantage of the unique experiment of nature, contributed by the special characteristics of exclusively visual knowledge such as color and individuals with congenital blindness, the studies reviewed here provide compelling positive evidence of fully disembodied knowledge derived from language in dorsal ATL and the related language network, along with sensory-derived knowledge in the higher-order sensory cortices. These findings indicate that two kinds of knowing, knowing by symbolic relations and knowing by experiencing, coexist in the human brain and jointly make up humans’ knowledge system. The dual-coding neural framework opens up new avenues of research (see [Outstanding questions](#)) and offers nature’s solutions to the classical challenges of different knowledge representation approaches: the problem of grounding [67] and the challenge of representing nonverbalized common-sense knowledge faced by the traditional symbolic approach in AI; and the challenge of elucidating the representation of abstract knowledge in the embodied approach [8,12,17]. The dual-coding neural framework also offers an empirical answer to the ‘Mary the color scientist’ thought experiment: when leaving the black and white room, Mary would develop an additional sensory-derived representation for color knowledge in lateral fusiform regions, supplementing her existing language-derived color knowledge representation in dorsal ATL.

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Outstanding questions

What are the relationships between sensory- and language-derived knowledge representations? Do they integrate to form a holistic representation? Do they modulate each other?

What are the functional roles of the two types of knowledge representations in various cognitive tasks, including relatively basic ones, such as perception and recognition, and high-level ones, such as reasoning and decision making? Is the sensory-derived representation more easily subject to sensory/motor biases and the language-derived one more ‘logical’?

Does individual variation in terms of language and sensory predispositions and/or experiences systematically affect knowledge representations?

Do cross-linguistic differences lead to systematic differences in knowledge representation? How does speaking two or multiple languages affect knowledge representation?

To what degree is the two-form knowledge representation framework human-specific? Do other animals such as rodents and nonhuman primates also have some kind of non-sensory, symbolic (yet non-linguistic) type of knowledge representations or do they only have representations derived from sensory experiences?

What are the developmental trajectories and mechanisms of these different knowledge-representation systems?

What is the relationship between the two knowledge coding systems in the human brain and the computational sensory models (e.g., vision, multimodal integration) and language models in AI?

Declaration of interests

No interests are declared.

References

- Jackson, F. (1982) Epiphenomenal qualia. *Philos. Q.* 32, 127–136
- Paivio, A. (1986) *Mental Representations: A Dual Coding Approach*, Oxford University Press
- Paivio, A. (2007) *Mind and Its Evolution: A Dual Coding Theoretical Approach*, Lawrence Erlbaum Associates Publishers
- Papineau, D. (2002) *Thinking About Consciousness*, Oxford University Press
- Binder, J.R. and Desai, R.H. (2011) The neurobiology of semantic memory. *Trends Cogn. Sci.* 15, 527–536
- Martin, A. (2016) GRAPES—grounding representations in action, perception, and emotion systems: how object properties and categories are represented in the human brain. *Psychon. Bull. Rev.* 23, 979–990
- Pulvermüller, F. (2013) How neurons make meaning: Brain mechanisms for embodied and abstract-symbolic semantics. *Trends Cogn. Sci.* 17, 458–470
- Barsalou, L.W. (2016) On staying grounded and avoiding quixotic dead ends. *Psychon. Bull. Rev.* 23, 1122–1142
- Lambon Ralph, M.A. et al. (2017) The neural and computational bases of semantic cognition. *Nat. Rev. Neurosci.* 18, 42–55
- Patterson, K. et al. (2007) Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat. Rev. Neurosci.* 8, 976–987
- Binder, J.R. (2016) In defense of abstract conceptual representations. *Psychon. Bull. Rev.* 23, 1096–1108
- Barsalou, L.W. (2008) Grounded cognition. *Annu. Rev. Psychol.* 59, 617–645
- Martin, A. et al. (1995) Discrete cortical regions associated with knowledge of color and knowledge of action. *Science* 270, 102–105
- Simmons, W.K. et al. (2007) A common neural substrate for perceiving and knowing about color. *Neuropsychologia* 45, 2802–2810
- Fernandino, L. et al. (2016) Concept representation reflects multimodal abstraction: a framework for embodied semantics. *Cereb. Cortex* 26, 2018–2034
- Binder, J.R. et al. (2016) Toward a brain-based componential semantic representation. *Cogn. Neuropsychol.* 33, 130–174
- Mahon, B.Z. and Caramazza, A. (2008) A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *J. Physiol. Paris* 102, 59–70
- Locke, J. (1690) *An Essay Concerning Human Understanding*, Oxford University Press
- Bedny, M. and Saxe, R. (2012) Insights into the origins of knowledge from the cognitive neuroscience of blindness. *Cogn. Neuropsychol.* 29, 56–84
- Landau, B. and Gleitman, L. (1985) *Language and Experience: Evidence from the Blind Child*, Harvard University Press
- Connolly, A.C. et al. (2007) Effect of congenital blindness on the semantic representation of some everyday concepts. *Proc. Natl. Acad. Sci. U. S. A.* 104, 8241–8246
- Mills, A.E. (1983) *Language Acquisition in the Blind Child: Normal and Deficient*, College-Hill Press
- Zimler, J. and Keenan, J.M. (1983) Imagery in the congenitally blind: how visual are visual images? *J. Exp. Psychol. Learn. Mem. Cogn.* 9, 269–282
- Shepard, R.N. and Cooper, L.A. (1992) Representation of colors in the blind, color-blind, and normally sighted. *Psychol. Sci.* 3, 97–104
- Marmor, G.S. (1978) Age at onset of blindness and the development of the semantics of color names. *J. Exp. Child Psychol.* 25, 267–278
- Sayani, A. et al. (2018) Colour envisioned: concepts of colour in the blind and sighted. *Vis. Cogn.* 26, 382–392
- Bottini, R. et al. (2020) Brain regions involved in conceptual retrieval in sighted and blind people. *J. Cogn. Neurosci.* 32, 1009–1025
- Bailari, M. et al. (2018) Is red heavier than yellow even for blind? *Perception* 9, 1–4
- Wang, X. et al. (2020) Two forms of knowledge representations in the human brain. *Neuron* 107, 383–393
- Bedny, M. et al. (2019) There's more to "sparkle" than meets the eye: knowledge of vision and light verbs among congenitally blind and sighted individuals. *Cognition* 189, 105–115
- Bedny, M. et al. (2009) Growing up blind does not change the neural bases of theory of mind. *Proc. Natl. Acad. Sci. U. S. A.* 106, 11312–11317
- Kim, J.S. et al. (2019) Knowledge of animal appearance among sighted and blind adults. *Proc. Natl. Acad. Sci. U. S. A.* 166, 11213–11222
- Wang, X. and Bi, Y. Idiosyncratic tower of babel: Individual differences in word meaning representation increase along abstractness. *Psychol. Sci.* (accepted) (bioRxiv preprint, doi: <https://doi.org/10.1101/2020.08.28.272997>)
- Turing, A.M. (1950) Computing machinery and intelligence. *Mind* 49, 433–460
- Striem-Amit, E. et al. (2018) Neural representation of visual concepts in people born blind. *Nat. Commun.* 9, 5250
- Kriegeskorte, N. et al. (2008) Representational similarity analysis - connecting the branches of systems neuroscience. *Front. Syst. Neurosci.* 2, 1–28
- Fedorenko, E. et al. (2010) New method for fMRI investigations of language: defining ROIs functionally in individual subjects. *J. Neurophysiol.* 104, 1177–1194
- Wang, J. et al. (2010) Neural representation of abstract and concrete concepts: a meta-analysis of neuroimaging studies. *Hum. Brain Mapp.* 31, 1459–1468
- Wang, X. et al. (2019) Close yet independent: dissociation of social from valence and abstract semantic dimensions in the left anterior temporal lobe. *Hum. Brain Mapp.* 40, 4759–4776
- Hoffman, P. et al. (2015) Differing contributions of inferior prefrontal and anterior temporal cortex to concrete and abstract conceptual knowledge. *Cortex* 63, 250–266
- Binder, J.R. et al. (2009) Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* 19, 2767–2796
- Sabsevitz, D.S. et al. (2005) Modulation of the semantic system by word imageability. *Neuroimage* 27, 188–200
- Zahn, R. et al. (2007) Social concepts are represented in the superior anterior temporal cortex. *Proc. Natl. Acad. Sci. U. S. A.* 104, 6430–6435
- Mellem, M.S. et al. (2016) Sentence processing in anterior superior temporal cortex shows a social-emotional bias. *Neuropsychologia* 89, 217–224
- Fang, Y. et al. (2018) Semantic representation in the white matter pathway. *PLoS Biol.* 16, e2003993
- Cangelosi, A. and Harnad, S. (2001) The adaptive advantage of symbolic theft over sensorimotor toil. *Evol. Commun.* 4, 117–142
- Paivio, A. (2013) Dual coding theory, word abstractness, and emotion: a critical review of Kousta et al. (2011). *J. Exp. Psychol. Gen.* 142, 282–287
- Fairhall, S.L. and Caramazza, A. (2013) Brain regions that represent amodal conceptual knowledge. *J. Neurosci.* 33, 10552–10558
- Marr, D. (1982) *Vision*, MIT Press
- Majid, A. et al. (2018) Differential coding of perception in the world's languages. *Proc. Natl. Acad. Sci. U. S. A.* 115, 11369–11376
- Majid, A. (2021) Human olfaction at the intersection of language, culture, and biology. *Trends Cogn. Sci.* 25, 111–123
- Lewis, M. et al. (2019) Distributional semantics as a source of visual knowledge. *Proc. Natl. Acad. Sci. U. S. A.* 116, 19237–19238
- Wang, X. et al. (2018) Organizational principles of abstract words in the human brain. *Cereb. Cortex* 28, 4305–4318
- Meersmans, K. et al. (2020) Representation of associative and affective semantic similarity of abstract words in the lateral temporal perisylvian language regions. *Neuroimage* 217, 116892

55. Günther, F. *et al.* (2019) Vector-space models of semantic representation from a cognitive perspective: a discussion of common misconceptions. *Perspect. Psychol. Sci.* 14, 1006–1033
56. Mitchell, T.M. *et al.* (2008) Predicting human brain activity associated with the meanings of nouns. *Science* 320, 1191–1195
57. Huth, A.G. *et al.* (2016) Natural speech reveals the semantic maps that tile human cerebral cortex. *Nature* 532, 453–458
58. Pereira, F. *et al.* (2018) Toward a universal decoder of linguistic meaning from brain activation. *Nat. Commun.* 9, 963
59. Anderson, A.J. *et al.* (2019) An integrated neural decoder of linguistic and experiential meaning. *J. Neurosci.* 39, 8969–8987
60. Carota, F. *et al.* (2017) Representational similarity mapping of distributional semantics in left inferior frontal, middle temporal, and motor cortex. *Cereb. Cortex* 27, 294–309
61. Carlson, T.A. *et al.* (2013) The emergence of semantic meaning in the ventral temporal pathway. *J. Cogn. Neurosci.* 26, 120–131
62. Fischer-Baum, S. *et al.*