

# Brain reflections of words and their meaning

Friedemann Pulvermüller

The neurobiological organization of meaningful language units, morphemes and words, has been illuminated by recent metabolic and neurophysiological imaging studies. When humans process words from different categories, sets of cortical areas become active differentially. The meaning of a word, more precisely aspects of its reference, may be crucial for determining which set of cortical areas is involved in its processing. Word-related neuron webs with specific cortical distributions might underlie the observed category-specific differences in brain activity. Neuroscientific principles can explain these differential topographies.

A few neuroscientific principles grounded in brain research could be sufficient to explain aspects of the physiology of word processing. Box 1 outlines four principles thought to reflect important aspects of the structure and function of the human cerebral cortex. These principles motivate the view that cognitive processes are realized as the activity of distributed neuron ensembles that act as functional units, called 'functional webs' here. The putative properties of distributed functional webs representing and processing words and concepts of different kinds are discussed in the light of recent neurophysiological and metabolic imaging studies.

## Functional webs in the cortex

Donald Hebb pointed out that synchronously activated neurons should link into cell assemblies and that these might underlie all higher cognitive processes<sup>1</sup>. Hebb's proposal differs radically from earlier neuroscientific approaches to information processing in the brain, because he postulated that higher brain processes are realized as functional units above the level of the neuron. Earlier proposals had stated that either individual neurons<sup>2</sup> or mass activity and interference patterns in the entire cortex<sup>3</sup> are the basis of cognition.

Hebb's view, which might appear to be a compromise between these views<sup>4</sup>, fits well with the neuroscientific insights that the cortex is a network of neurons characterized by: (1) ordered input and output connections in modality-specific areas; (2) heavy information mixing through short- and long-distance cortico-cortical connections; and (3) correlation learning (Box 1). Object features, for example of the shape, smell, purr and smooth fur of a cat, relate to information from different modalities that is processed in distant cortical areas that are, however, linked through long-distance connections.

For such a network, the correlation learning principle implies the build-up of distributed object representations with neurons in all cortical areas where correlated activity occurs. A web of strongly connected neurons, each of them contributing to specific sensory and motor processes related to an object, may thus become the cortical representation of this object. Binding of the features of the cat-concept would be established by mutual links within a widely distributed 'functional web' characterized by a defined cortical distribution. Synaptic strengthening caused by correlation of neuronal activity – both between and within motor and sensory cortical areas – would thus be a major driving force of the formation of distributed functional webs.

## Evidence for distributed functional webs realizing active memory

Which critical predictions are implied by the idea of distributed functional webs? Lesion of a significant portion of the neurons of a functional web must impair its function. If the functional web is distributed over a set of cortical areas, substantial lesions everywhere within this set of areas should degrade the web's function. If the web is intact, its neurons in different areas should also share functional properties and should, for example, be activated by the same stimuli. Thus, if the functional web is distributed over frontal and temporal areas, neurons in both areas should (1) exhibit the same stimulus-specificity, and (2) show this only if the respective other area is intact.

These predictions have been tested in macaque monkeys using a memory paradigm where the animal has to keep in mind the shape or color of a stimulus and perform a concordant matching response after a delay of several seconds (delayed matching to sample task)<sup>5</sup>. Throughout the memory period, where the animal has to keep in memory, for example, that the stimulus shown was red, neurons fired at an enhanced level. Their firing was specific in the sense that they did not respond, or responded less, when a stimulus of another color had been shown. Neurons with this stimulus-specific response pattern were found in the prefrontal cortex and in the inferior temporal lobe. Temporary lesion by cooling of the neurons in one area led to loss of stimulus-specificity of the neurons in the respective other area. This is support for the notion of distributed functional webs, because neurons in both areas, temporal and frontal, (1) exhibited the same stimulus-specificity, and (2) showed this stimulus-specificity only if the respective other area was intact<sup>5,6</sup>.

## Functional cortical webs and their putative role in language processing

The cortex, a neuroanatomically defined associative memory obeying the correlation learning principle, allows for the formation of distributed functional webs. The postulate is that the mechanisms described

Friedemann Pulvermüller  
MRC Cognition and  
Brain Sciences Unit,  
15 Chaucer Road,  
Cambridge, UK CB2 2EF.  
e-mail:  
friedemann.pulvermuller  
@mrc-cbu.cam.ac.uk

## Box 1. Neuroscientific principles

Four principles established by neuroscientific research are outlined that may be relevant for explaining language and other cognitive mechanisms in the brain.

### I. Ordered afferent and efferent cortical projections

Most afferent fibers transmitting information from the sensory organs to the cortex reach primary sensory areas, including the visual (Brodmann area 17), auditory (area 41), and somatosensory (areas 1–3) cortex (Fig. 1a). Most efferent fibers through which the cortex controls muscle activity originate in the primary motor area (area 4). Each primary area is characterized by topographical order of projections. This means that adjacent sensory cells project to adjacent cortical neurons, and adjacent body muscles are controlled by adjacent neurons in the motor cortex. The somatotopy of the primary motor cortex<sup>a</sup> is illustrated in Fig. 1b.

### II. Information mixing in the cortex

Massive fiber tracts reciprocally connect many cortical areas, and calculations show that every cortical neuron is likely to be linked through a small number of synaptic steps to any other cortical cell<sup>b</sup>. Neuroanatomists have proposed that the cortex has the function of an information mixing device<sup>c</sup>, where information from different modalities is being merged and interacts. Cortical neurons with multimodal response properties<sup>d-f</sup> strongly support the idea that the cortex is an information mixing device allowing single neurons to represent and process merged information from various motor and sensory modalities.

Looking more closely at the neuroanatomical structure of the cortex, it becomes obvious that most primary cortical areas are not linked by strong direct connections<sup>g,h</sup>, the primary motor and sensory cortices (which are next-door neighbors) representing the only exception. Thus multimodal information mixing is not done by direct links between primary areas, but necessitates intermediate neuronal steps. The intervening neurons between sensory and motor neurons in the cortex allow for

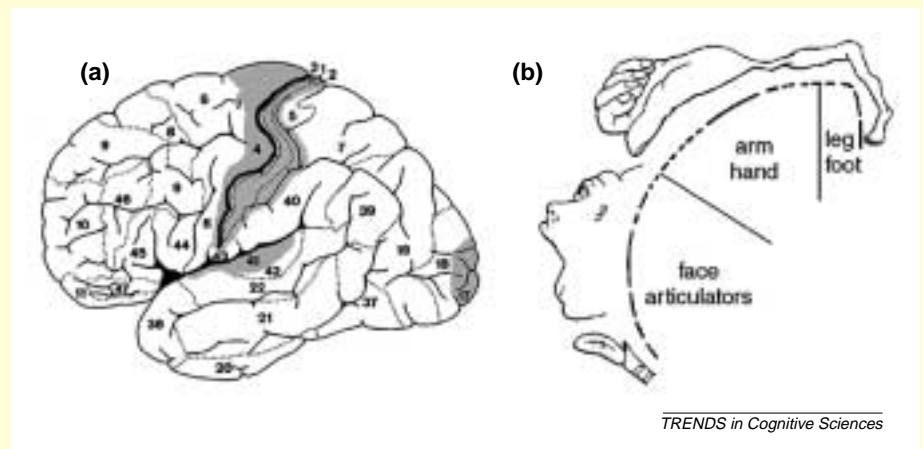


Fig. 1. (a) A lateral view of the human cortex with Brodmann's areas indicated. Primary motor and sensory areas relevant for language perception and production are shaded in gray. (b) The somatotopic organization of the primary motor cortex (area 4). (Adapted from Ref. a.)

complex reciprocal mappings of information patterns between modalities.

### III. Correlation learning

Donald Hebb postulated 'that any two cells or systems of cells that are repeatedly active at the same time will tend to become 'associated', so that activity in one facilitates activity in the other' (Ref. i, p. 70). This postulate receives strong support from intracortical neurophysiological recordings<sup>k</sup>. The correlation of neuronal firing of connected cortical cells is, so to speak, translated into their connection strength.

### IV. Functional laterality

Language laterality has been well-known since the first scientific investigations of language loss as a result of stroke<sup>l</sup>, but the causes of this laterality have not yet been revealed. Language laterality was also reflected in brain physiology revealed by modern neuroimaging techniques<sup>m-o</sup>.

Language laterality can be graded, that is, signs of activity usually appear in both hemispheres and the left dominant hemisphere is more active than the right<sup>p</sup>. The neuronal mechanisms underlying lateralized cortical processes (language, but also face perception, hand preference etc.) is still not sufficiently understood. It is necessary to attempt at grounding the laterality principle in more fundamental neuroscientific knowledge<sup>p</sup>.

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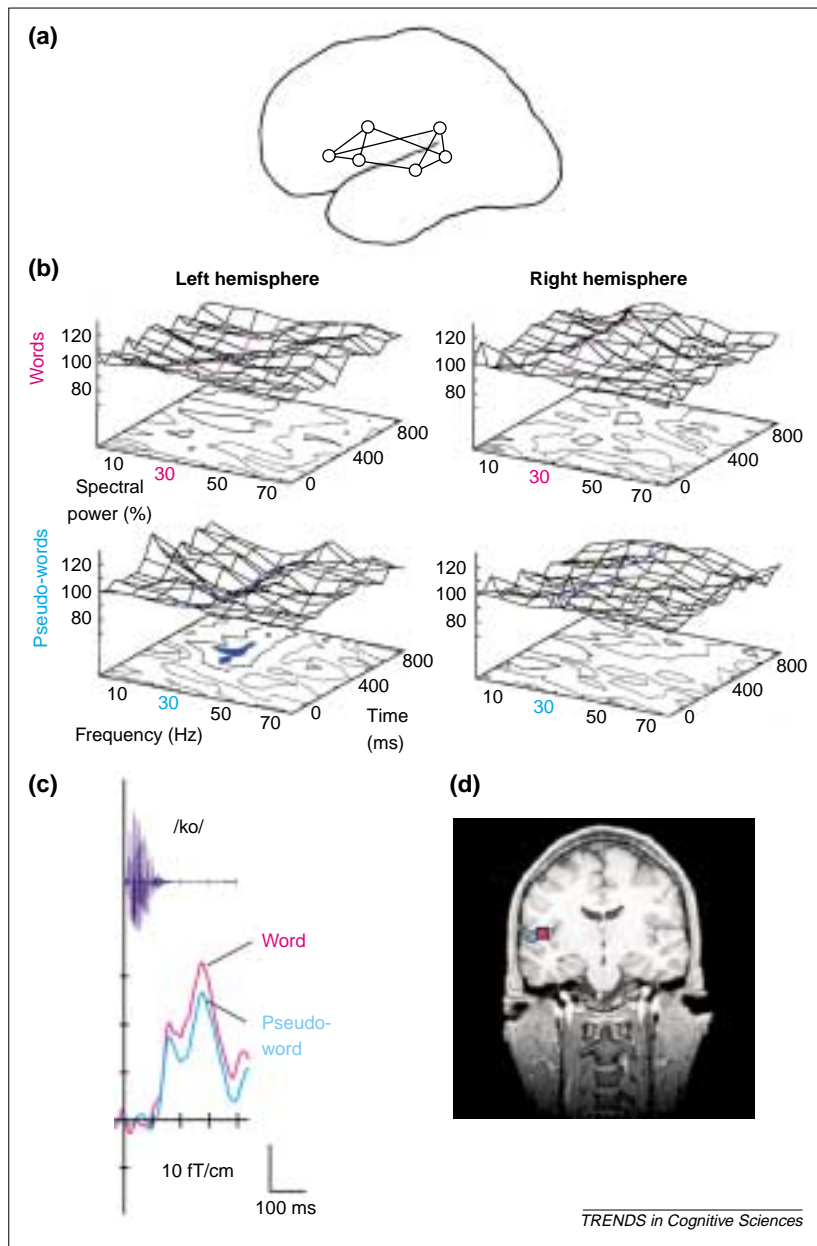


Fig. 1. (a) The functional webs realizing phonological word forms might be distributed over the perisylvian areas of the dominant left hemisphere. Circles represent local neuron clusters and lines represent reciprocal connections between them. (b) Recordings from the left hemisphere induced stronger gamma-band responses in the 30 Hz range to word presentation (red line, graph at upper left) than to pseudoword presentation (blue line, graph at lower left). Reverberatory circuits within word webs could underlie the enhancement of high-frequency responses to words compared with pseudowords. (c) The magnetic correlate of the Mismatch Negativity, the MMNm, was stronger in response to words compared with pseudowords. Significant differences appeared already around 150 ms after the word recognition point, suggesting that the activation of word-related functional webs (lexical access) is an early process. (d) The main generator of the word-evoked magnetic mismatch response was localized in the left superior temporal lobe. (Adapted from Refs 14, 27)

by principles I to IV (Box 1) yield functional webs representing language in the cortex, in particular networks linking phonological and phonetic information related to the articulatory and acoustic pattern of a word form, and word webs storing form-meaning contingencies. Each type of functional web can be characterized by a specific cortical distribution, cognitive function, and kind of information it processes and stores<sup>7</sup>.

### Evidence for word webs

Early babbling and word production require neuronal activity in cortical areas controlling face and articulator movements and actions; these areas are in the inferior motor cortex and adjacent inferior prefrontal areas. The articulations cause sounds and these activate neurons in the auditory system, including areas in the superior temporal lobe. Strong fiber bundles between inferior frontal and superior temporal areas provide the substrate for associative learning between neurons controlling specific speech motor programs and neurons in the auditory cortical system stimulated by the self-produced language sounds. The correlation learning principle implies the formation of such specific associations resulting in functional webs distributed over the perisylvian cortex – which includes the inferior-frontal and superior-temporal core language areas (Fig. 1a).

As detailed in Box 1, a laterality principle can be postulated that summarizes the well-established fact of the laterality of language mechanisms, which implies that the distributed functional webs realizing word forms include more neurons in the dominant than in the non-dominant hemisphere (although comprising neurons in both hemispheres)<sup>8</sup>. The lateralized perisylvian neuron ensembles would later provide the machinery necessary for activating a word's articulatory program as a consequence of acoustic stimulation with the same word form, a feature necessary for the ability to repeat words spoken by others. The emergence of this ability should therefore coincide with that of language-specific cortical memory traces for phonemes, syllables, and word forms. Babbling, the infant's earliest language-like behavior, starts around the sixth month of life. Interestingly, the development of electrophysiological indicators of memory traces for phonemes<sup>9,10</sup>, follows in the subsequent months of life, together with that of the infant's ability to repeat words and syllables spoken by others<sup>11</sup>.

Massive reverberatory circuits making up functional webs representing objects and words may produce precisely timed high-frequency rhythms when active<sup>12,13</sup>. A critical prediction would therefore be that word stimuli activate the corresponding functional webs thereby eliciting strong high-frequency rhythms. By contrast, phonologically and orthographically regular pseudowords that are not part of the language would fail to activate a word-related functional web, and the high-frequency activity in the perisylvian areas should therefore be relatively low.

This prediction was put to a test using magnetoencephalography (MEG). Recordings from the perisylvian language areas in the left (but not right) hemisphere revealed significant differences between acoustically presented words and pseudowords in a frequency band around 30 Hz (Ref. 14). Word-induced high-frequency responses were stronger than pseudoword-induced activity

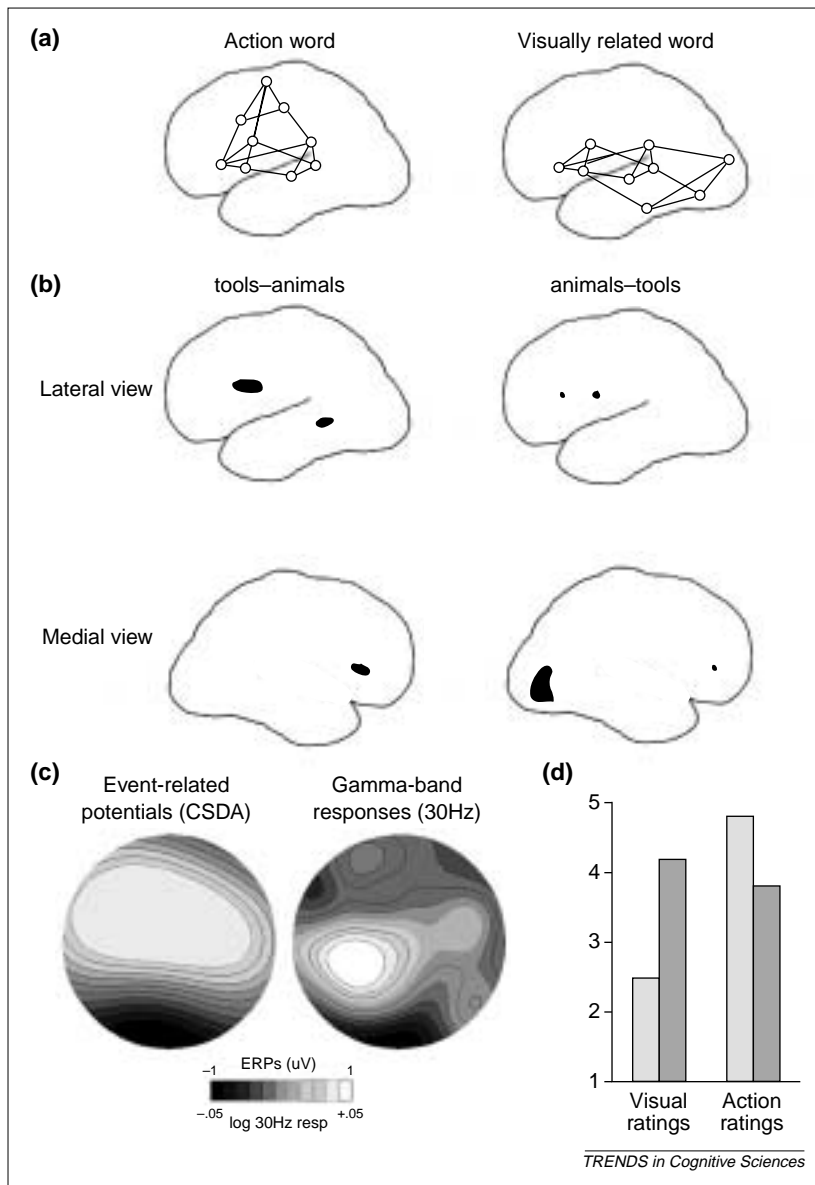


Fig. 2. (a) Action and visual associations of words might be mapped by functional webs extending over perisylvian language areas and additional action- and visually-related areas in the temporo-occipital and fronto-central areas. The cortical topography of functional webs representing words primarily characterized by visual associations might therefore differ from those of words with strong action associations. (b) Differences in metabolic brain activation related to the processing of nouns referring to animals and tools in a naming task. Whereas tool naming more strongly activated a premotor region and an area in the middle temporal gyrus (left), animal naming most strongly activated occipital areas (right). (c) Electrophysiological differences between nouns and verbs in a lexical decision task recorded at central (close to motor cortex) and posterior (above visual cortex) recording sites. Gamma-band responses in the 30 Hz-range were stronger close to the motor cortex for action verbs, but greater above visual areas for nouns with strong visual associations. A similar difference was revealed by Current Source Density Analysis (CSDA) performed on event-related potentials. (d) Behavioral experiments showed that the stimulus nouns (dark bars) elicited strong visual associations whereas the verbs (lighter bars) were primarily action-related. (Adapted from Refs. 34, 44.)

(Fig. 1 b)<sup>14–18</sup>. The word-related enhancement of high-frequency responses in the gamma band (> 20 Hz) may indicate the activation of word webs with multiple reverberatory circuits that fail to become fully active if pseudowords are perceived<sup>12,13</sup>, an assumption consistent with neurocomputational models of cell assemblies in the brain<sup>19</sup>.

Neurophysiological and metabolic imaging studies have also revealed physiological word-pseudoword

differences<sup>20–23</sup>. Event-related potential (ERP) studies revealed such differences as early as 100–200 ms after stimulus onset<sup>20</sup> and therefore substantially earlier than the differential high-frequency responses in the gamma-band. Recently, the Mismatch Negativity, MMN, and its magnetic equivalent called MMNm, well-known indicators of the presence of experience-dependent cortical memory traces for acoustic stimuli<sup>24,25</sup>, were used to investigate word processing. MMN and MMNm were both found to be larger in response to spoken words than in response to pseudowords<sup>26,27</sup>.

When a critical syllable completed a word, the MMN(m) it elicited was larger than it was when the same syllable occurred in a pseudoword context (Fig. 1c). The difference was found to be largest 100–200 ms after a word's recognition point<sup>27</sup>, the earliest point in time when subjects reliably recognize an acoustic input as a specific word<sup>28</sup>. It thus appears that the brain distinguishes a word from a pseudoword early after the information necessary for identifying the word is presented in the input. The main cortical generator of the word-induced MMNm was localized in the left superior temporal lobe (Fig. 1d). This source was stronger for words than pseudowords. There was no evidence that its locus changed with lexical status<sup>27</sup>.

The early enhancement of the MMN(m) to words was seen although participants in the experiment were instructed to direct their attention away from the acoustic input and watch a silent movie. Together with results from metabolic imaging studies<sup>29</sup>, this physiological distinction of words and pseudowords indicates that focussed attention to words is not necessary for activating their cortical memory traces<sup>26,27</sup>.

In summary, physiological studies are consistent with word representations in the brain that are activated early and regardless of whether subjects focus their attention on the stimuli or not<sup>25</sup>. The late word-related enhancement of high-frequency responses is consistent with coordinated fast reverberatory neuronal activity generated by functional webs, a putative correlate of active memory<sup>6</sup>.

#### Referential semantics and the cortical distribution of word webs

The correlation learning principle and the long-range cortical connections between motor and sensory systems imply that word-use in the context of objects and actions leads to associations between neurons in the cortical core language areas and additional neurons in areas processing information about word-related objects and actions. Functional webs representing words and aspects of their meaning, called 'word webs' here, would therefore provide the basis for the association, in the psychological sense, between an animal name and the visual image it relates to, or between an action verb and the action it normally expresses.

Word webs would include neurons in perisylvian areas storing word form information and, in addition, neurons in more widespread cortical areas critically involved in processing information about perceptions and actions. The sensory/action modalities through which the referent of a word is known appear to be relevant. Fig. 2a sketches the postulated neuronal architectures of functional webs representing words with strong visual versus action associations, respectively. These diagrams might suggest the existence of words with either visual or action associations only. In fact, most, if not all, concrete words elicit both visual and action associations, but frequently with gradual differences; for example, strong visual associations but only weak associations to actions. Correspondingly, the density of neurons in visual and action-related areas should gradually differ between a primarily action-related word and a primarily visually-related one. The postulated differential topographies of word webs imply meaning-related processing differences between word categories.

A major source of evidence for such differences are neuropsychological patient studies where, for example, the production or comprehension of nouns and verbs, or animal and tool names, was found to be differentially affected by disease of the brain<sup>30–32</sup>. These dissociations between kinds of words and conceptual categories can be understood on the basis of the assumption of distributed neuron ensembles reflecting *perceptual* attributes, including visual features and the degree of overlap between exemplars, and the *functional* attributes, the actions to which the words and concepts relate<sup>30–33</sup>.

It can also be asked whether the intact brain demonstrates differential activation of brain areas when action- or perception-related words are being processed. Category-specific activation was found in the premotor cortex and the middle temporal gyrus when tools had to be silently named, and in the occipital and inferior temporal lobe when animals had to be named<sup>34</sup> (Fig. 2b). The premotor activation may be related to action associations of tool names, as the activation in inferior-temporal and occipital areas may be related to visual attributes of animal names. The additional activity in the middle temporal gyrus in tool naming may be related to movement perceptions characterizing the tools and the actions typically performed with them. These results were confirmed, in part, by other metabolic imaging studies of category-specific processes<sup>35–38</sup>.

Neurophysiological investigations of noun and verb processing provided further evidence for category-specific brain processes relevant for language<sup>39–44</sup>. In one of these studies, differential visual and action associations of stimulus nouns and verbs were demonstrated by a rating study performed by all participants in the experiment<sup>44</sup> (Fig. 2d). Event-related potentials (ERPs) and high-frequency cortical responses revealed a physiological double

dissociation consistent with differential activation of fronto-central action-related areas and occipital visual areas (Fig. 2c).

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## 'Information about the body parts with which actions are being carried out may be woven into the word-related cortical networks.'

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The physiological distinction between visually-related nouns and action verbs could be replicated by EEG studies of visual and auditory word processing, and differential activation similar to that of the noun-verb comparison was also found between visually-related and action-related nouns<sup>45,46</sup>. In contrast, action verbs and nouns with strong action associations did not yield significantly different brain responses<sup>45</sup>. Furthermore, nouns with both strong visual and action associations elicited greater magnetic brain responses than either visually-related nouns or action verbs<sup>47</sup>. These results indicate that the differential activity pattern is not grammatically-related (noun versus verb), but rather reflects semantic properties of the stimulus words. As the topographical differences of activity patterns evoked by action-related and visually-related words resembled those observed between the corresponding pictures<sup>46</sup>, the results are consistent with the view that words and the concepts relating to their meaning are processed by largely overlapping, or even identical, cortical webs<sup>48</sup>.

### Brain physiology and the referential meaning of action verbs: walking versus talking

More fine-grained predictions are possible on the basis of the postulate that topographies of word webs reflect aspects of the words' referential meaning. Action verbs can refer to actions performed with the legs (walking), arms (waving), or mouth (talking). The motor cortex is organized somatotopically, that is, adjacent body muscles are represented in neighboring areas within the motor cortex (see Box 1, Fig. 1)<sup>49</sup>. The correlation learning principle therefore predicts differential topographies for cell assemblies organizing leg-, arm- and face-related words (Fig. 3a). Differential action-related associations of sub-categories of verbs could be demonstrated by behavioral studies (Fig. 3b).

In an EEG study using 64 recording electrodes, we compared face- and leg-related action verbs ('walking' versus 'talking'). Current source density maps revealed differential activation along the motor strip. Words of the 'walking' type evoked stronger in-going currents at dorsal sites, over the cortical leg-area, whereas those of the 'talking' type elicited the stronger currents at inferior sites, next to the motor representation of the face and articulators<sup>50</sup> (Fig. 3c). A similar study comparing arm- and leg-related

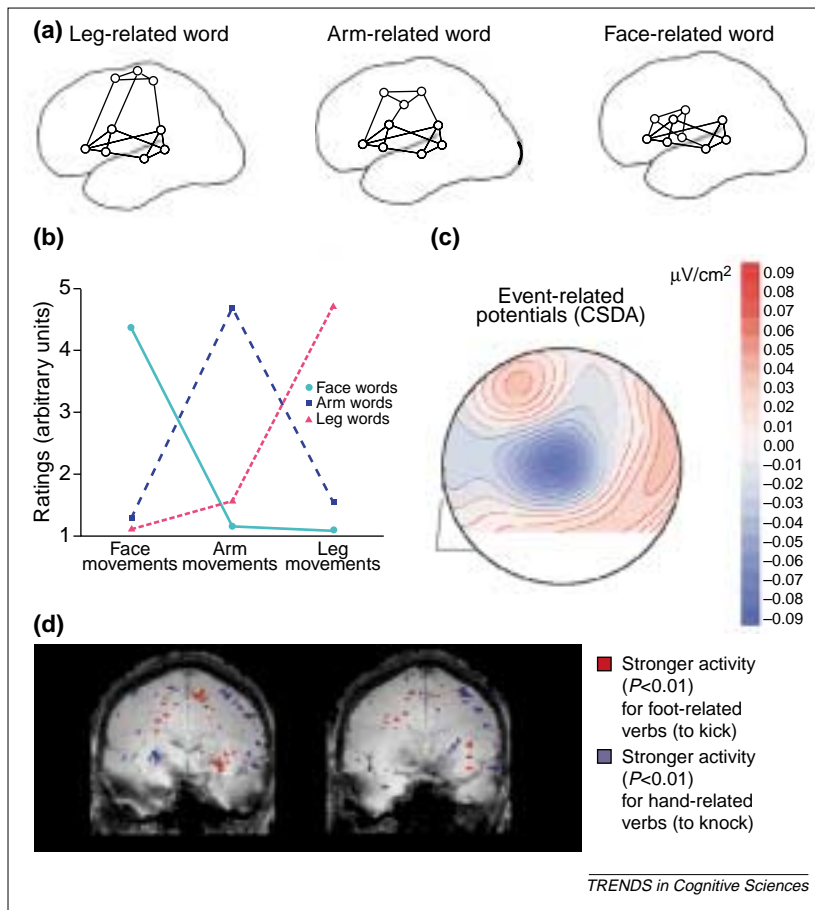


Fig. 3. (a) Cortical topographies of functional webs representing different types of action verbs might differ. Action words can refer to actions executed by contracting face, arm or leg muscles (*to lick, to pick, to kick*). Different neuron ensembles in the primary and higher-order motor cortex might therefore be woven into the word-related neuron ensembles. (b) Ratings of face-, arm-, and leg-associations confirming differential referential semantics of three action-verb groups. (c) Results from an EEG study. Topographical differences between brain responses to face- and leg-related verbs are shown in a view of the left side of the head (the triangle at lower left indicates the nose). Stronger in-going currents were seen close to the vertex for leg-related items (red spot at the top) and at left-lateral sites, close to the face representation, for face-related words (blue spot). (d) Result from an fMRI study comparing arm- and leg-related verbs (single subject data). Differences were seen in the left hemisphere. Blue pixels indicate stronger activation for arm-words and red pixels indicate stronger activation for leg-words. Note the accumulation of blue pixels in a lateral area and that of red pixels in a medial area. (Adapted from Refs. 50,51.)

words was performed using fMRI. The data shown in Fig. 3d are again consistent with the view that the body parts involved in the actions action verbs refer to are reflected in the cortical neuron webs these words activate. Information about the body parts with which actions are being carried out may be woven into the word-related cortical networks<sup>51</sup>.

#### Time course of lexical and semantic activation

Semantic aspects, in particular the cortical areas typically involved in processing information about word referents, appear to crucially determine brain responses to words. The differences between semantic word categories can appear early in the neurophysiological brain response (100–200 ms after stimulus onset)<sup>47,52</sup>, as early as the first differences related to lexical status (words versus non-words)<sup>20,27</sup>. Because differences related to lexical and semantic status appeared in the same time range, the

neurophysiological data support models proposing that information about a word's meaning can be accessed near-simultaneously with information about its form, a conclusion proposed earlier on the basis of behavioral studies<sup>28</sup>.

Whereas the semantic and form-related parts of distributed word webs are activated near-simultaneously, there is evidence that different physiological processes appear in sequence in the same cognitive neuronal representations. A stage of access to the representation reflected in early event-related potentials (word recognition; latency 100–250 ms), might be followed by sustained reverberatory activity of the word web, which is reflected in high-frequency responses in the gamma band (active memory for words; > 250 ms)<sup>44,53</sup>. This suggests that lexical and semantic brain processes occur near-simultaneously, but that lexico-semantic activation has two distinct steps: access or ignition, followed by active memory or reverberation.

#### Conclusion

Four neuroscientific principles – ordered projections, information mixing, correlation learning, and functional laterality (Box 1) account for the main findings summarized here, namely: (1) differential neurophysiological responses to words and pseudowords; (2) differential topographies of brain responses to action- and visually-related words; and (3) differential topographies of brain responses to action verbs related to different body parts. Still, these neuroscientific principles do not explain the entire range of brain regions found to be active during category-specific processing. For example, the differential activation of left- and right-hemispheric parietal areas by names of body parts and numerals<sup>54</sup>, cannot be explained by the four principles alone.

It is likely that additional as yet not fully understood principles of cortical function are relevant for accounting for these data. Furthermore, the semantic category of the stimulus words is clearly not the only variable determining the topography of brain activation, but modality of stimulation (visual or auditory, words or pictures) and task context (lexical decision, reading, naming, etc.) are also relevant<sup>35,55</sup>. The present approach implies, and the summarized data indicate, that sometimes fine-grained category-specific differences are present between word and conceptual kinds across tasks and stimulus modalities<sup>45,46</sup>.

The present neurocognitive model of word processing takes into account the cortical areas where information from different modalities (e.g. action versus vision) is being processed. It has been argued that, apart from the involvement of different semantic systems, action- and visually-related words and concepts, for example animals and tools, can be distinguished on the basis of their conceptual structure. For example, some visual features are shared between numerous animals, whereas there is less overlap and inter-correlation between features of tools.

## Questions for future research

### Location (*Where* questions)

- Can the differential activation of focal frontal and temporal areas by words of different semantic categories (e.g. action-/perception-related; foot- and mouth-related) be confirmed. What is the full list of semantic categories that differentially activate brain areas?
- What is the role of the primary sensory and motor cortices in word-category-specific processing?
- Does the right hemisphere not dominant for language participate in word-category-specific processing, is it necessary for it, and which role does it play?

### Timing (*When* questions)

- Does the brain distinguish between semantic word kinds ~100–200 ms after word-specific information becomes available in the input?
- What is the temporal relationship between lexical access – as reflected in the neurophysiological difference between words and pseudowords – and specific semantic processes – as reflected in the neurophysiological distinction of semantic word categories? Do these processes occur in sequence or in parallel?

- What is the exact difference of the onset of brain indicators of lexical and semantic processing?
- Can physiological signs of cortical activation reveal information about the point in time of the recognition of individual words?

### Mechanism (*How* questions)

- Can the concept of functional webs, (a) which are distributed over defined cortical areas, (b) whose component neurons show similar response properties, (c) whose component neurons are mutually functionally dependent, be further established by neuroscientific research?
- Are words processed by functional webs that store information about word forms along with information about word semantics?
- How is serial order being established in a network composed of functional webs?

### Explanation (*Why* questions)

- Which aspects of word processing in the brain can, and which cannot, be explained on the basis of principles (I)–(IV) in Box 1?
- Which additional principles of neuronal architecture and functioning are relevant for an explanatory theory of language mechanisms in the human brain?

In line with the correlation-learning principle, the inter-correlation of semantic features of concepts may be one factor contributing to neuropsychological dissociations between word and conceptual categories<sup>32,56</sup>. Some colleagues<sup>57,58</sup> have argued that a single semantic system – without separate topographically ordered compartments devoted to action- and perception-related information – is sufficient for modeling category-specific processes on the basis of the inter-correlation of features (but see Ref. 59). However, it is difficult to see how a single-system approach can explain the results of neurophysiological and metabolic imaging studies summarized here, in particular the differential

activation of frontal and temporo-occipital areas by visually and action-related word and picture stimuli, and of fronto-central cortex during the processing of different kinds of action verbs.

A multiple semantic systems account formulated in terms of distributed functional webs with defined cortical topographies explains these data. In this framework, the correlation of neuronal activity related to semantic features, within and between modalities, is but one crucial factor explaining category-specific brain mechanisms, and the contribution of information laid down in the genetic code<sup>60</sup> – determining, for example, the order of cortical projections – is also acknowledged.

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