Review

How neurons make meaning: brain mechanisms for embodied and abstract-symbolic semantics

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How brain structures and neuronal circuits mechanistically underpin symbolic meaning has recently been elucidated by neuroimaging, neuropsychological, and neurocomputational research. Modality-specific 'embodied' mechanisms anchored in sensorimotor systems appear to be relevant, as are 'disembodied' mechanisms in multimodal areas. In this paper, four semantic mechanisms are proposed and spelt out at the level of neuronal circuits: referential semantics, which establishes links between symbols and the objects and actions they are used to speak about; combinatorial semantics, which enables the learning of symbolic meaning from context; emotional-affective semantics, which establishes links between signs and internal states of the body; and abstraction mechanisms for generalizing over a range of instances of semantic meaning. Referential, combinatorial, emotional-affective, and abstract semantics are complementary mechanisms, each necessary for processing meaning in mind and brain.

Symbolic and embodied semantic systems

What is the brain basis of meaning or semantics? Cognitive psychologists have proposed that semantic and conceptual processes can be attributed to a dedicated 'symbolic semantic system' specialized for handling information about meaning and concepts related to signs [1,2]. However, brain imaging work and patient studies suggest that several different brain areas play a central role in semantic processing [3–5], thus casting doubt on the existence of a single focal 'hub' for semantic integration [6]. At the theoretical level, a theory of meaning of symbols needs to solve the semantic grounding problem, namely, how words and other symbols are related to specific types of perceived objects and executable actions [7,8]. Theories that rely on a symbolic system functionally detached from sensory and motor mechanisms cannot explain semantic grounding [9–11]. Therefore, an alternative proposal emphasizes semantic grounding of symbols in perception and action systems of the mind and brain [12–14]. Because words are used to speak about different types of objects and actions, this approach implies specific semantic mechanisms that depend on word category (e.g., object vs action words, animal

Glossary

Action and action schema: an action is a motor act connected to a goal. Individual actions, which take place at a specific time and place, can be classified into types or action schemas (e.g., GRASPING, DONATING).

Amodal: amodal meaning (or semantics) is defined in abstract space, for example in terms of abstract semantic features (e.g., BACHELOR = [+human, +adult, +male, −married]). It has been proposed that an amodal semantic system processes meaning independently of information from the senses. Some researchers also refer to 'amodal brain areas', although every area in cortex in fact receives information from the senses and connects, at least indirectly, to the motor output.

Arcuate fascicle: fiber bundle that connects the inferior frontal, inferior parietal, and superior/middle temporal cortex of the human cortex. It is especially well developed in the left hemisphere.

Combinatorial (or distributional) meaning (semantics): the meaning of words that becomes evident from the other words with which they typically combine in constructions and larger discourse (e.g., for 'strawberry': red, sweet, enjoy, buy).

Concept and meaning: the meaning of a word is sometimes seen as the concept related to it. Concepts and meanings can be concrete (EYE, GRASP) or more abstract (GAME, BEAUTY).

Compositional meaning (semantics): derivation of the meaning of constructions from the meaning of their constituent words plus general combinatorial principles.

Constituent words: words as parts of a larger construction.

Construction: structurally coherent aggregate of words with specific meaning.

Disembodied: disembodied meaning does not include sensorimotor representations, although it may be grounded in action and perception. Disembodied meaning processing in multimodal cortex areas is sometimes connected to the idea of an amodal semantic system, but is equally consistent with semantic grounding in action and perception.

Embodied: embodied meaning (or semantics) includes representations of action and object schemas and is assumed to be processed in sensory, motor, and multimodal areas of cortex.

Grounded: grounded meaning (semantics) is intrinsically related to perceptions and actions. The link can be referential (between 'eye' and the respective referential objects) or more distant ('beauty' and the variable objects, action schemas, and scenes to which this word applies). It has been stated that symbol grounding is necessary for semantics.

Modality-specific, modality-preferential: some parts of cortex are primarily dedicated to one sensory or motor modality (see sensory, motor). These are frequently called modality-specific. Because some multimodal convergence exists in sensory and motor areas, the term modality-preferential areas is more accurate.

Motor: motor areas include primary motor, premotor, and supplementary motor cortex (Brodmann areas 4, 6, and 44; Figure 1, top left). Neural processes in these areas control motor acts and contribute to actions.

Multimodal: multimodal areas of cortex are equally dedicated to processing information from different sensorimotor modalities (e.g., dorsolateral prefrontal cortex, angular gyrus; Brodmann areas 10, 46, and 39).

Object and prototype: objects in the world can be subsumed under certain words and concepts (e.g., EYE, GAME). A prototype is a particularly typical and frequently encountered instantiation of a concept (e.g., brown eyes in southern countries).

Perisylvian cortex: inferior frontal, inferior parietal, and superior temporal areas surrounding the Sylvian fissure (Figure 1, top left). In almost all right-handed and most left-handed people, the perisylvian cortex of the left hemisphere is most relevant for language.

Semantic hub: unique brain area equally necessary for processing all types of meaning.

Semantics: the (science of the) meaning of words and constructions.

Sensory: sensory areas include primary and adjacent higher visual, auditory, somatosensory, olfactory, and gustatory cortex. Activity in these areas is necessary for sensory perception.

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vs tool names) [15,16]. Support for different category-specific semantic brain mechanisms comes from patients with focal brain lesions and category-specific semantic deficits [17,18] and from neuroimaging work that demonstrates activation of sensory and motor areas that reflect aspects of word and sentence meaning [10,12,19,20]. These results support models of category-specific semantic grounding and meaning embodiment in sensory and motor systems. However, it has also been argued that lesions sometimes compromise sensory or motor processing without impacting on semantics and some semantic deficits appear without concordant sensorimotor impairment, thus supporting 'disembodied' semantic mechanisms that can dissociate from sensorimotor functions and brain areas [3,21].

To explain semantic processing and representation in the human mind and brain, the new data and positions that have emerged in this 'embodiment debate' need to be integrated with each other. In this review, four different semantic mechanisms are identified as essential and spelt out neuromechanistically in an attempt to develop an integrative neurosemantic proposal that covers both embodied and abstract-symbolic processes in both modality-specific and multimodal areas of the brain. First, referential semantic mechanisms for linking symbols to objects and actions are contrasted with mechanisms for combining symbols with each other. Then symbol grounding in emotion and the wide applicability spectrum of some terms are discussed in an attempt to account for aspects of abstract concepts. A final section focuses on the interplay between 'embodied' and 'disembodied' semantic systems in abstract sentence processing.

Semantic hubs and the symbolic system

Semantic processing may occur in an integration center or 'semantic hub' that joins together the various aspects of a word's meaning [3], for example, in the case of the word 'fish', about shape, color, smell and taste. Although a specialized area is in fact not necessary for integration of semantic information – because the binding of multimodal semantic features into one coherent representation may rely on long-range cortico–cortical connections [16] – it is possible that such a single hub exists. However, neuroimaging and neuropsychological studies have revealed several cortical regions that may support general meaning processes (Figure 1, top):

(i) Inferior frontal cortex (iFC): the anterior part of Broca's area and adjacent tissue in left iFC (Brodmann areas, BA, 44, 45, and 47) are active in semantic processing and functional changes in iFC impact on them [4,22].
(ii) Superior temporal cortex (sTC): Wernicke's area, the classic posterior language area in and adjacent to the superior temporal gyrus and sulcus [23], has been emphasized as a semantic processor on the basis of lesion, perfusion, and imaging data [24–26].
(iii) Inferior parietal cortex (iPC): angular and adjacent supramarginal gyrus in iPC provide another candidate region for a semantic hub [6,27] that is most strongly active during semantic processing of cross-modal spatial and temporal configurations [6,28].
(iv) Inferior and middle temporal cortex (m/iTC): a general semantic binding site between words and their meaning in left [5] or bilateral [29] m/iTC has been suggested on the basis of neuroimaging results; lesion evidence also supports this position.
(v) Anterior temporal cortex (aTC): semantic dementia (SD), a severe and specific semantic deficit, is characterized by severe lesions of both temporal poles (TPs) [3]; some neuroimaging results also point to a role of TPs in semantic processing. Recent work shows the best correlation between semantic deficit and reductions in metabolic brain activation in anterior fusiform gyrus rather than TP [30]; data from stroke patients indicate similar roles of left aTC and other semantic areas in causing semantic errors [31].

Although each candidate semantic hub is, by itself, consistent with the idea of an amodal semantic system [1,2], all the results taken together suggest that a wide variety of areas are important for general meaning processing, and this undermines the idea of a unique local center for semantic integration. Semantic integration mechanisms draw on higher association areas of the neocortex, that is, the multimodal convergence zones in prefrontal, posterior parietal, and anterior, inferior, and posterior temporal cortex, and possibly even anterior and posterior cingulate and other corticolimbic structures [6], where sensory, motor, and affective emotional information converges. These areas are known to function as convergence zones of information from several modalities, rather than as functionally isolated modules of amodal information processing [32].

Semantic category specificity and embodiment

On closer examination, all of the candidate semantic hubs appear to contribute to semantics differentially. Typical lesions in each of the five potential hubs do not affect all words alike; instead, words from one semantic category may suffer more than words from other categories. Concordant with these observations, neuroimaging studies show that semantic areas are activated to different degrees when different semantic types are being processed:

(i) Left iFC and bilateral frontocentral motor systems become most strongly active in the processing of action-related words and phrases, and lesions in these areas, as seen with stroke and dementia, lead to relatively pronounced impairments in processing of action-related words and concepts compared to matched control items (Box 1) [12,33–37].
(ii) Bilateral sTC is especially active in response to words related to sounds, and lesions in left sTC impair sound word processing more than that for other (matched) words [20,38].
(iii) Left iPC, especially supramarginal gyrus, is most strongly activated by spatial language, and iPC lesions most strongly affect spatially related language, including prepositions [39,40]. Angular gyrus and intraparietal sulcus in iPC are of special importance for processing number words and concepts [41,42].
(iv) Different parts of m/iTC show category-specific effects for animal, tool, and person names, color- and form-related words, and emotion terms in both activation and lesion studies [12,18,32,43].

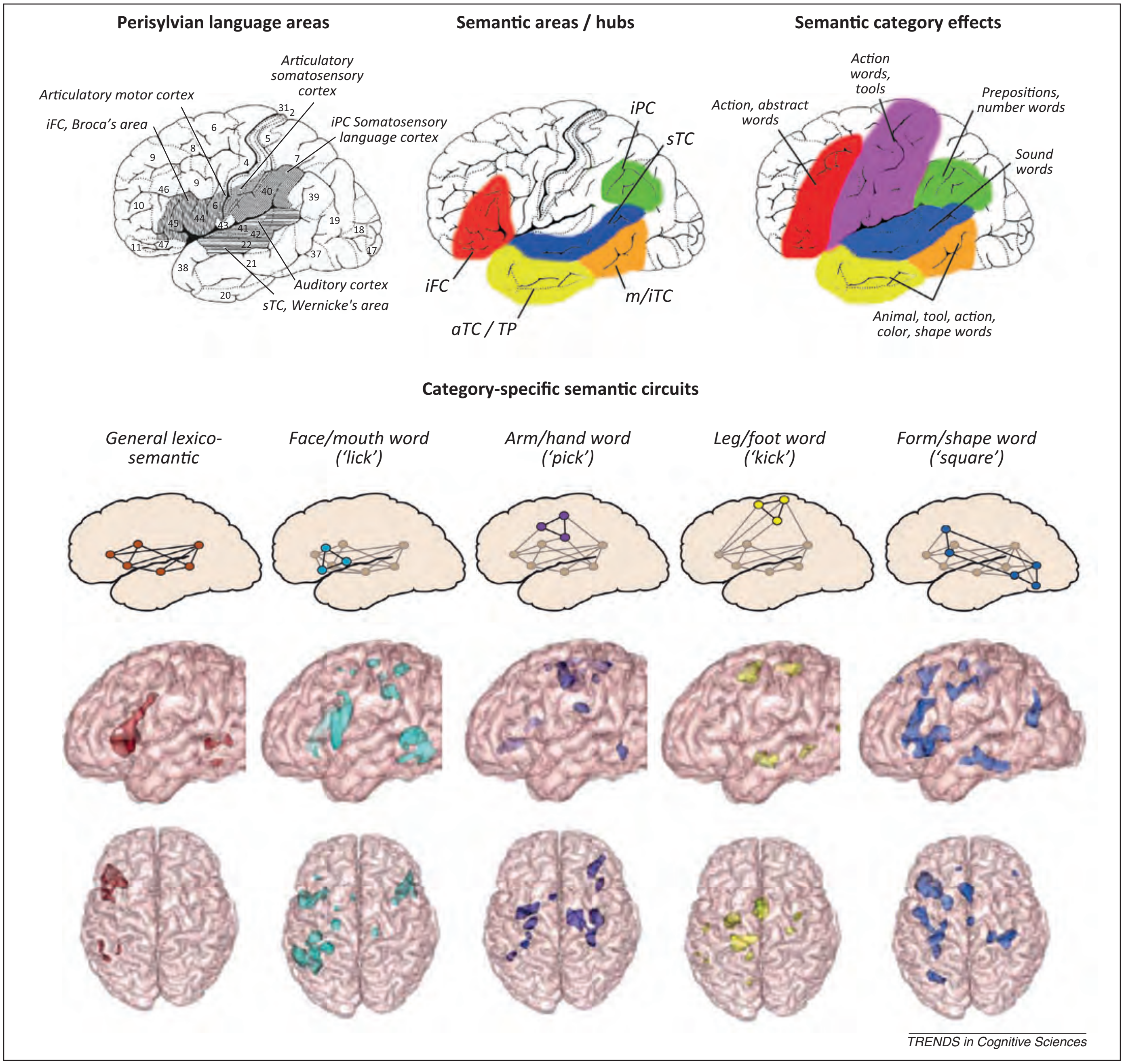


Figure 1. Semantic brain mechanisms: hubs, category specificity, and semantic circuits. Top left: Left cortical hemisphere with Brodmann area numbers indicated; the left-perisylvian language areas are highlighted (adapted from [55]). Top middle: Areas of particular importance for general semantic processing as proposed in the literature. Top right: Cortical areas for which semantic category-specific effects have been reported in the literature. Middle panels: Model of general lexico–semantic circuits (leftmost graph) and referential–semantic circuits for four different semantic word types (as indicated). Bottom panels: Results of functional magnetic resonance imaging (fMRI) cluster analysis (views from left and from top) revealing activation clusters common to all word types tested (leftmost graph) and category-specific activation to four different semantic word types. Cluster analysis contrasts activation patterns elicited by individual word categories (each tested against a control condition of matched meaningless symbol strings) with each other and with those activations shared by combinations of semantic categories (adapted from [79]). Category-specific semantic circuits are distributed over different areas of both hemispheres and lexico–semantic circuits shared by all words are localized in left perisylvian areas. Note the rich category-specific activations, which confirm some of the model predictions, but also call for model extensions. Abbreviations: iFC, inferior frontal cortex; iPC, inferior parietal cortex; sTC, superior temporal cortex; m/iTC, middle/inferior temporal cortex; aTC, anterior temporal cortex; TP, temporal pole.

(v) Differences in the ability to process semantic categories have also been observed after lesion in aTL [17,32] and in SD due to TP lesion [44,45].

Thus, all putative semantic hubs seem to show at least a degree of category specificity. It is possible that some of these category differences can potentially be explained by close adjacency of true hubs and category preferential areas, but the data are equally open to the possibility that potential hub areas preferentially process specific semantic types.

Category-specific semantic effects also appear for regions far beyond the hub candidates, in and close to modality-specific – or, more accurately, modality-preferential – sensory and motor areas. In superior temporal auditory and inferior temporal visual areas, sound and visually related words such as 'bell' and 'grass' yield the strongest activation, and focal lesions can cause semantic

Box 1. Action semantics in the dorsal stream

Some brain language models attribute semantics to areas in the temporo-occipital ventral stream of processing of visual object-related information (yellow/orange areas in top middle and right panel of Figure 1). However, recent evidence showed that frontoparietal areas in the dorsal stream (red, purple, and green areas) are also active in semantic processing and that lesions here lead to severe linguistic–conceptual impairments, especially in the processing of action-related meaning [12,20,33,35]. For example, motor neuron disease, a degenerative brain disease that affects frontoparietal cortex including precentral motor systems, is characterized by motor deficits and concordant conceptual–semantic deficits in the processing of action information [35]. In functional imaging studies, semantic somatotopy was found in precentral motor and premotor cortex, showing that words (both verbs and nouns), phrases, and sentences semantically related to different parts of the body (e.g., 'talk', 'fork', and 'walk') activate ventral face/mouth, lateral arm/hand, and dorsal leg/foot motor regions, respectively [80]. Semantic–somatotopic activation has been confirmed by a range of fMRI studies (Figure I; [81]) and in MEG and EEG studies it emerged as rapidly as the earliest signs of cortical meaning processing reported so far (pre-N400 responses with a latency of 100–250 ms), thus arguing that meaning-related motor activity indexes early semantic access rather than late post-understanding inferences [20,82,83]. Furthermore, experimental studies have demonstrated a causal effect of focal motor systems activation – induced by magnetic brain stimulation [84,85] and behavioral procedures [50,86,87] – on the processing of action-related language.

There are two main reasons why dorsal-stream action semantics is important for cognitive theory. First, claims about semantic category specificity and its relationship to motor and sensory brain systems had remained suggestive because most category-specific deficits were seen for large lesions [17] and category-specific functional activation was typically seen adjacent to, but not in, sensory regions [43]. Crucially, motor activation of action-semantic processing was found in regions of interest defined by motor localizer tasks, thus strengthening the argument for embodied semantics grounded in action and perception systems of the brain and mind [12,13]. Second, after behaviorism had been overcome by the cognitive revolution of the 1950s, motor processes had been seen as epiphenomenal to cognitive and mental mechanisms. However, on the basis of theoretical arguments, semanticists had long emphasized the important criterial role of action and interaction for semantics [71,72,88], an insight whose re-entry into the cognitive field was, in part, sparked by empirical evidence of action semantics in the context of emerging interest in embodied cognition [13,14,20,68,89–91].

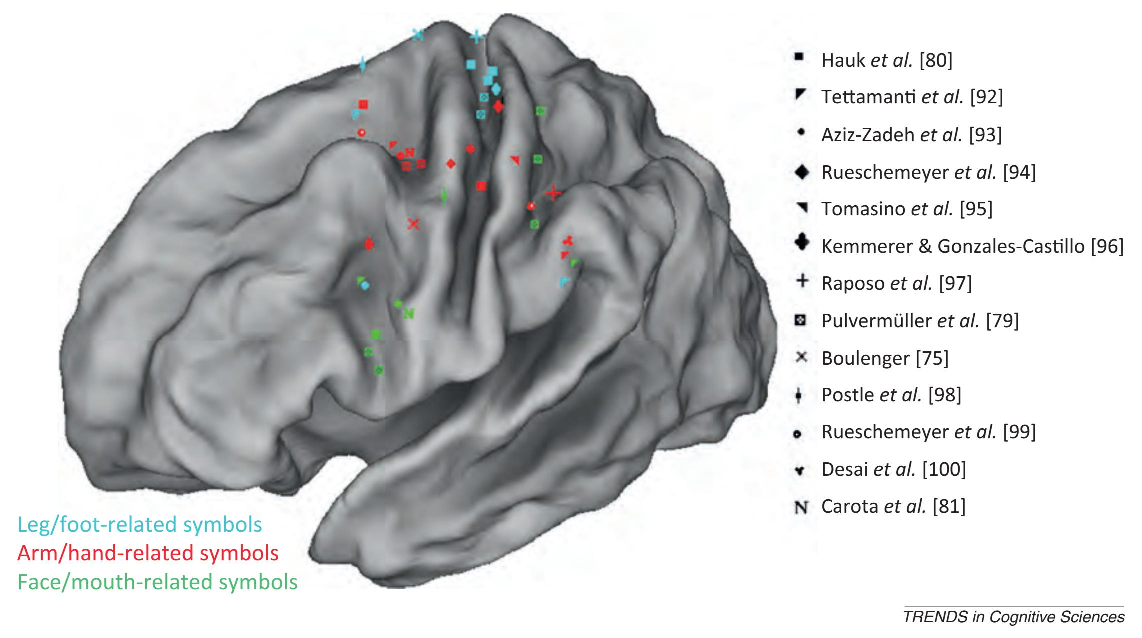
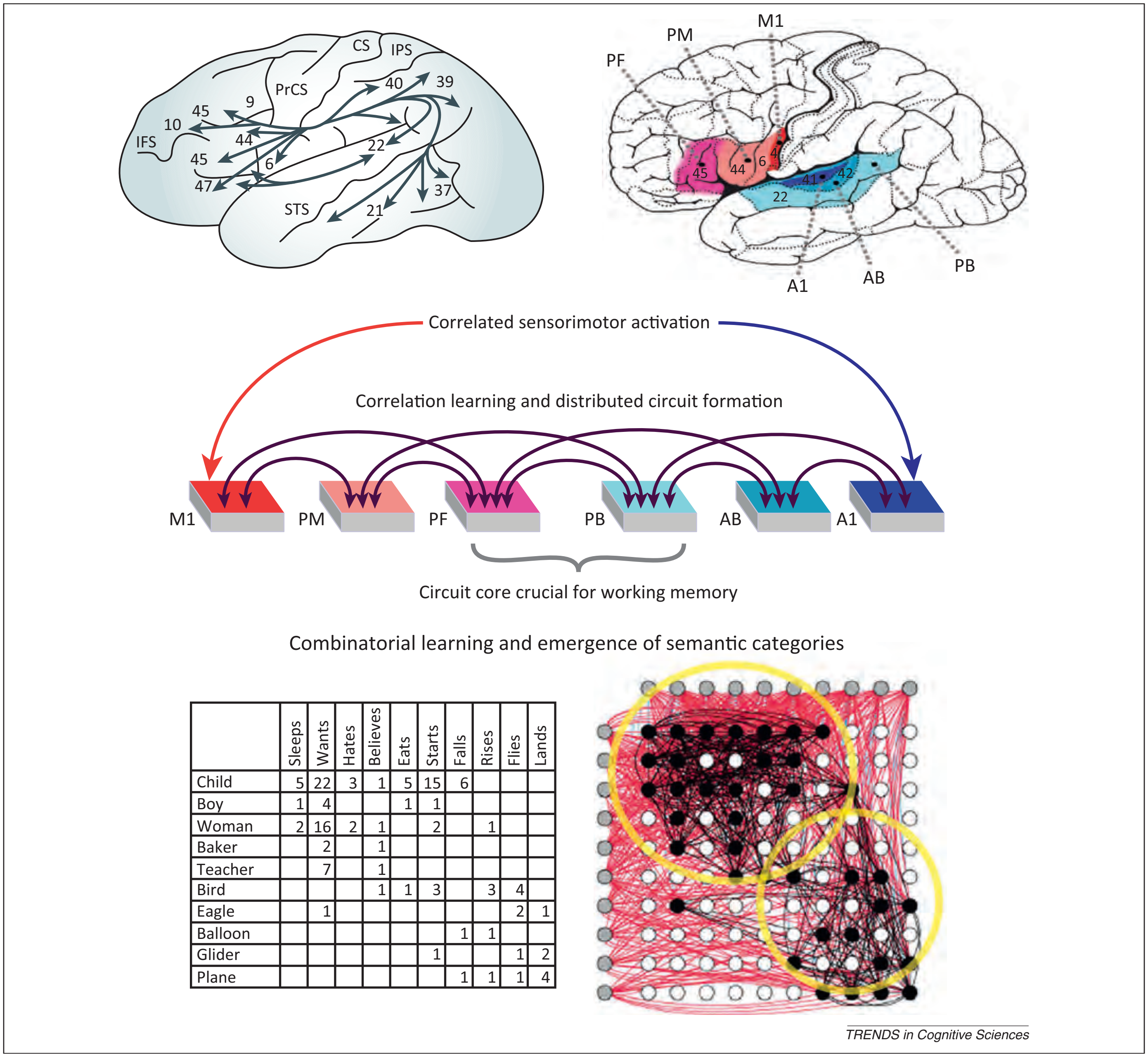


Figure I. Semantic somatotopy in the motor system. Activity foci observed in studies of action word and sentence processing semantically related to actions preferentially performed with the face/mouth (symbols in green), arms/hands (red) and legs/feet (blue). Note that neural indices of semantic body-part relationships are present in central and precentral frontal, but not in postcentral parietal areas. Adapted, with permission, from [81]. The data displayed are from [75,79–81,92–100].

and conceptual deficits for these categories [20,38,44]. Category specificity is present in and close to the piriform and anterior insular olfactory cortex, where odor words such as 'cinnamon' lead to greater activation than control words do [46]; in the gustatory cortex in anterior insula and frontal operculum, where taste words such as 'sugar' lead to relatively strong activation [47]; and in the ventral, lateral, and dorsal motor system, including primary motor and premotor, along with adjacent prefrontal and anterior parietal areas. In motor cortex, a fine-grained semantic map reflects the body-part relationship of action-related words, phrases, and sentences, and potentially additional features of the action schemas these signs relate to semantically (Box 1).

Neuroscience integration of semantic models

The overlap and adjacency of many of the category-specific semantic areas with sensory and motor areas suggests common mechanisms for action, perception, and semantic processing [20,48], a postulate also immanent to cognitive theories of semantic embodiment [49–51]. Arguably, the observation of disembodied semantic functions in multimodal association cortices far removed from sensory and motor fields contradicts this view [52]. To understand semantic mechanisms, an integration of these positions with each other is required, as is an explanation of why different aspects of semantics relate to different multimodal and modality-preferential brain parts (Figure 2).



Correlated sensorimotor activation

Correlation learning and distributed circuit formation

Circuit core crucial for working memory

Combinatorial learning and emergence of semantic categories

	Sleeps	Wants	Hates	Believes	Eats	Starts	Falls	Rises	Flies	Lands
Child	5	22	3	1	5	15	6			
Boy	1	4			1	1				
Woman	2	16	2	1		2		1		
Baker		2		1						
Teacher		7		1						
Bird				1	1	3		3	4	
Eagle		1							2	1
Balloon							1	1		
Glider						1			1	2
Plane							1	1	1	4

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Figure 2. Cortico–cortical connectivity, word form circuit formation, and combinatorial semantic learning. Top left: Long-range cortico–cortical connections within the perisylvian language cortex and adjacent areas. Abbreviations: IFS, inferior frontal sulcus; PrCS, precentral sulcus; CS, central sulcus; IPS, intraparietal sulcus; STS, superior temporal sulcus. Numbers indicate Brodmann areas (reproduced, with permission, from [54]). Top right: Neuroanatomical subdivision of inferior frontal and superior temporal cortex into six areas: M1, primary motor; PM, premotor; PF, prefrontal; A1, primary auditory; AB, auditory belt; and PB, auditory parabelt areas (adapted from [61]). Middle: Schematic connection structure of the six areas highlighted in the top right panel. Correlated activation in M1 and A1 during articulations leads to spreading activation in the network and distributed circuit formation for syllables and words. Their richer connectivity determines that PF and PB develop memory-active circuit cores [67], by means of which word-form circuits become linked to each other in combinatorial learning. Bottom: Combinatorial learning of noun–verb co-occurrences in an auto-associative neuronal network model. Word pair co-occurrence data are shown in the table on the left (verbs in top row, nouns in left column; numbers denote co-occurrences in the British National Corpus). The bottom right panel shows neuronal elements for the same words and connections between neural elements detecting individual pair sequences. Black lines show learnt connections between sequences including semantically similar nouns and verbs. The formation of *ad hoc* semantic categories (yellow circles, e.g. nouns for humans vs flying objects and human-specific actions/mental activities vs flying actions) results from mapping of word–word correlations (adapted from [66]).

An explanation of the location of semantic brain processes is offered by semantic theory at the level of neuronal circuit structure and function. Neuroanatomy offers important brain structural information about within- and between-area connections in the cortex. Neurophysiology revealed equally important neurofunctional principles that specify the way learning is realized at the level of nerve cells and neuronal populations. A neural key to learning is the correlation learning principle: neurons that fire together wire together and neurons out of sync delink [53]. Together with structural knowledge about long-distance cortico–cortical connections – especially about the human-specific dorsal left-lateralized arcuate fascicle linking together inferior frontal and temporoparietal cortex (Figure 2, top left) [54] – this principle offers a range of explanations for brain topographies of linguistic and semantic processes [12,16,55].

Pronouncing a word form requires activation patterns in (frontal) articulatory motor systems of the speaker and leads to specific (temporoparietal) activation of auditory

Box 2. Automatic versus context-modulated semantics

It has been argued that linguistic and semantic brain activations are to some degree independent of attention [48,102,103]. This means that neuronal, behavioral, and cognitive signs of semantic activation can be observed even if subjects do not attend to symbols or their meaning. Several studies using fast neurophysiological brain imaging have demonstrated such automatic semantics [82,104,105]. However, the fact that attention-to-stimuli is not necessary still allows the possibility that task, behavioral, and linguistic contexts influence and modulate neurocognitive semantic processes. To what degree are semantic processes flexible and how can such flexibility be explained? This question has recently been addressed by numerous studies of action semantics. The results suggest several mechanisms.

Masking by motor responses: Semantic activations in motor areas are small and can be overridden by motor-related brain activity. Overt motor tasks strongly activate the motor system and preparatory motor activity is present when subjects are in a state of readiness to act, even in the absence of immediate overt responses [106]. Concordant motor preparation processes may explain why action-semantic responses are sometimes missing in precentral areas but still persist in inferior parietal areas when subjects perform button press tasks [100]. Therefore, several studies revealing action-semantic brain activation used non-response tasks [80]. Moving a finger in the context of a button press task may even cancel semantic activation of left-hemispheric hand/arm areas while still allowing leg- or face-word-related activation of dorsal or ventral motor systems to appear [107].

Attention to signs and meaning: A range of studies have shown that task-induced attention to aspects of meaningful stimuli can alter the brain response to these items. According to current theory [108] and neurcomputational work [61], attention boosts the local cortical response, for example, by adjusting the gain of activation-level control and competition mechanisms. Local modulations of brain manifestations of action semantics seen for attention and task [95,109,110] are consistent with this position.

Semantic priming: Even if the same neurosemantic circuit ignites each time a target word appears in the input, the degree of pre-activation explains why the neuronal circuit of a target is activated more rapidly after a semantically related prime-word [111] and with less additional cortical activity compared to an unprimed presentation [112]. Note that it is normally the difference between baseline responses and those to critical target stimuli that is interpreted as the neurocognitive response to the target. Therefore, pre-activation (priming) of semantic brain systems (including motor systems) due to semantic priming during baseline reduces the relative activation to the target [105,113].

Syntactic and semantic context: Syntactic and semantic context modifies action semantic processes. Such modulation has been shown for verbs appearing in the first versus the third person [114], action sentences including nouns and verbs with and without overtly realized grammatical endings [115], statements attributing actions to humans versus animals [83], and positive versus negation action statements [116,117]. These intriguing results are of great relevance for understanding the interplay between action semantics and other facets of language processing. For example, the reduction of semantic brain responses in motor systems and temporal poles to sentences including grammatical materials (Figure I [115]) may be due to perisylvian grammatical circuit activations competing with, and partly suppressing, semantic circuits. Likewise, the down-modulation of motor processes with negation may index interactions between semantic circuits for negation and action representations [116,117].

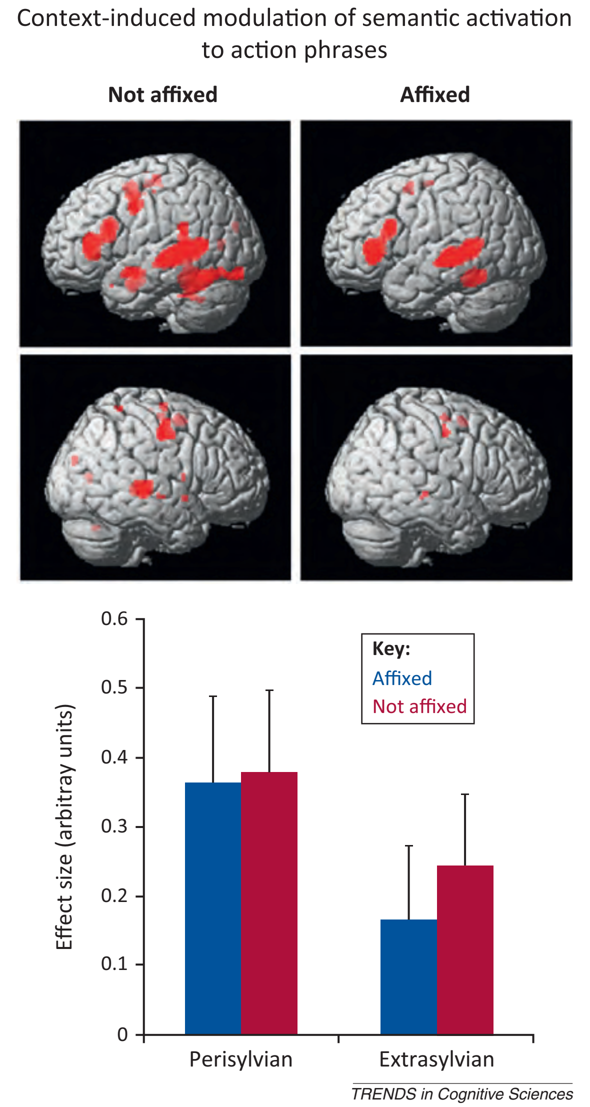

Figure I. Grammatically driven flexibility of semantic activation in the motor system and anterior temporal cortex. Simple action sentences (her/they grasp; top left panels) produce stronger semantic activations in precentral and anterior temporal cortex than similar sentences that include additional grammatical materials (with inflectional affixes on the nouns and verbs, e.g., she/their grasps; top right). Such grammatical modulation occurs in extrasylvian areas that index semantic processing (bottom, blue bars) but not in perisylvian language areas (red bars; reproduced, with permission, from [115]).

and somatosensory systems due to self-perceived sounds and movements. Fronto–temporal connections are typically left-lateralized, so the left hemisphere takes a lead role in mapping correlated articulatory–auditory information [56]. The emerging circuits are localized in frontotemporal perisylvian cortex, with an important contribution of motor areas [57], and can be seen as cortical correlates of spoken word forms (Figure 2, top and middle panels). If word meaning is grounded in the visual shapes of objects, the word form circuit is active together with neural activity in the ventral–temporal visual stream related to the processing of visual object information. Correlation learning links the word and object circuits, resulting in an embodied object-semantic representation. Likewise, correlations between word and sound-, smell-, taste-, or action-related information lead to the establishment of embodied referential semantic circuits, including perisylvian neuronal populations, along with circuits in auditory, olfactory, gustatory, and motor cortex. Action–perception correlation thus explains category-specific semantic grounding and embodied brain correlates of semantic word types in specific sensorimotor areas (Figure 1, middle panel; Box 2) [12,20].

How would this mechanistic approach address semantic processing in multimodal areas outside sensory or motor systems? The key to this question is cortical connectivity. Distant primary cortices do not strongly link to each other directly; major connections are via intermediary areas. For activity to travel between primary auditory and motor cortices, a number of areas need to be traversed, including premotor and prefrontal cortex in the frontal lobe, and the auditory belt and parabelt in superior temporal cortex (Figure 2, middle panel) [54,58–61]. Likewise, the connection between primary visual cortex and language areas is indirect, for example, via hubs, that is, interlinking relay areas, in temporo-occipital and middle temporal cortex [62]. To link the spoken word form 'grasp' to the concordant motor movement, or the articulation pattern for pronouncing the word 'grass' to specific visual knowledge about color and shape, nerve cells in motor and sensory areas are necessary; in addition, intermediary area neurons are equally required to build circuits that bind sensory and motor information. Neuroanatomical structure determines that the emerging circuits include neurons in modality-nonspecific areas of cortex. Therefore, semantic grounding, that is, the linking of symbols to information in the senses and the motor system (and thus correlated activation in perisylvian and modality-preferential brain systems), necessarily recruits 'higher' multimodal relay areas that bridge different modality-preferential systems (Figure 2, middle panel) [9,16]. As a result, semantic circuits are distributed over both types of areas. Convergence and divergence of connections between modality-preferential and -general areas explains why sensorimotor semantic activation is particularly specific to semantic category, whereas intermediary convergence area activity is less so, and thus sometimes creates the impression of general semantic hubs.

Whether specific areas of cortex tend to respond to specific word types or rather to all words alike can be explored objectively using cluster analysis performed on functional magnetic resonance imaging (fMRI) data.

There are indeed category-specific areas that preferentially respond to one semantic word type, and these are seen across the entire cortex (Figure 1, bottom panels). There are also areas that respond similarly to different semantic word types; these latter areas are multimodal and in the periphery of or adjacent to the perisylvian language areas in iFC, sTC, and m/iTC (shown in brown in Figure 1, bottom left). These results support both semantic embodiment and disembodiment at the neural level.

Combinatorial semantics

A wealth of semantic information is captured in the way words are combined with other words in sentences and texts. Combinatorial (sometimes also called distributional) semantic models express meaning similarity in terms of vectors derived from the probability of the co-occurrence of words with other words in texts [63]. Learning from context is sometimes seen as a paradigm case of acquiring disembodied semantics. However, it must be acknowledged that if a stock of words is semantically grounded in action and perception knowledge, these words can form the basis of a form of secondary grounding (or 'symbolic theft') [11,64]. Correlation learning implies such semantic links between co-active novel word-form circuits and embodied referential representations activated as part of previously learnt semantic circuits.

Because correlated activation of neuronal circuits strengthens the connections between them, the cortex appears to be an ideal device for mapping the co-occurrence probabilities of words. Indeed, neural networks that learn to connect word forms by Hebbian mechanisms can map combinatorial properties of language [65]. Interestingly, even such combinatorial learning *per se* leads to the emergence of *ad hoc* semantic categories (Figure 2, bottom) [66]. Because all words share circuits in left-perisylvian language areas, disembodied combinatorial information is best mapped in or close to these regions, although the possibility exists that additional areas become involved, especially in binding between words with similar referential meaning. Partly in line with the left-perisylvian predominance of combinatorial mechanisms, two of the putative semantic hubs, in anterior inferior frontal cortex and superior temporal cortex, fall on the rim of the perisylvian cortex (Figure 1, top middle). However, why they do not fill the entire perisylvian space still awaits explanation, which is possible based on the internal dynamics of linguistic circuits: because convergence zones (relay areas) typically show richer neuroanatomical connectivity with other relevant areas than sensorimotor areas do, they may be more efficient in maintaining activity after circuit activation [67]. Prolonged activity of iFC and sTC neurons constituting the cores of linguistic circuits may thus underlie learning of word co-occurrences in contexts (Figure 2, middle).

From motion to emotion: from action to abstraction

A classic argument against embodiment in its strict form is based on abstract meaning. Whereas the meanings of the words 'eye' and 'grasp' can be explained, to a degree, by pointing to objects and actions, those of 'beauty' and 'freedom' cannot. It may be that some common sensorimotor knowledge is immanent in FREEING actions or instantiations of BEAUTY [68], but it seems likely that additional semantic binding principles are behind such concepts. So might it be necessary, after all, to place abstract semantics in an amodal meaning system? A remarkable observation has recently been offered that may be of the essence in this context: abstract terms show an over-proportionally strong tendency to be semantically linked to knowledge about emotions [10,69]. This additional embodied–semantic link accounts for advantages in processing speed for abstract emotional terms over otherwise matched control words [69]. In addition, abstract words strongly activate anterior cingulate cortex, a site known to be relevant for emotion processing [70]. Thus, it appears that at least some abstract words are semantically grounded in emotion knowledge.

Abstract emotion words as a test case for semantic theories

If abstract emotion words indeed receive their meaning through grounding in emotion [69], it is of crucial relevance

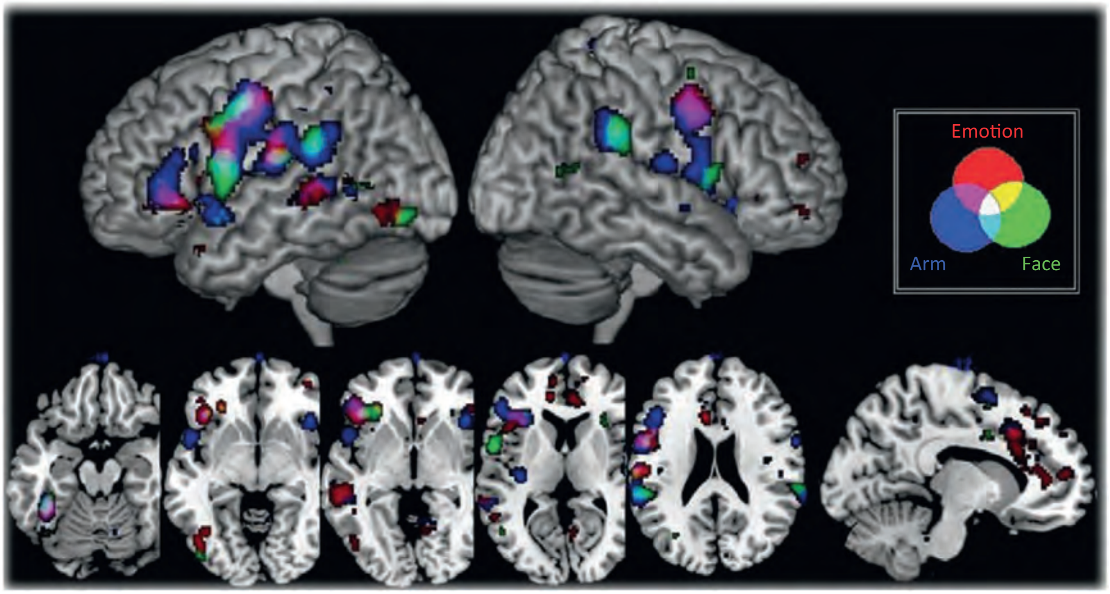

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Figure 3. Semantic embodiment of abstract emotion words. Brain activation (event-related functional magnetic resonance imaging) to face-related action words (in green), arm-related action words (in blue), and abstract emotion words (in red), each contrasted with activation for matched meaningless strings of repeated familiar symbols. Note that the inferior motor and premotor cortex sparked by face and arm words is also active for abstract emotion words. In addition, there is activation of the anterior insula and a range of other limbic structures. Reproduced, with permission, from [73].

to explain how emotion grounding is established. Note that an amodal semantic system account does not address this question. Even if such a system contained an inborn emotion concept of JOY, it is left unexplained how the learner knows to relate the concept to its corresponding word, and not, for example, to 'grief'. The classic answer in semantic theory is that this is possible, because abstract emotions and other internal states have characteristic ways in which they are manifested in the actions and interactions in which the learner engages with speakers of the language

Box 3. Grounding by correlation: mechanisms for concrete and abstract semantics

Both concrete and abstract words and constructions can be learnt when they are being used to speak about real-life events, actions, and objects or their features. A major difference lies in the variability of the sensorimotor patterns that foster semantic grounding, which is typically low for concrete and high for abstract symbols. This difference in correlation structure may yield different neuronal and cognitive mechanisms for concrete and abstract meaning.

Concrete semantics: The concrete word 'eye' is used to speak about objects with similar shapes and a range of colors. At the neurocognitive level, this leads to exemplar representations that strongly overlap in their sensorimotor semantic feature neurons, possibly dominated by a frequently processed prototype. The upper panel in Figure I schematically illustrates such sensorimotor semantic overlap (some of which may be carried by visual center-surround cells that respond to a circle in one color on a background of a different one) and feature neurons more specific to individual exemplars (e.g., to a specific color). In concrete semantic learning, neurons of the circuit overlap and frequently occurring prototypical exemplars strongly interlink with the word form circuit owing to the high correlation of their activations.

Abstract semantics: The instantiations of abstract words such as 'games' and 'beauty' are quite variable, exhibiting a 'family resemblance' pattern of partial semantic similarity [71]. The bottom panel in Figure I schematically shows the putative neural correlate of such family resemblance, where sensorimotor semantic feature neurons are only shared between subsets of exemplar representations of variable instantiations of the concept. The low correlation of activations of neuronal circuits for word forms and for each exemplar representation results in weak links between neural representations of sensorimotor knowledge (in modality-preferential areas) and those of verbal symbols (in perisylvian cortex). Abstract semantic connections can draw on partial-overlap feature neurons (as shown) and indirect connections by way of neurons in multimodal cortex that happen to link to several sensorimotor instantiations of an abstract meaning (not shown; [11,118]).

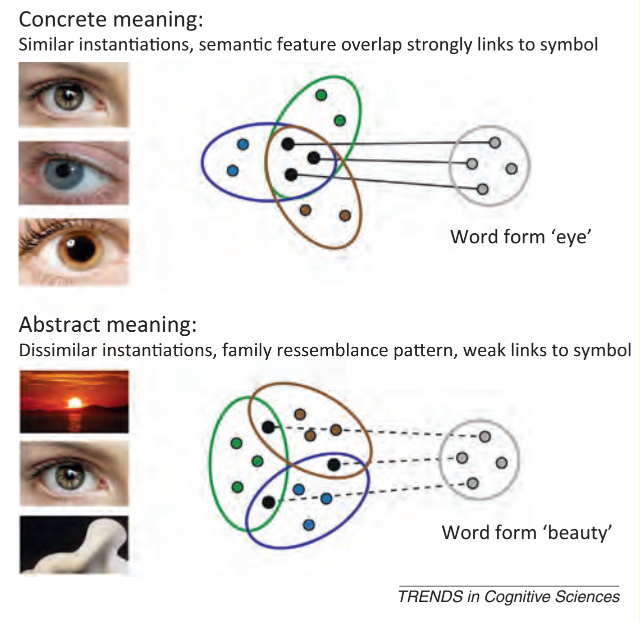

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Figure I. Sketch of putative neurobiological mechanisms for concrete and abstract meaning processing.

[71,72]. Therefore, the link between an abstract emotion word and its abstract concept is via manifestation of the latter in prototypical actions. The child learns an abstract emotion word such as 'joy' because it shows JOY-expressing action schemas, which language-teaching adults use as criteria for correct application of the abstract emotion word [71,72]. Thus, the manifestation of emotions in actions becomes the crucial link between word use and internal state, and hence between sign and meaning. Only after a stock of abstract emotion words has been grounded in emotion-expressing action can further emotion terms be learnt from context.

This proposal generates critical predictions testable in neuroscience experiments. In particular, over and above activating limbic emotion-related circuits, abstract emotion words should specifically excite the motor system that controls the face and arms, with which emotions are typically expressed. Motor system activation for emotion-expressing body parts was indeed found when adults passively processed abstract emotion words [73], suggesting that, for one important class of abstract concepts, semantic grounding in emotion-expressing action is of the essence and can, in part, explain the meaning–symbol link (Figure 3).

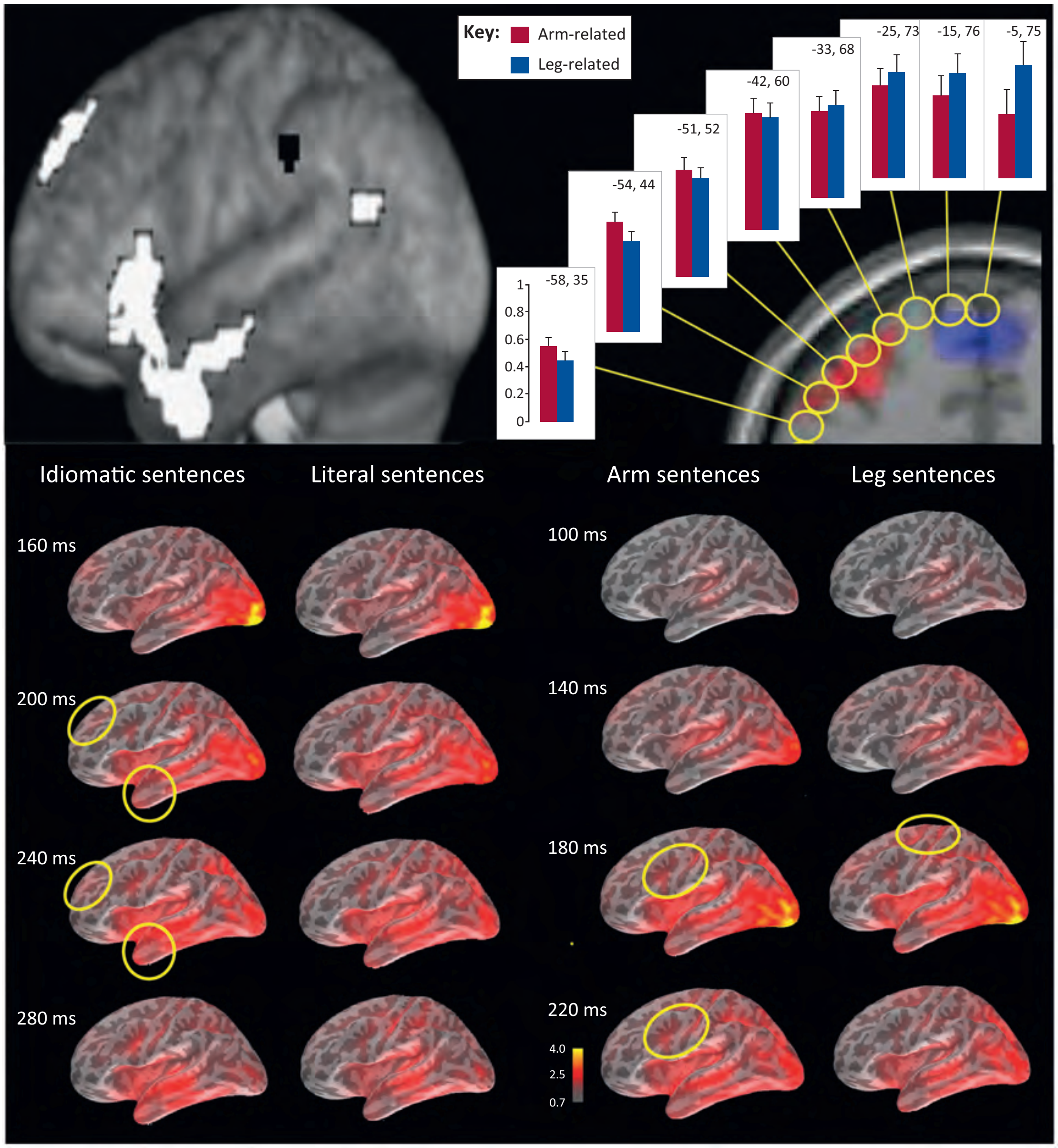

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Figure 4. Brain activation for idiomatic and literal sentences recorded using functional magnetic resonance imaging (top) and magnetoencephalography (bottom). Top left: comparison of brain activation elicited during idiomatic and literal sentence processing (white, idiomatic>literal; black, literal>idiomatic; reproduced, with permission, from [78]). Top right: activation for literal and idiomatic sentences that include arm- (red bars) and leg-related words (blue bars); the red and blue areas indicate where finger and foot movements elicited activity (reproduced, with permission, from [75]). Bottom left: activation time course for idiomatic and literal action sentences (arm and leg sentences collapsed). Bottom right: activation time course for arm and leg sentences (idiomatic and literal collapsed). Note that constructional idiomaticity and compositional action-relatedness effects were present simultaneously early on (150–200 ms), suggesting that action-embodied compositional and disembodied constructional semantic processes emerge instantaneously at the same time (reproduced, with permission, from [101]).

Variability and abstraction

As concrete words fall into different semantic classes, so may abstract words. Indeed, neuroimaging results suggest very different brain correlates for subtypes of abstract words and constructions [74,75]. A characteristic feature of some abstract utterances is the variability of entities they are typically used to speak about. For most words related to concrete objects, such as 'eye', the entities they are used to speak about may vary to a degree (in size, form, and color), but it is normally possible to identify a semantic schema that can be illustrated by a prototype, a typical best representative of the schema [76]; less typical variants may activate the schema representation less than the prototype itself [77]. For some terms, this model fails, because their meanings cannot be explained by a single prototype, but require several of them. Consider the case of the word 'game' [71,72,77], which can refer to diverse activities ranging from cooperative to competitive, from group to solitary, and from playful to more serious action. No single prototype can represent this space of action schemas, and although prototypical members may be similar (European and American football), others are very different (football and tetris). To capture such variable family resemblance, the semantic representations need to link up with variable action and perceptual schemas. At the neurobiological level, variability means low correlation between words and their possible semantic instantiations, implying that, although word meaning may originally be grounded in specific action and perception schemas, the semantic representation in a sense is detached from specific action-perception knowledge. This process of variability-related disembodiment, which is implied by correlation learning (note the 'out of sync, delink' rule), may be effective for many abstract words and concepts. Therefore, abstract words grounded in perceptual schemas (e.g., 'beauty') may detach from their perceptual schemas stored in posterior inferior temporal cortex, thus leaving relatively anterior temporal representations weakly linked to these concrete instantiations, whereas abstract action terms (e.g., 'free' and 'game') may show the same process of variability disembodiment in prefrontal and parietal areas adjacent to sensorimotor cortex. Weak links between neuronal representations of abstract terms and their multiple and variable sensorimotor instantiations may be a hallmark of abstract meaning and key to the retreat of abstract semantic circuits to multimodal prefrontal, parietal, and temporal convergence areas (Box 3).

Interplay between embodied and disembodied semantics

Acknowledgment of both grounded embodied and disembodied semantic mechanisms will mean that new experimental investigations of the interplay between both will be possible. A crucial question in the embodiment debate is whether one of these mechanisms drives the other and might therefore serve a primary role in semantic processing, whereas that of the other might be secondary and potentially under the control of the primary one. It has been discovered that abstract idiomatic sentences (e.g., 'Mary cooked her mother's goose') activate inferior and dorsolateral prefrontal and inferior parietal and anterior temporal areas more strongly than concrete idiomatic sentences do [75,78], consistent with disembodied semantic processes of abstract constructions (i.e., the entire idiomatic sentences) in these multimodal regions. By contrast, aspects of the embodied meaning of action words included in both idioms and literal sentences (e.g., 'cooked' in 'Mary cooked her mother's meal/goose' or 'ran' in 'Anna ran for exercise/president') was manifest in motor system activation [75]. Because such motor-system activation that reflects the meaning of constituent action words was present at the point in time at which idiomatic and literal sentence meaning were disambiguated, the data suggest a degree of semantic compositional processing of the action-embodied meaning of constituent words (i.e., of the embedded action words 'cook' and 'run') in idiomatic sentence comprehension. Crucially, precise mapping in time using magnetoencephalography (MEG) showed that the brain correlates of abstract idiomaticity and those of action-grounded constituent word meaning occurred at the same time, at 150–200 ms after onset of the critical, sentence-disambiguating words ('goose'/'meal' in the above examples, Figure 4). These results further confirm early semantic activations with the same latency in sensorimotor and multimodal cortices, and argue against the possibility that sensorimotor semantic activation might be an epiphenomenon, just following after, or spilling over from, semantic system activation elsewhere. If prefrontal and anterior temporal activations are interpreted as indexes of disembodied symbolic system activation, they are manifest together with embodied semantic activation of the action system. Furthermore, these results suggest that compositional semantic processing of action-related words (precentral

Box 4. Outstanding questions

General questions

- How many semantic mechanisms are there? Is it sufficient to distinguish modality-preferential referential, combinatorial, emotional, and variable-abstract semantic mechanisms?
- What roles do sensorimotor and multimodal association areas play in processing of meaning?
- To what degree is meaning learnt and generalized from experience or preprogrammed in the genetic code?

Specific questions

- Does semantic learning from experience and from context lead to different semantic representations in mind and brain?
- What is the activation time course for modality-preferential and multimodal regions in referential and abstract semantic processing?
- Is the influence that sensorimotor and language regions have on each other during semantic processing facilitatory or inhibitory? What factors determine the sign of the influence?
- To what degree do modality-preferential and multimodal brain systems contribute to early and late brain responses known to be related to processing of meaning (e.g., N160 and N400)?
- What types of abstract words and meanings can be distinguished according to neurocognitive criteria?
- Do subjects with a developmental deficit in motor function have problems in processing language that is semantically related to actions and to abstract emotions?
- When words are used to perform specific social communicative actions, how does the relevant knowledge about interaction structure and theory of mind become manifest in the brain?

cortex) and semantic processing of abstract idiomatic constructions as a whole (prefrontal and anterior temporal areas) simultaneously and jointly contribute to idiom comprehension.

Concluding remarks

Semantic processes draw on left-perisylvian language regions and include adjacent areas, multimodal hubs, and sensory, motor, and limbic areas of the human brain. Sensorimotor and limbic areas are essential for grounding language in action, perception, and emotion; the periphery of the perisylvian cortex engages in combinatorial semantics; and multimodal convergence zones in prefrontal, anterior temporal, and inferior parietal cortex are essential for processing of abstract meanings generalized over variable concrete instantiations. Thus, widespread cortical regions and cortico–cortical long-distance connections provide the machinery for holding together and integrating semantic representations and circuits. However, different areas make very specific contributions to meaning processing, as evidenced by area-specific signatures of category-specific impairments and activations. Future research may further scrutinize the differential contributions of cortical areas to semantic processing and especially their functional interplay in symbol and construction understanding (Box 4).

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