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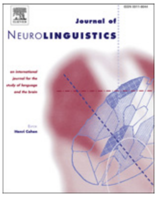

Meaning and the brain: The neurosemantics of referential, interactive, and combinatorial knowledge

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ABSTRACT

Which types of nerve cell circuits enable humans to use and understand meaningful signs and words? Philosophers were the first to point out that the arbitrary links between signs and their meanings differ fundamentally between semantic word types. Neuroscience provided evidence that semantic kinds do indeed matter: Brain diseases affect specific semantic categories and leave others relatively intact. Patterns of precisely timed brain activation in specific areas of cortex reflect the comprehension of words with specific semantic features. The classic referential link between words and the objects they are used to speak about can be understood as a result of associative learning driven by correlated neuronal activity in perisylvian language areas and sensory, especially higher visual but also olfactory, somatosensory and auditory, areas. However, the meaning of words used to speak about actions calls for a different account. *For learning their meaning, specific action and interaction contexts are critical, and neuronal links between language and action systems of the human brain likely store such action-semantic information*. In fact, after learning, the action system is sparked when such words and utterances are being used or understood, and, correspondingly, functional changes in the brain's motor system influence the recognition of action-related expressions. These results show that language is "woven into action" at the level of the brain. *Word-object, word–action and word-word contexts are discussed in view of further facets of semantics* and their brain basis, including emotional-affective, abstract and combinatorial aspects of

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meaning. All of these aspects and corresponding neuronal circuit types interact in the processing of the meaning of words and sentences in the human mind and brain.

1. Introduction

Semantic theory and neuroscience can mutually benefit each other. The aim of this paper is to show that semantic theories, theories about the nature of word meaning, were essential for progress in the cognitive neurosciences. It will also be asked whether neuroscience theory and data might be relevant for semantic theory.

1.1. Overview

This paper first presents an outline of classic approaches to semantics, with an emphasis on fundamental differences between meaning types (Section 2). I will then switch to brain science, laying out neuroscience principles for a brain-based theory of language along with their implications for the brain mechanisms for word forms in the human brain (Sections 3, 4). This will be complemented with some empirical support and an extension addressing words with affective and emotional function (Section 5). The focus will then be on the question of meaning in the human brain, arguing that much current research in neuroscience on this topic is guided by very specific types of meaning, and that a more accurate perspective on the nature of meaning makes different types of predictions (Sections 6). A model of category-specific semantic circuits of nerve cells will be presented, taking into account the many-many relationship between semantic kinds and brain loci revealed by neuroimaging and neuropsychological research (Sections 7, 8). The underlying principal idea is that semantic action and object relationship of signs are brain-grounded in the action and perception circuits of the brain that also underpin the execution of relevant actions and perception of referent objects. To what degree these action-perception circuits are essential for semantic processing will be in the focus of further discussion (Section 9). The brain basis of referential, action-related and emotional meaning will be contrasted with that of abstract semantic processing (Section 10) and mechanisms for storing and processing combinatorial semantic information (Section 11). Object- and action-related meaning along with combinatorial semantic knowledge are interpreted as the consequences of established neuroscience principles, of correlation learning – between words and the world, between words and aspects of actions and interactions, and, similarly, between words and other words – in a pre-structured network whose anatomical properties co-determine the learning.

1.2. Cognitive-semantic questions, conceptual issues

When discussing the brain basis of semantics, a range of semantic questions will be addressed. Here is a (non-complete) selection: Can word meaning be defined in terms of contextual relationships between words or is some additional grounding necessary, whereby word meaning is directly linked to information about objects and actions the words are typically used to speak about? Is the semantic system a unitary entity employing the same type of linking mechanism to yield abstract and concrete symbol meaning relationships? Is it necessary to divide up the symbol inventories of languages according to categories of meaning and, if so, what are the principles determining the division criteria? Which examples of semantic “kinds of words” and “vocabulary types” can be distinguished and supported by neuroscience evidence? Are semantic distinctions inborn or do they rather emerge naturally as a consequence of perceptual differences and action types? Are semantic and symbol processing systems modular, so that each of them computes an output without being influenced by the other; or are linguistic and semantic systems rather tightly interwoven and interdependent functionally? When looking at brain activation patterns, some of these questions find a straightforward answer or appear in a new light.

A conceptual issue arises when speaking about the brain basis of language and therefore of communicative actions. We are being made responsible for our own actions, implying some freedom of choice, whereas the brain is a machine governed by the laws of nature. This creates conceptual tension. The solution here is to consider specific brain circuits as necessary for relevant linguistic actions and linguistic actions to be accompanied by, or manifest in, specific brain processes, without touching upon the issue of causation. If a neuronal activity in a specific part of the brain is necessary for an action and its activation typically accompanies that action – as it is the case, for example, for a certain part of the motor cortex and movements of the index finger – the neuronal activity (or the nerve cell circuit carrying it) will occasionally be said to "represent" the action. This use of the word "represent" therefore abbreviates for "is necessary for and accompanies", thus avoiding mereological fallacies such as the implication that the brain (rather than the individual) performs the action (for discussion of this important issue, see Baker & Hacker, 2009; Bennett & Hacker, 2003).

2. Meanings of "meaning"

What is meaning? The answer to this question determines not only the target of semantic theory but, in the very same way, the study object of one of the most exciting domains in the cognition and brain sciences.

An early answer to the ultimate question of meaning was suggested by St. Augustine in his *Confesiones*, where he described word learning when parents point out objects while using their names (Augustine, 1992). In this context, words are used to speak about objects, an idea which later-on sparked a range of theories of referential meaning (Alston, 1969; Frege, 1980; Locke, 1909/1847; Quine, 1960). The simple equation "meaning $=$ object reference" was criticised, for example by Frege, who pointed out semantic differences between utterances that share their referent object (Frege, 1980). As "morning" and "evening star", which both refer to the same object, the Venus, are not equivalent semantically, object reference does not capture some relevant aspect of meaning (or "sense"). An even more fundamental critique of the "meaning $=$ object" equation was presented by the late Wittgenstein, who pointed out that Augustine's perspective on meaning might work to some degree for certain nouns, such as "table", "chair" and proper names, but would fail for other "kinds of words" (Wittgenstein, 1953). Among the kinds of words he mentioned are action verbs, adjectives referring to object properties, words that relate to feelings or so-called "inner states", other abstract words including logical particles, modal verbs and further semantically highly complex items.

Wittgenstein's notion of "word kinds" with fundamentally different semantics is at the heart of the idea that there are different kinds of meaning and, correspondingly, different conceptual kinds, which draw on different parts of the brain, This latter idea inspired and propelled an enormous research effort in both modern neuropsychology (Gainotti, 2006) and human cognitive neuroscience (Martin, 2007; Pulvermüller & Fadiga, 2010). Later sections of this paper will highlight this research (Sections 6–10).

How might the meaning of other "kinds of words" be conceived? Wittgenstein complemented the classic paradigm of learning meaning in the object context with other word learning paradigms, for example a paradigm of language-action learning: As a feeling, emotion or other so-called "inner state" of the body is not overtly accessible, it cannot be labelled by a name in a similar manner as it is possible for an object. Wittgenstein's solution is that the "inner state" is naturally expressed by complex behaviours, the overt actions having the status of criteria for the presence of the "inner" state, the sensation or emotion. In this context, meaning learning is conceived as the linking of new language signs to an already available action repertoire expressing the "inner" state or emotion. "The child has hurt himself and cries; and then adults speak to him and teach him exclamations and, later, sentences. They teach the child new pain behaviour" (§ 244, Wittgenstein, 1953). *In this case, a link is established between a non-linguistic action scheme, expressing an "internal" state or emotion, and the utterance of a sign, whose meaning is therefore being connected to the feeling and emotion. Such signs then allow for communicating feelings, thus transforming the "internal" states into the public realm via language.*

This type of semantic learning applies to symbol types for which movement, behaviour, and the *individual's actions and interactions with others* are important semantically and serve as criteria for appropriate application of the sign (for further explanation, see Baker & Hacker, 2009). Such symbols are part of spoken and written language and of gesture and sign systems too. In contrast to the classic model, where language signs are linked to objects, this new view draws attention to the links between signs and actions. *The meaning of a sign is intrinsically based on its use and the role it plays in action contexts, in "language games", in which sign usage and other (also non-linguistic) actions, along with relevant objects of these actions, are embedded and relevant for semantics.* In this sense, language is, according to Wittgenstein, "woven into action" (§ 7, Wittgenstein, 1953). *The general argument that action-linkage is of semantic relevance applies to a range of very different word types, including items used to speak about emotions, actions, mental states, and abstract ideas.*[1]

Since Wittgenstein, semantic theories have developed further the concept of meaning as word usage. Accordingly, the meaning and pragmatic function of a symbol or utterance is defined as its use in specific action contexts and sequences, when given constellations of shared knowledge apply and specific communicative intentions guide the interaction (Alston, 1969; Baker & Hacker, 2009; Ehlich, 1991; Fritz & Gloning, 1992; Pickering & Garrod, 2004; Sacks, 1995; Tomasello, 2005).

3. Neuroscience principle and insights relevant for language theory

Neuroscience research has revealed a range of by now well known insights and general principles relevant for a theory of language at the level of cortical circuits and, more specifically, a neuronal model of word meaning. These insights and principles concern the structure and function of the brain and are therefore anatomical and physiological in nature.

Information processing in the brain[2] is carried by nerve cells or neurons that send signals, action potentials, in a binary fashion – by way of sometimes long processes called axons – to adjacent neurons and even distant ones in other areas of the brain. Whether or not they fire a signal, called an action potential, depends on whether the amount of stimulation they receive from other neurons reaches a critical activation threshold. Already the single nerve cell may therefore be considered a discrete unit which is either active or inactive.

An important physiological principle is that of *correlation learning*. As hypothesized by Donald Hebb and many before him, neurons that fire together for a while strengthen their mutual connections and therefore become more tightly associated, a process called long term potentiation today (Artola & Singer, 1993; Hebb, 1949; Tsumoto, 1992). However, the fire-together-wire-together rule is not the only brain principle of learning at the level of plasticity of the synapses, the contacts between nerve cells. If neurons fire alternatingly so that one is unusually silent when the other is active, their mutual connections weaken; this process is called long term depression (Artola & Singer, 1993; Tsumoto, 1992). Together, long-term potentiation and depression imply that the correlation of activation of nerve cells is mapped onto their connection strength. The fine-grained timing of the firing of neurons can also influence synaptic learning, so that synaptic plasticity becomes spike-time dependent (Bi, 2002). Rapid learning, as it is required to explain language acquisition, for example when infants pick up new words within minutes, suggests correspondingly rapid synaptic learning, which has also been documented experimentally (Reynolds, Hyland, & Wickens, 2001; Shtyrov, Kujala, & Pulvermüller, 2010; Wickens, Reynolds, & Hyland, 2003). The mapping of correlated activation onto the strength of neuronal links during wakefulness is complemented by reactivation mechanisms during sleep leading to memory consolidation (Davis, Di Betta, Macdonald, & Gaskell, 2009; Davis & Gaskell, 2009; Dumay & Gaskell, 2007; Huber, Ghilardi, Massimini, & Tononi, 2004; Wilson & McNaughton, 1994). In sum, a range of neurobiological learning mechanisms are available for storing dynamic activation patterns by strengthening synaptic links between nerve cells.

Linguistic and semantic-conceptual processes are frequently modelled using learning principles similar to those of synaptic plasticity, but implementing them in networks with little if any resemblance to the neuronal structures relevant for language. The brain structure most relevant for language is the cortex, which includes a few tens of billions of neurons divided up into areas with

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[1] Wittgenstein has argued that, in order to establish the referential semantic link between nouns and objects, specific action contexts (for example the language game of naming) relevant (not necessary).

[2] If a nerve cell responds to a given input (for example a straight black line being shown to the individual), but remains silent when such a stimulus is absent, the nerve cell is said to *process the information* that the input is present.

similar anatomical features (Amunts, Schleicher, & Zilles, 2007; Brodmann, 1909). Adjacent neurons in cortex have a high probability of being connected (Braitenberg & Schüz, 1998) and connections within an area of a few square centimetres and between adjacent such areas are still rich (Pandya & Yeterian, 1985; Young, Scannell, & Burns, 1995). The links between areas more distant from each other are however rarer and it is here where relevant structural information is required to make learning possible. Critically, the human cortex has strong connections between a range of distant areas, linking neurons in its frontal, temporal, parietal and occipital lobes. This is functionally important because motor commands leave the cortex from fronto-central areas and most sensory information enters the cortex at the back, in temporal (acoustic), parietal (somatosensory) and occipital areas (visual information) (Pandya & Yeterian, 1985; Young et al., 1995). Anatomical links between nerve cells processing motor and sensory information make it possible to learn and map the relationship between specific bits of action- and sensory related information by strengthening corresponding connections. The neurons involved are therefore no longer specific to motor or sensory processes, but "mix" sensorimotor information by becoming active both in the programming of actions and in the perception of corresponding scenes. The discovery of Mirror Neurons (Rizzolatti & Craighero, 2004) and other multimodal cells in cortex (Fuster, 2003) lends great support to this idea of information mixing (Braitenberg & Schüz, 1998). Neuroanatomists had been arguing for some time that the structure of the cortex suggests that it is an information mixing device ideal for cross-modality learning (Braitenberg & Schüz, 1998). Physiological evidence from basic neuroscience now strongly supports this view.

Evidently, it is of great importance to take into account documented anatomical links and structural information when theorising about the brain basis of language and semantics (Garagnani, Wennekers, & Pulvermüller, 2008). An important step in the evolution of language seems to have been the strong linkage of the lower part of the frontal cortex – inferior-frontal cortex – to the upper temporal areas – superior-temporal areas, especially in the left language-dominant hemisphere. The link between these structures, especially one carried by a fibre bundle called the arcuate fascicle – seems to be unavailable in monkeys, weakly developed in apes and strong in humans (Rilling et al., 2008). The inferior-frontal and superior-temporal cortex are also connected by way of other connections (Petrides & Pandya, 2009; Saur et al., 2008), and via the inferior-parietal cortex (Catani, Jones, & Ffytche, 2005). All three regions together, inferior-frontal, inferior-parietal and superior-temporal cortex, along with deep cortical structures below them (operculum and insula) are sometimes called the perisylvian cortex. The perisylvian cortex in the left language-dominant hemisphere is also called the "(core) language cortex" (Fig. 1). Other parts of cortex can also play a linguistic role (Section 5ff).

4. Steps towards a neurobiological model of language

The neuroscientific principle of correlation learning and the knowledge about long-distance connectivity in human cortex have important implications for the brain basis of meaningful language units, words and morphemes. Fundamental and specific learning capacities are apparent from the fact that vocabularies of ten thousands of words are easily acquired by humans, whereas other primates typically only manipulate small numbers of meaningful signs (Tomasello, 2005). What is the neuronal machinery of the brain that underlies the learning and processing of signs as phonological, articulatory and acoustic units, which become elements of a store of complex signs, the lexicon of a language? Basic neurobiological mechanisms underlying phonological and lexical learning will be discussed in this section, before semantic issues will be addressed.

When a word form is being articulated, this relates to neuronal activation in the lower motor cortex. Motor cortex activation is coordinated and controlled by premotor circuits, which are, in turn, orchestrated and influenced by activity in adjacent inferior prefrontal areas (red areas M1, PM and PF in Fig. 1). In addition to this activity in the inferior-frontal cortex, speech produced leads to auditory input, which specifically activates superior-temporal auditory cortex and, via short distance connections, the adjacent auditory belt and parabelt areas in superior-temporal gyrus and sulcus (blue areas A1, AB and PB). There are strong and reciprocal neuronal links between superior-temporal lobe and inferior-frontal areas and, therefore, the co-activation of neurons in these areas, which is characteristic of the production of a spoken word, leads to synaptic strengthening. A word-related

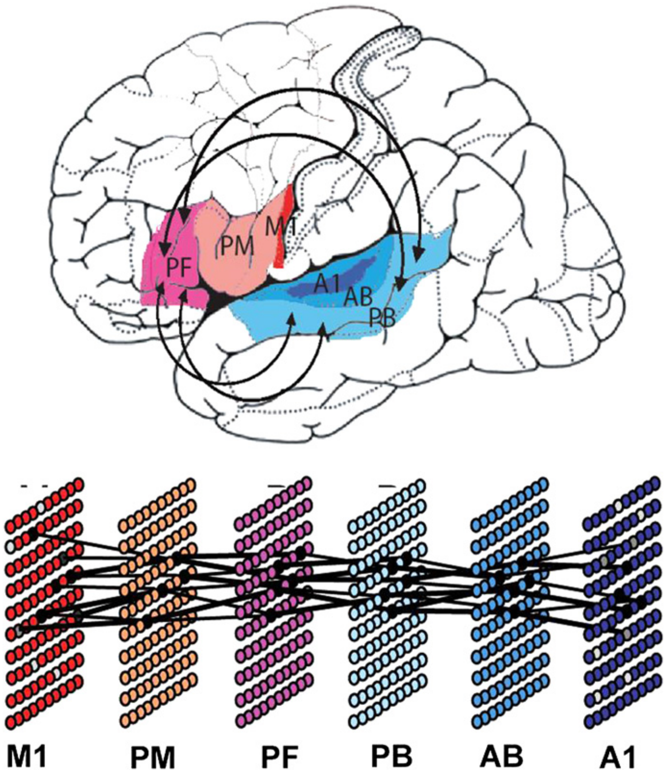

Fig. 1. Diagram at the top: Lateral view of the left hemisphere with core language areas indicated in colour. Blue areas in the superior-temporal cortex include the primary auditory cortex (A1), the auditory belt (AB) and parabelt (PB) regions and red areas in the inferior-frontal cortex include inferior prefrontal (PF), premotor (PM) and primary motor cortex (M1). Connections between these areas by way of white matter fibre tracts (arcuate fascicle, extreme capsule) are shown schematically by arrows. Language-relevant areas in the inferior-parietal cortex are not highlighted. Diagram at the bottom: The neural model of the language cortex (Garagnani et al., 2008) is shown, which mimics relevant areas and connections and is used to simulate language learning and brain responses to linguistic materials. Highlighted neural elements (circles) and connections (lines) indicate a distributed cell assembly linking action and perception circuits. This type of distributed circuit may underlie the production and recognition of spoken words. Note that correspondences between brain and model areas are indexed by colours. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

neuronal assembly distributed over different parts of perisylvian cortex develops (Pulvermüller, 1999; Pulvermüller & Preissl, 1991). As the inferior-frontal and superior-temporal neuron populations – which, before learning, had either been controlling articulation movements or had specifically responded to the acoustic features – are being linked together by the learning process, the resulting connected assembly can be considered an action–perception–circuit, or APC, in which action-related and perceptual information is being merged or mixed. Somatosensory input from receptors close to the articulators are likewise informative about articulatory movements; therefore, this argument can be extended to the inferior-parietal cortex, where somatosensory information is being processed (Ito, Tiede, & Ostry, 2009). The action–perception–circuit emerging during word production would therefore be the brain basis of a specific spoken word form and ground it in distinctive articulatory-motor, articulatory-somatosensory and acoustic phonetic features. In order to include the processing of written words, the circuits need to include neuronal populations in areas where information about the visual form of words is being processed (visual cortex, fusiform gyrus and temporo-parieto-occipital junction) along with neuronal ensembles in motor regions coordinating and controlling writing gestures (Pulvermüller, 1992, 1999).

Note that the sketched scenario answers the question why humans are able to build large vocabularies whereas other primates cannot. Connections between superior-temporal and inferior-frontal areas, which are especially rich in humans, provide the machinery for associating a wide range of complex action-perception patterns for developing vocabulary elements. Monkeys and even the great apes are able to learn some sensorimotor mappings (e.g., involving symbols or objects) but not a rich sign inventory (Tomasello & Call, 2007), possibly because their links between the critical areas are weaker, especially those provided by the arcuate fascicle (Rilling et al., 2008).

That some kind of sensorimotor learning takes place in language development is uncontroversial, for example to map speech sounds to articulations. Uncontroversial is also that such sensorimotor learning is carried by connections in perisylvian cortex (Fig. 1), by neuronal links between specific neuronal populations in superior-temporal and inferior-frontal, possibly also inferior-parietal cortex. Whether these neurons in different areas form a functional unit, a cell assembly, whose concerted action is required for both speech production and perception is, however, still a matter of debate. The neurobiological theory holds that, after linkage of acoustic and articulatory circuits, the whole distributed circuit acts as a closed functional system, which competes with other similar action-perception circuits in the process of speech perception and likewise in speech production (Garagnani et al., 2008). Activity anywhere in the circuit would therefore have an effect on both speech production and perception processes and a lesion anywhere in the network, in frontal or temporal areas, would imbalance the competition between action-perception-circuits in both production and perception.

These predictions have been validated using formal neuronal network simulations in which areas of perisylvian language cortex are replicated and systematically lesioned (Pulvermüller & Preissl, 1991). The results replicate the well-known multimodal character of most language deficits caused by lesion of the brain. Neuropsychological studies have shown that lesions in inferior-frontal cortex indeed lead to production problems along with quantifiable deficits in understanding sentences and even single words (Moineau, Dronkers, & Bates, 2005; Utman, Blumstein, & Sullivan, 2001; Yee, Blumstein, & Sedivy, 2008) and likewise superior-temporal lesions have an impact not only on perception and comprehension but also on language production (Lichtheim, 1885).

Further properties of word- and speech sound-related action-perception circuits emerging during language acquisition can be summarized as follows: Although the neurons included in these circuits are located in areas distant from each other, they are linked together strongly, as a consequence of pre-established connections and their strengthening following associative learning. Because of their strong internal connections, these circuits act functionally as *discrete* systems. Each circuit includes only a small fraction of the neurons of the network, thus constituting *sparse* representations. If stimulated, the circuits reach a point of no return after which they *ignite* and become fully active. This ignition process may be the brain basis of recognition of a linguistic item, for example a word. After ignition has taken place, activity will not immediately cease in the circuit, but activity will *reverberate* in the circuit due to the strong connections. Reverberation is a candidate mechanism of working memory (Fuster, 1995). Neurocomputational simulations using an artificial model of the language cortex make these postulates more plastic and generate precise and testable model predictions on brain activation patterns observable during language processing (Garagnani et al., 2008).

The discrete functionality of action-perception circuits is manifest in a certain degree of stability of their activation processes. Because circuit activation is carried by strong assembly-internal connections, inhibitory and excitatory processes elsewhere in the network have a reduced impact on it. This surfaces in relative insensitivity of the activation processes to variable attention levels, a feature first predicted by network simulations and then confirmed in neurophysiological experiments (Garagnani, Shtyrov, & Pulvermüller, 2009; Shtyrov et al., 2010). From a linguistic perspective, functional discreteness is important for phonological, lexical and syntactic-semantic representations and processes. Many neural network models of language use fully distributed non-sparse representations, which do not support discrete processes, therefore making it difficult to store several items at the same time in the same network (for discussion, see Jackendoff, 2002; Pinker & Prince, 1988). The action-perception circuits discussed in this review allow for discrete processes, multiple circuit activation and working memory (reverberatory activation), thereby providing a mechanistic basis of symbols (Pulvermüller, 2003). Distributed cortical circuits in this sense share important properties with mechanisms envisaged by Donald Hebb and labelled *cell assemblies* (Hebb, 1949) and with more recently proposed mechanisms labelled *reverberatory synfire chains* (Abeles & Prut, 1996; Shmiel et al., 2005), *cognits* (Fuster, 2003), *large-scale neurocognitive networks* (Mesulam, 1990) and *neuronal assemblies* (Palm, 1982).

The postulate that spoken word forms, for example "crocodile", are grounded in discrete action-perception circuits, whereas meaningless but pronounceable and phonotactically legal pseudowords not used in the language, such as "crodobile", are not, has led to a range of empirical predictions, which were tested in neuroimaging experiments. According to one proposal, the reverberatory activity of a memory circuit is manifest in synchronous oscillations at high frequencies (von der Malsburg & Schneider, 1986). Evidence for this proposal comes from animal research (Singer & Gray, 1995) and could be found also in non-invasive recordings, EEG and MEG (e.g., Lutzenberger, Pulvermüller, Elbert, & Birbaumer, 1995; Müller et al., 1996; Tallon-Baudry & Bertrand, 1999). When investigating high frequency cortical responses to words and meaningless word-like items, induced high-frequency (high beta and gamma band) responses were found to be enlarged to the lexical items and relatively small for the meaningless novel ones (Eulitz et al., 2000; Krause, Korpilahti, Porn, Jantti, & Lang, 1998; Lutzenberger, Pulvermüller, & Birbaumer, 1994; Pulvermüller, Birbaumer, Lutzenberger, & Mohr, 1997; Pulvermüller et al., 1996; Pulvermüller, Preissl, Lutzenberger, & Birbaumer, 1995). This was so for different languages (e.g., English, German, Finnish), in both major language modalities (spoken and written language) and in a range of tasks and paradigms (lexical decision, reading, listening, active and passive oddball tasks). The difference in gamma-band responses was usually most pronounced over, or in, the left language-dominant hemisphere. Similar effects as reported earlier for words and pseudowords were also seen for phonemes of a language vs. non-language sounds and for familiar vs. unfamiliar letters (Ihara & Kakigi, 2006; Palva et al., 2002). These results indicate the existence of memory circuits in the human brain generating coordinated high-frequency responses. The circuits may have developed for meaningful elements the individual is familiar with, including words and objects. The recent criticism that saccades and other muscle related activity may underlie high-frequency dynamics recorded in the EEG and MEG (Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008) does not apply to several of these linguistic studies, as frequency ranges where muscles contribute most had been systematically monitored (for discussion, see Pulvermüller et al., 1997).

A further prediction of the model is that, due to their strong internal connections, action-perception circuits in cortex act like amplifiers of cortical activity, so that, when processing resources are limited, input amplified by circuit ignition leads to a stronger brain response (input plus cell assembly activation) than an input that fails to activate such a network (response to sensory input only). A well-known indicator of cognitive processes is the Mismatch Negativity, or MMN, elicited by auditory stimuli (Näätänen et al., 2007). The MMN is indeed larger to familiar sounds of one's own language than to phonemes of a foreign language (Näätänen et al., 1997). In the same way, familiar non-language sounds, such as familiar clicks or whistles, elicit a larger MMN compared with physically matched unfamiliar sounds (Frangos, Ritter, & Friedman, 2005; Hauk, Shtyrov, & Pulvermüller, 2006). Crucially, if a syllable or language sound is placed in a context where it is critical for understanding a meaningful word, its MMN is enhanced compared with a condition in which the same phonologically regular stimulus completes a pronounceable but meaningless pseudoword (Endrass, Mohr, & Pulvermüller, 2004; Korpilahti, Krause, Holopainen, & Lang, 2001; Kujala et al., 2002; Pettigrew et al., 2004; Pulvermüller, Kujala et al., 2001; Pulvermüller, Shtyrov, Kujala, & Näätänen, 2004; Shtyrov & Pulvermüller, 2002; Sittiprapaporn, Chindaduangratn, Tervaniemi, & Khotchabhakdi, 2003). This lexical enhancement of the MMN is best explained by the full activation (ignition, Braitenberg, 1978) of a cell assembly triggered by a meaningful word, but not by an unfamiliar meaningless item. A similar explanation in terms of memory networks for phonemes and other familiar sounds is also established (Näätänen, 2001; Näätänen, Paavilainen, Rinne, & Alho, 2007; Pulvermüller & Shtyrov, 2006).

The results summarized support cell assembly activation following word presentation and a lack thereof when pseudowords are being presented. An additional model prediction is that action-perception network activation includes near simultaneous ignition of both inferior-frontal output control circuits and superior-temporal comprehension processors. During listening to syllables and words, the left-inferior frontal and premotor cortex was indeed found active along with the superior-temporal areas in the vicinity of the auditory cortex (Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Pulvermüller, Shtyrov, & Ilmoniemi, 2003; Watkins & Paus, 2004; S. M. Wilson, Saygin, Sereno, & Iacoboni, 2004; Zatorre, Evans, Meyer, & Gjedde, 1992). During speaking, the superior-temporal cortex was active along with areas in inferior motor, premotor and prefrontal cortex, although it was ensured that self-produced sounds could not be perceived through the auditory channel (Paus, Perry, Zatorre, Worsley, & Evans, 1996). Furthermore, as mentioned above, it is well-known that lesions in superior-temporal or inferior-frontal cortex cause language deficits, aphasias, which impair both speech production and comprehension. These results converge on the conclusion that interactive neural systems distributed over the inferior-frontal and superior-temporal cortex contribute to both speech production and perception. During spoken word recognition and understanding, these systems become active near-simultaneously and largely in parallel, with a peak activation delay in the inferior frontal cortex of ~20 ms after the activation peak in superior-temporal areas (Pulvermüller & Shtyrov, 2009; Pulvermüller et al., 2003). These results suggest tight and rapid functional links between speech perception and speech production processes, as postulated by neurobiological (Braitenberg & Schüz, 1992; Fry, 1966; Pulvermüller & Preissl, 1991) and psycholinguistic theories (Fowler, 1986; Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967). It is noteworthy that temporal and inferior-frontal activity even emerged when subjects did not attend to and were distracted from incoming speech stimuli, thus supporting the automaticity of inferior-frontal activity in speech processing (Pulvermüller et al., 2003). Over and above their apparently automatic emergence, attention to speech enhances these inferior-frontal activations, especially when meaningless pseudowords are presented (Garagnani et al., 2008; Shtyrov et al., 2010).

That the links between superior-temporal perceptual circuits and the inferior-frontal speech production machinery are functionally effective has been demonstrated by experiments using transcranial magnetic stimulation (TMS). When spoken words and language sounds (phonemes) that strongly involve the tongue are being perceived, TMS applied to the inferior motor cortex elicits stronger muscle responses of the articulators compared with control conditions (Fadiga et al., 2002). Interestingly, this effect was most prominent when the critical phonemes were presented in meaningful word context, suggesting that cell assemblies for meaningful words play a role in linking articulatory gestures and auditory signals at the cortical level (see Pulvermüller & Preissl, 1991). The specific role motor circuits play in speech perception has recently been demonstrated using TMS. Weak magnetic stimulation of the lip and tongue areas in the left dominant hemisphere biases the perceptual system to “hear” the concordant speech sound ([p] in case of lip motor area stimulation) and to incorrectly perceive incongruent phonemes ([t] to lip TMS) (D’Ausilio et al., 2009). The neuronal correlate of phonetic features, (such as [+bilabial] and [+alveolar]) provides a neuroscientific basis for linguistic-phonetic theory (for further discussion, see D’Ausilio et al., this volume).

In summary, these neuroscience data provide support for the position that word forms are brain-based on specific action-perception circuits distributed over inferior-frontal and superior-temporal areas of cortex. At the purely cognitive level, this suggests that spoken words as entries of a “mental lexicon” are embodied as complex articulatory gestures and as complex auditory spectrotemporal patterns and, most importantly, as the specific functional connections between the two. Considering written language, additional specific links to circuits for visual patterns, written word forms, and writing gestures are necessary. One may want to call the resulting action-perception networks modality-unspecific representations of *abstract* word forms, but, as concrete and specific articulatory, gestural, acoustic and visual features characterize word forms, it is equally accurate to speak of *multimodal* or *transmodal* circuits.

Whereas the above considerations and data address simple monomorphemic words, the present neurobiological approach provides a perspective on other sign types, too, including human-produced sounds that do not belong to a language system (whistle, finger click), hand and whole body gestures, and written symbols. It has also been extended to morphologically complex words, postulating discrete neuronal circuits, respectively, for roots, derivational and inflectional affix and particles (Cappelle, Shtyrov, & Pulvermüller, 2010; Pulvermüller, 1999). Likewise, the question of how the word-related cortical circuits may be embedded into larger syntactic and combinatorial networks has been addressed elsewhere (Section 11, Pulvermüller, 2003).

5. Semantic word kinds and the brain

In Section 2, different views on the nature of word meaning have been outlined and, in Sections 3–4, a neurobiological approach to linguistic brain circuits was sketched, focussing on the level of single mono-morphemic word forms. The next step will now be to integrate word form circuits with putative brain mechanisms of semantics, taking into account the different views on semantics. Some philosophical and linguistic theories of meaning have focussed on the relationship between signs and the objects they are used to speak about. If we accept such a limited perspective, the task a semantic brain theory might be expected to solve, is to investigate the connections between the brain bases of sign and object knowledge. (Note, however, the limitations of such an approach pointed out throughout this article.) In terms of neuronal circuits, the brain correlate of words can be conceived as left-lateralised perisylvian circuits, possibly with subcortical addenda (Section 6). Seeing an object activates a range of cortical areas in the primary visual cortex and adjacent higher visual areas, along with areas of the inferior-temporal cortex where object-type-specific activation patterns have been documented (see Martin, 2007). The word–object learning paradigm – adults naming objects while the child focuses on and attends to them (cf. Augustine's example) – leads to correlated activation patterns in left-lateralised perisylvian and bilateral temporal-occipital visual areas. As connections are available between these sets of areas, the correlated activation patterns elicit strengthening of neuronal connections and therefore merging of the neuronal assemblies storing word form and object information.

In this biological framework, neuronal correlation is a driving force of semantic linkage. The probabilistic nature of the learning process and the emphasis of correlation may help to overcome some problems of classic theories of reference. A classic problem for learning by ostensive definition had been that using the word "cow", while pointing to an animal leaves it open whether the whole entity or its subparts, eyes or tail, are being named (see, for example, Quine, 1960). In a neurobiological framework, disambiguation of word-object relationships is achieved by correlation of neuronal firing during word usage and visual object information processing over several learning events. Psychologists have argued that this problem may, in part, be solved by a default to relate new words to entire objects, rather than their parts (Bloom & Markson, 1998), an approach which, however, makes the learning of part names especially difficult to explain. The correlation concept provides a solution. Because the individual words ("eye", "tail", "cow") would each co-occur with different sets of visual inputs (where not all eyes are cows' eyes), the induced reference-object links will differ between them. *As neuronal correlation is crucial for the modification of the strength of cortical connections, the circuit for the word "cow" would therefore detach from the eye-object circuit when this word is used in context of eyes belonging to a sheep (for discussion, see Pulvermüller, 1999).* A similar solution seems feasible for the so-called semantic subset problem, that category terms can be at various levels of specificity, from hyperonyms, basic category names and hyponyms (animal, bird, duck) down to the level of proper names (Donald Duck). A solution comes from activation correlation between sets of neural elements realising visual-perceptual features and word-form-related circuits. For "duck", a range of visual feature neurons are frequently active in the Augustinian learning situation together with the word form circuit. Birds look differently and only the neurons responding to characteristic features of the family will be linked strongly to the word-related circuit (see Pulvermüller, 2003). Thus, while prototypical category members will be connected strongly to the category term, the less prototypical items will be linked in less strongly. The importance of a probabilistic approach to language learning has been pointed out in the psycholinguistic literature (L.R. Gleitman, 1990).

The left panel of Fig. 2 shows the kind of cortical network emerging after merging of perisylvian word form circuit and temporal-occipital object circuit. We may call this an Augustinian semantic network, or object word circuit.

As emphasised previously, a learning paradigm highlighted by Wittgenstein emphasise action embedding of language. *The child performs an action (with criterium-status for the presence of a feeling) and hears words spoken by adults, thus allowing the learning of word–action correspondence. Also aspects of the meaning of action words (such as "run" and "grasp") can be extracted from situations where the learner is told the word while performing the action.* Children do indeed learn action words in contexts where they perform actions semantically related to these words and caretakers use words to speak

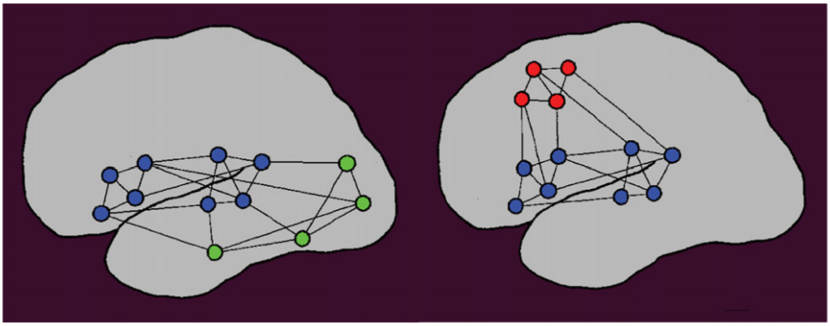

Fig. 2. Schematic illustration of cortical cell assemblies linking perisylvian word form circuits to semantic circuits in the inferior-temporal object perception stream (diagram on the left) and in the fronto-central motor systems (right). Neuroscience principles of synaptic learning and cortical connectivity imply that these types of circuits emerge, respectively, during word-object learning and during learning of word–action correspondences. At the psychological level, the semantic circuits can be understood as schematic representations of actions and objects.

about these actions – for example "run" when the child is running (for data on both ostensive and non-ostensive verb learning situations, see Tomasello & Kruger, 1992). Brain-wise, correlation of neuronal activity *is a by-product of such interactions; in this case, correlated activity is present* in the left-perisylvian language system and in areas controlling and coordinating action performance.[3] These areas are in the central "motor strip" and the premotor cortex anterior to it, also including areas dorsal to the perisylvian ones (Fig. 2, panel on the right). *When observing an action performed by somebody else, there is similar activation in premotor mirror neurons as during action execution, thus offering an additional route for learning word action correspondences (Rizzolatti & Craighero, 2004). Furthermore, neuronal circuits and cortical areas relevant to knowledge storage and to predicting other people's actions and intentions are also relevant in this context (Tomasello, 2005).*

The object-related (Augustinian) and the action-related (Wittgensteinian) word learning paradigms lead to fundamentally different predictions on the brain circuits involved in the binding of word form and meaning knowledge. Whereas one places semantic links in the posterior perception-related brain areas, especially in the "ventral" stream in temporal cortex, the other emphasises the role of fronto-central action-related and motor areas in meaning processing (Fig. 2). Each view seems to be appropriate for specific kinds of words (Pulvermüller, 1999). Importantly, however, it is necessary to recognise differences between semantic word kinds, as suggested by Wittgenstein, and the neurobiological model may provide a guideline for distinguishing some of the relevant types. Note that the general distinction between action- and perception-related knowledge and corresponding semantic types is directly reflected in the brain's subdivision into frontal, action-related and posterior (temporal, parietal and occipital), perception-related areas.

Although the word-object paradigm of word learning has been amply criticised by linguists and psycholinguists, it is striking that, in spite of its limitations, it has attracted much attention in these disciplines. For example, Pinker (Pinker, 1984, 1989) specified *perceptual* elements which, in his view, are sampled over verb learning situations – or, in case of mismatches, eventually discarded. However, it may seem that perceptual features are insufficient for learning the meaning of verbs and that action features are equally critical (Section 9). Gleitman (L.R. Gleitman, 1990) mentioned that it is difficult if not impossible to learn any *perceptual* distinction relevant for discriminating between the meanings of "paired verbs describing single events", "give" and "take", or "buy" and "sell". As these items are

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[3] It has been pointed out that word-world correlations cannot provide an explanation of semantic learning in Wittgenstein's framework or elsewhere (Baker & Hacker, 2009). However, what is relevant in the present context are correlations between linguistic actions and other actions, and, correspondingly, between the brain circuits that underlie them. As a consequence of the words' embedding in specific action sequences in language games, neuronal correlations of word- and action-circuit activations necessarily emerge, which, in turn, lead to synaptic strengthening between these circuits. These are brain-mechanistic correlates of word learning which weave the word, in a very concrete sense, into action.

applicable to the same scenes and perceptions, Gleitman argued that word–world contingencies cannot account for the difference in word meaning. However, the solution of an action-centred approach is obvious: The infant's actions (handing over or receiving an object) clearly differ between first-person-usage of "give" and "take" and this disambiguating action-related information can come into play in learning.[4] Word learning relies on both word-object and word–action contingencies, although the latter have not been considered to a similar degree as the former.

As Wittgenstein's example of learning the meaning of the word "pain" illustrates, the word kinds for which word–action contingencies are crucial do not just include action verbs that are typically used to speak about overt body actions of human beings (thus including "walking" and "talking", but not normally "tail-waggling" and "barking"). *A wide range of word types is in fact semantically related to action and interaction knowledge.* As one can "*stop* a car by *raising* the arm by *moving* a specific set of muscles" the action verb can be from the low (rightmost) end of the "by" chain (the so-called basic action, e.g., "move") or can, alternatively, be typically used to speak about higher-order intentional actions, further to left in the chain (e.g., "stop"). Words used to speak about automatic unintentional behaviours are also included ("shriek", "shiver"). The category of action related words include verbs that relate to actions ("to walk", "to hammer") and also nouns with a clear action component to their meaning ("the walk", "the hammer"). Note that this covers words used to speak about objects whose role is defined in an action context, such as tool names. Emotion terms and other "inner state" words are included as well (e.g., "pain", "joy"). Other "mental" verbs, nouns or adjectives ("think", "thought", "thoughtful") are included to the degree as there are behavioural criteria for the semantically appropriate use of the terms: An adult may be able to recognise from the actions of an infant that it is thinking – even though the related action schemes are sometimes complex. Usage of external, action based criteria by the adult is key to learning the meaning of a range of very different types of terms, including even abstract ones.

Word kinds differ not only in the way their meaning is learned and in their semantic properties. The idea that, similar to these semantic and developmental distinctions, the underlying neural circuits may also differ between word kinds has led to an exciting research stream in modern neuropsychological research. Brain lesions of different kinds were found to impair semantic processes in a category-specific manner (Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; Humphreys & Forde, 2001; Warrington & McCarthy, 1983; Warrington & Shallice, 1984). These findings led to the postulate that different semantic types or categories and their related concepts draw on different parts of the brain. Sections 7–10 of this paper will focus on some word types distinguishable on brain grounds and on areas involved in category-specific semantic processes.

6. Emotional meaning

As Wittgenstein put a focus on words typically used to speak about feelings, which had once been thought to "refer" to "internal states" of the body, some comments below will address affective and emotional meaning. This topic is closely related to the question: Is language related to processes in cortex exclusively or are other brain structures also relevant?

Although most brain-language theories do not pay special attention to subcortical mechanisms, it is evident that language mechanisms are not restricted to the cortex (Crosson, 1985; Dominey & Inui, 2009). All cortical areas project to the basal ganglia, the neostriatum and pallidum, from which fibres project to thalamus and from there back to cortex. The cortico-striato-thalamic loop is important for cortical function and it is therefore not surprising that lesion to subcortical key nuclei (thalamus, striatum) lead to language deficits (Nadeau & Crosson, 1997), although it has been argued that concurrent lack of blood supply in cortex critically contributes to these deficits (Hillis et al., 2002). In one proposal, each cortical cell assembly representing and processing a linguistic unit has an associated subcortical, striato-thalamic

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[4] Gleitman and colleagues (Gleitman, 1990; Gleitman, January, Nappa, & Trueswell, 2007; Landau & Gleitman, 1985) used their criticism of the word-object learning framework (which they attribute to Locke, 1909/1847) as a springboard to argue that, apart from learning word-world contingencies, structural information may aid semantic knowledge acquisition. This point is well taken. Chapter 11 will discuss the neurobiological basis of such contextual semantic learning, which is important and complementary to word-object and word–action learning.

loop attached to it, which is important for self-supporting the circuit's activity and for competing with other circuits (Gurney, Prescott, Wickens, & Redgrave, 2004; J. Wickens, 1990).

In their neurobiological model of language acquisition, Pulvermüller and Schumann postulated that this subcortical loop provides a relay station for linking linguistic information and emotional meaning (Pulvermüller & Schumann, 1994; Schumann et al., 2004). Correlation between activity in the limbic system, the distributed brain system processing affective and emotional information, and language areas of cortex lead to the association of cortical lexical circuits and emotion circuits. These "limbic tails" are important for later learning, because cortical circuits can activate, via their limbic tails, subcortical nuclei that send dopamine to the forebrain. Dopamine is an enhancer of synaptic learning at certain synapses (especially in basal ganglia structures such as the Nuclus accumbens) and the limbic tails may therefore be relevant for later learning. Pulvermüller and Schumann used these "emotional tails" of cortical circuits to provide a tentative account for the differential success of second language learners who have started to learn their second language late in life, after puberty (Johnson & Newport, 1989). Some results indicate that success in acculturation and integration into a foreign society predicts the very variable proficiency level finally achieved in late foreign language learners (Schumann, 1976, 1997). Note that an influence can be documented in both directions. Especially efficient language learning has been reported in well-acculturated subjects with ample positive language-related emotional experiences, whereas chronic pidginization and virtual absence of syntactic learning was seen in individuals that did not acculturate and evaluated the foreign culture and language as negative (J. Schumann, 1978). The neurobiological hypothesis states that the link between success in second language learning and emotional-affective evaluation of foreign society and language is provided by the "limbic tails" of cell assemblies for foreign language elements. If available, these facilitate further language learning, and if not, learning will be harder (Pulvermüller & Schumann, 1994).

Since this model had been proposed, several neuroimaging studies addressed the critical question whether limbic structures are indeed active during processing of words carrying emotional meaning. The variables reflecting affective and emotional meaning were inspired by work in psychology according to which meaning can be captured by three dimensions, *arousal*, the degree to which a word, symbol or picture (or the entity it depicts or relates to) is experienced as activating, *valence*, the degree to which it is positive or negative, and *potency*, the degree to which it is considered strong or weak (Lang & Bradley, 2009; Osgood, Suci, & Tannenhaus, 1975). For example, when investigating the arousal dimension of individual words, brain activation in a range of limbic areas was found to be stronger for highly arousing words as compared with low-arousal ones (Kensinger & Corkin, 2004; Kuchinke et al., 2005; Maddock, Garrett, & Buonocore, 2003). The limbic structures activated included frontal and parietal cingulate along with orbito-frontal and fronto-polar cortex, thalamus, caudate nucleus, amydgala and insula. Words semantically related to odours, which almost always carry emotional load, specifically activate the primary olfactory (pyriform) cortex along with the limbic structures amygdala, insula, cingulated gyrus, caudate nucleus and thalamus (González et al., 2006). These results are consistent with and in support of the postulate that words with high emotional value and high arousal have brain correlates reaching into limbic structures (Pulvermüller & Schumann, 1994). An early study had shown that the learning of associations between words and slightly painful stimuli enhances the left-lateralised brain response to the words, suggesting that the learning-induced addition of a limbic tail to a word-related circuit can amplify cortical activation (Montoya, Larbig, Pulvermüller, Flor, & Birbaumer, 1996).

These postulates and insights about brain circuits, emotional meaning and their possible relationships to each other do not address the question of why emotional meaning does come about, and, how the meaning of a word could possibly be linked to an "inner state" such as an emotion. Wittgenstein's theorising shows that, for linking the word "pain" to the feeling of pain, it is essential to have available the complex behaviour that mediates between the "inner" state and the word's usage. The meaning of feeling-related and emotion words can only be learned interactively, based on the actions that provide the criteria for attributing "internal" states. To validate this statement, it is of relevance to investigate the semantic properties of these words and to relate action and emotional aspects of their meaning to each other.

In psychology, a range of methods are used to assess semantic properties of words and symbols. Subjects can be asked to judge aspects of the meaning of words or their semantic similarity. Although these techniques have limitations – the information subjects give can only be as good as the questions they are asked – the empirical methods provide an objective way of assessing semantic features of symbols and their consistency in a speech community. If a range of subjects consistently rate, for example, a given word as both highly affective-emotional in meaning and semantically related to actions, it is plausible that these features apply for a large class of uses of this sign. General semantic features such as imageability, concreteness, action-relatedness, valence and arousal are frequently assessed for word stimuli and, after such evaluation, one can ask how these features relate to each other. If Wittgenstein's proposal that words used to speak about feelings can only be learned in action contexts is correct, one would expect high correlations between semantic action-relatedness of words and their emotional meaning (as emotions are one type of feeling). When performing Pearson correlation analysis between a range of different semantic rating values, the only significant correlation of the emotional-affective variable arousal emerged with action-relatedness ($r = 0.51$). A multiple regression analysis using the variables imageability, action relatedness, word frequency and word length to predict arousal values confirmed a close and specific relationship of the arousal variable to action relatedness ($beta=0.57$, significant at $p < 0.05$, all other $betas<0.1$, n.s.; $R = 0.52$, $F(4,297) = 26.78$). These empirical data are consistent with the view that the semantic relationship of words to "internal states" of a specific kind, emotions, is systematically linked to their action relatedness. The presence of this link at the semantic level is critical for the Wittgensteinian idea that the semantic connection between word and feeling is being established by using overt action as the criterion of the presence of "internal" states.

7. Semantic category-specificity: action and object words

The cell assembly model and other theories of perception and action-related category-specificity predict differential distribution of the neuron populations organizing action- and object-related words and similar differences can be postulated for other semantic categories (Fig. 2, Pulvermüller, 1996, 1999). Many nouns are typically used to speak about visually perceivable objects and are therefore characterized by strong semantic links to visual knowledge (e.g., about objects shape and colour), whereas most verbs are action verbs and link semantically to action knowledge (e.g., about how to kick or pick). Like action verbs, nouns that refer to tools are usually also rated by subjects to be semantically linked to action knowledge, but most animal names are rated to be primarily related to visual information (Preissl, Pulvermüller, Lutzenberger, & Birbaumer, 1995; Pulvermüller, Lutzenberger, & Preissl, 1999; Pulvermüller, Mohr, & Schleichert, 1999). Note therefore that semantic ratings of action-relatedness miss important distinctions, for example the principal difference between the direct action-relatedness of verbs used to speak about actions and the comparably indirect action-relatedness of tool nouns used to speak about objects that can be used for actions. Common to both is a semantic relationship to action knowledge.

A range of neuroimaging studies using EEG, PET, fMRI and MEG techniques found evidence for category-specific activation in the human brain for the processing of action- and visually-related words and concepts (e.g., Cappa, Perani, Schnur, Tettamanti, & Fazio, 1998; Chao, Haxby, & Martin, 1999; Kiefer, 2001; Preissl et al., 1995; Pulvermüller, Lutzenberger et al., 1999; Pulvermüller, Mohr et al., 1999). The results were largely consistent with the model of semantic category-specificity briefly outlined in Section 5. Processing of action-related words, be they action verbs, tool names or other action-related lexical items, tended to activate fronto-central cortex, including inferior-frontal and premotor areas, more strongly than words lacking comparable semantic action links. The same was found for temporo-occipital areas involved in motion perception. On the other hand, words used to speak about objects unrelated to actions tended to activate visual occipital and inferior-temporal cortex or temporal pole more strongly than the action-related words. Together with the neuropsychological results from patients with category-specific deficits (see previous section), this differential activation was interpreted as evidence for semantic category-specificity in the human brain at the neurofunctional level (Martin, 2007; Martin & Chao, 2001; Pulvermüller, 1999).

In summary, results from metabolic and neurophysiological imaging demonstrate the activation of neuronal assemblies with different cortical distributions in the processing of action- and visually-related words and concepts. *Other word types used to speak about sounds (or objects with characteristic sounds) and about odours also produce their own specific brain responses reflecting their semantic relationship to sound or odour information (Gonzalez et al., 2006; Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008).* However, it has been asked whether the reason for the differential activation observed for these word types would necessarily reflect semantic or conceptual brain processes. Could there be alternative explanations?

Although the broad majority of the imaging studies revealed different patterns of brain activity for different semantic categories, there is work that could not provide converging evidence (Devlin et al., 2002; Tyler, Russell, Fadili, & Moss, 2001). These authors used well-matched stimuli, so that word length, frequency and other psycholinguistic factors could not account for possible differences in brain activation, and argued that a lack of such matching might account for differences between "semantic" categories reported previously. Although some earlier studies reporting semantic category differences had actually performed meticulous stimulus matching for a range of psycholinguistic variables, including, for example, word length and frequency included (Kiefer, 2001; Preissl et al., 1995; Pulvermüller, Lutzenberger et al., 1999; Pulvermüller, Mohr et al., 1999), the majority of studies had not controlled for these factors. Furthermore, as pointed out previously (Bird, Lambon-Ralph, Patterson, & Hodges, 2000), nouns tend to have more highly imageable meaning than verbs, whereas verbs tend to have higher word frequency and also a more complex grammatical role than nouns. Any difference in brain activation, and also any differential vulnerability to cortical lesion, could thus be explained, for example, as an imageability-frequency dissociation, rather than in terms of semantic categories. Similarly, animals tend to be more similar to each other than tools from a visual and also conceptual point of view, and it has therefore been argued that perceptual and conceptual structure – or within-category similarity – could contribute to the explanation of dissociations between these categories (G.W. Humphreys & Riddoch, 1987; Rogers et al., 2004; Tyler, Moss, Durrant-Peatfield, & Levy, 2000). On these grounds, at least some evidence for category-specificity has therefore been criticized as being not fully convincing.

What makes things worse is that predictions on where category-specific activation should occur in the brain have usually been not very precise. Whereas rough estimates, such as the prediction that action semantics involves frontal areas and visual semantics temporo-occipital ones, could be confirmed, the more precise localization of category-specific activation foci was sometimes surprising and not a-priori predicted. It would be desirable to have evidence for category-specific semantic activation at precisely the locus a brain-based action-perception theory of semantic processing would predict. Such a perspective has been opened by looking at subtypes of action words. Furthermore, a brain-inspired more fine-grained subdivision of the semantic space into subtypes of the large categories might be of potential interest for semantic theory.

8. Fine-grained semantic distinctions and their brain mapping: the case of action words

Action words are characterised by semantic links to action knowledge. The neurons that process their word forms are likely interwoven with neurons controlling actions. The motor cortex is organized in a somatotopic fashion with the mouth and articulators represented at the bottom, close to the sylvian fissure, the arms and hand at dorsolateral sites and the foot and leg projected to the top, to the vertex and interhemispheric sulcus (Penfield & Rasmussen, 1950). Additional somatotopic maps exist in the fronto-central cortex (He, Dum, & Strick, 1993), among which a prominent one lies in the premotor cortex in the lateral precentral gyrus and resembles the map in the primary motor cortex (Matelli, Camarda, Glickstein, & Rizzolatti, 1986; Rizzolatti & Luppino, 2001). As many action words are preferably used to speak about movements of the face or articulators, arm or hand, or leg or foot, the distributed neuronal ensembles would therefore include motor-scheme-related semantic neurons in perisylvian (face words), lateral (arm words) or dorsal (leg words) motor and premotor cortex (Pulvermüller, 2001). This is the essence of the somatotopy-of-action-word model, which implies differently distributed networks for the English words *lick, pick* and *kick* (Fig. 3). This model allows for general predictions on action-word-related cortical activity within the limits of the well-known inter-individual variation of cortical maps, most notably as a result of practice-related reorganization (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995), and is open to further elaboration taking into account additional mapping rules, for example the topography of coordinated actions in a body-centred workspace (Graziano, Taylor, & Moore, 2002). Steps for such extensions of the model have been taken recently (Kemmerer & Gonzalez-Castillo, 2010; Pulvermüller, 2005; Pulvermüller & Fadiga, 2010).

A crucial prediction of the semantic somatotopy model is that spoken or written action words activate cortical areas involved in action control and execution in a category-specific somatotopic fashion, depending on the meaning of the action words. As the cortical areas of action control and

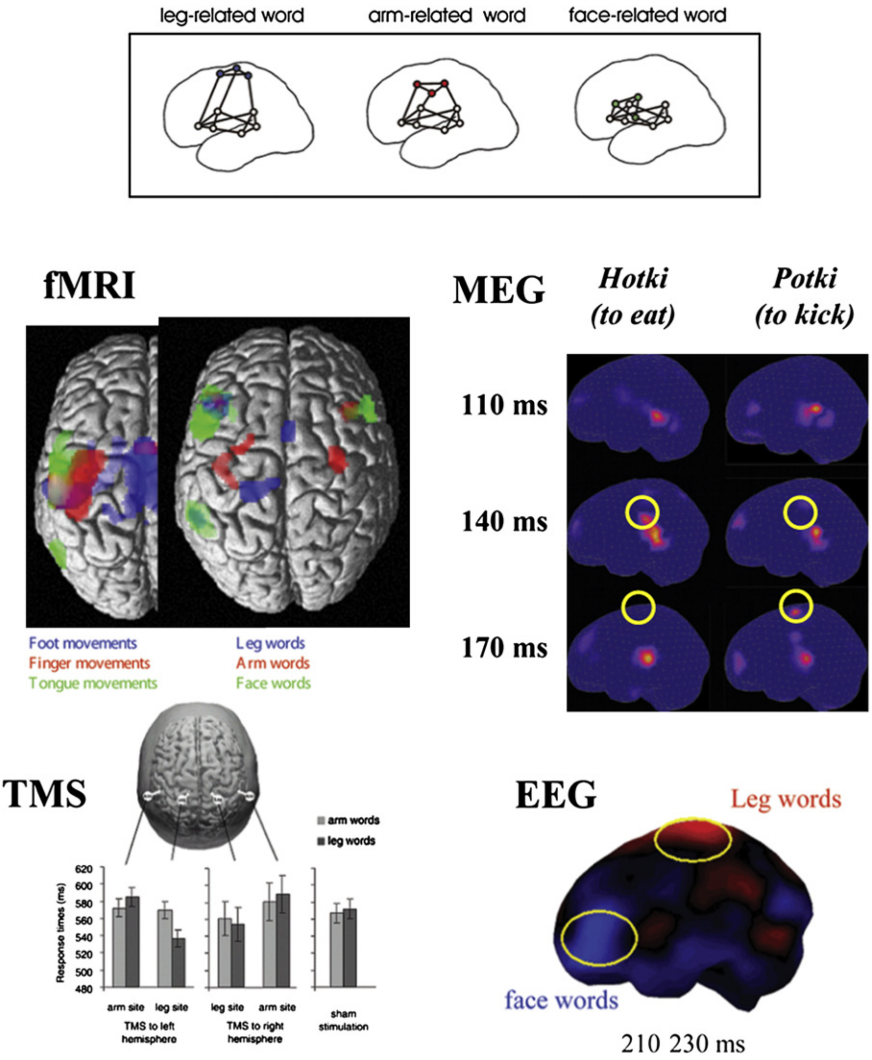

Fig. 3. Semantic somatotopy model and supporting data from neuroscience experiments. Top: Semantic somatotopy model of cortical circuits underlying the processing of words typically used to speak about actions preferentially involving the face/articulators (e.g., *lick*), arm/hands (*pick*), or leg/feet (*kick*) (modified from Pulvermüller, 2001). Semantic circuits are postulated in different parts of the motor and premotor cortex. Middle left: Activation of the motor system, as measured with fMRI, by passively reading face (in green), arm (red) and leg words (blue) and, partly hidden, during motor movements of the tongue (green), index finger (red) and foot (blue) (modified from Hauk et al., 2004). Bottom left: Differential facilitation of arm/leg words by magnetic stimulation of the motor cortex controlling the finger/foot using TMS. The brain diagram indicates stimulation loci; bars give average response times of lexical decisions responses expressed by tongue movements (error bars give standard errors) (modified from Pulvermüller, Hauk et al., 2005). Middle right: Rapid activation of frontocentral areas by face/arm (left panels) and leg verbs (right) 120–200 ms after the recognition point of spoken face/arm related words (left column) and leg words (right column), as measured with MEG. Yellow circles indicate early activations of inferior-central areas to face/arm items and, slightly later, dorso-central activation to leg words. Latencies are given relative to word recognition points (modified from Pulvermüller, Shtyrov et al., 2005). Bottom right: Rapid differential activation of inferior-frontal and superior-central areas by face (in red) and leg words (blue) 200–220 ms after visual word presentation as calculated from EEG recordings (modified from Hauk & Pulvermüller, 2004). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

execution can be defined experimentally, one can use action localizer experiments to predict the loci of semantic activation for different aspects of action-related meaning.

In functional neuroimaging experiments, elementary repetitive movements of single body parts activate motor and premotor cortex. For example, Hauk and colleagues reported functional MRI data showing that tongue, finger and foot movements lead to the somatotopic activation pattern illustrated in Fig. 3. When the same subjects were instructed to silently read action words related to the face, arm and leg that were otherwise matched for important psycholinguistic variables (such as word frequency, length and imageability) a similar pattern of activation emerged along the motor strip (Hauk, Johnsrude, & Pulvermüller, 2004). Consistent with earlier findings (Pulvermüller et al., 2003; Wilson et al., 2004; Zatorre et al., 1992) , all word types equally activated areas in the temporal cortex and also in the inferior frontal cortex. The additional category-specific somatotopic activation in response to face-, arm- and leg-related words seen in the motor system was close to and overlapped with the motor and premotor representations for specific body part movements obtained in the motor localizer tasks. These results indicate that specific action representations are activated in action word understanding. The fact that the locus of semantic activation could be predicted by a theory of action-perception circuits provides strong evidence for this theory in particular and for the grounding of aspects of semantics in action mechanisms in general (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Kemmerer, Castillo, Talavage, Patterson, & Wiley, 2008). In the context of the debate about the category-specificity of semantic brain processes highlighted in Section 7, recent work on fine-grained subcategories of action words substantially strengthened the sensorimotor account (Warrington & Shallice, 1984), because cortical loci involved in category-specific semantic processing could be predicted a priori by action-perception theory (Pulvermüller, 2005; Pulvermüller & Fadiga, 2010).

An experiment similar to the one reported by Hauk et al. (2004) was carried out with action words embedded into spoken sentences. In this case, subjects heard action descriptions such as “The boy kicked the ball” or “The man wrote the letter” while their brain metabolism revealed differential activation of premotor cortex (Tettamanti et al., 2005). Such differential motor systems activation was also shown using transcranial magnetic stimulation of different parts of the motor cortex while subjects listened to arm and leg related sentences (Buccino et al., 2005). These results are consistent with the view that word-related semantic circuits play a role in computing sentence meaning. Interestingly, not only simple concrete action sentences, but also idiomatic sentences including verbs related to actions preferentially performed with the arm or leg (“She grasped the idea”, “He kicked the habit”), elicited somatotopic semantic activation in the precentral cortex (Fig. 4, Boulenger, Hauk, & Pulvermüller, 2009). This specific activation was strongest after the end of the sentences, not when action words were perceived, thus suggesting a role of previous action word meaning in the understanding of abstract idiomatic sentence meaning.

These results allow for different interpretations of the precise role constituent word meaning may play in sentence comprehension. They can certainly be interpreted in the sense of theories of compositional semantics, because they suggest that the meaning of single words plays a role in composing over-learned abstract sentence meanings, which are not fully derivable from the meanings of sentence constituents (e.g., Gibbs & O’Brien, 1990). The results can also be interpreted in the framework of construction grammar and embodied theories of meaning assuming that the semantics of the abstract idioms under investigation is based on motor schemata derived from concrete motor meaning (Gallese & Lakoff, 2005; Lakoff, 1987).[5] *In future, it will be important to investigate the precise contribution composite words make to idiom comprehension along with the exact time course of motor area activations in the processing of idiomatic and other abstract sentences.*

The small-category differences between subtypes of action verbs have been complemented by specific activation to other narrowly defined semantic word kinds. Colour words activated areas in the

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[5] A recent study also investigating idioms including action words related to arm and leg actions failed to replicate motor somatotopy for abstract idioms (Raposo, Moss, Stamatakis, & Tyler, 2009). This study used sentences such as "The spiteful critic *trampled* over Sarah’s feelings", triggering fMRI responses to (here italicized) *action words* rather than to the (here underscored) critical words disambiguating idiomatic sentences. Note that with the expression kitchen floor at its end, the sentence would not be idiomatic, so the brain response brought about by *trampled* does (contrary to the authors’ assumption) not reflect idiomatic sentence processing. Note furthermore that sequential probability of strings was not controlled in this study, making it difficult to separate effects of close probability and semantics.

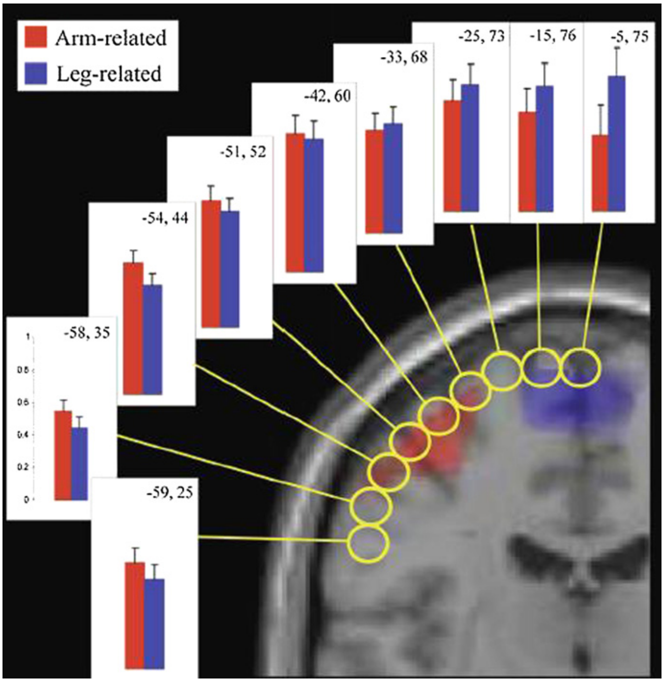

Fig. 4. Brain activation elicited by idiomatic sentences containing action words. Subjects read sentences such as “He *grasped* the idea in no time” or “She *kicked* the habit without any effort”. After the end of the critical words revealing the idiomatic nature of the sentences (“idea” or “habit”), activity developed in the motor system. Interestingly, this activation reflected the body part relationship of the action verbs at the beginning of the sentences. Note the stronger activation of “leg sentences” (bars on the right, in blue) in dorsal leg areas and the stronger activation of “arm sentences (bars on the left, in red) in lateral arm areas. The brain slice shows areas activated during finger (red) and foot movements (blue). The results suggest that constituent word meaning is being processed and may possibly play a role in the compositional computation of abstract sentence meaning (after Boulenger et al., 2009). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

inferior-temporal cortex and fusiform gyrus, which were also seen active in a colour discrimination task (Simmons et al., 2007), and differences in area-specific activation patterns in inferior-temporal cortex were seen between matched colour- and form-related words ((Moscoso Del Prado Martin, Hauk, & Pulvermüller, 2006; Pulvermüller & Hauk, 2006). The activation patterns elicited by specific word types were not only characterized by one category-specific activation focus, but by a set of foci. Also in the case of hand- or leg-related action words, the characteristic motor and premotor activations seem to be only one of many systematically occurring local activation differences, which discriminate between the word-category. In addition to word-kind-specific fronto-central foci, differential activation was evident in inferior-temporal cortex (Fig. 5, Pulvermüller, Kherif, Hauk, Mohr, & Nimmo-Smith, 2009).

Taken together, these fMRI results indicate that rather fine-grained semantic aspects of words can find their correlate in locally specific brain activation. Somatotopic activations of motor circuits reflect aspects of word and sentence meaning, possibly even aspects of abstract semantic processing. Such specific activation can be elicited by spoken and by written language.

As already mentioned, the semantic sub-classification of action-related words according to their action-relevant body parts is only one example of a distinction motivated by brain theory. Apart from action words, object terms have been sub-divided into animal and tool, fruit and vegetable, small man-made and nature-made object words, colour- and form/shape-related words and different patterns of functional activation and lesion-elicited deficits have been reported for these sub-types (see, for example, Martin, 2007). Further sub-categorisations are possible according to sensory modality, into word kinds whose meaning implies acoustic (for example, *click*), somatosensory (*heat*), olfactory (*cinamon*), or gustatory (*sweet*) semantic knowledge (e.g., Gonzalez et al., 2006; Kiefer et al., 2008). *The*

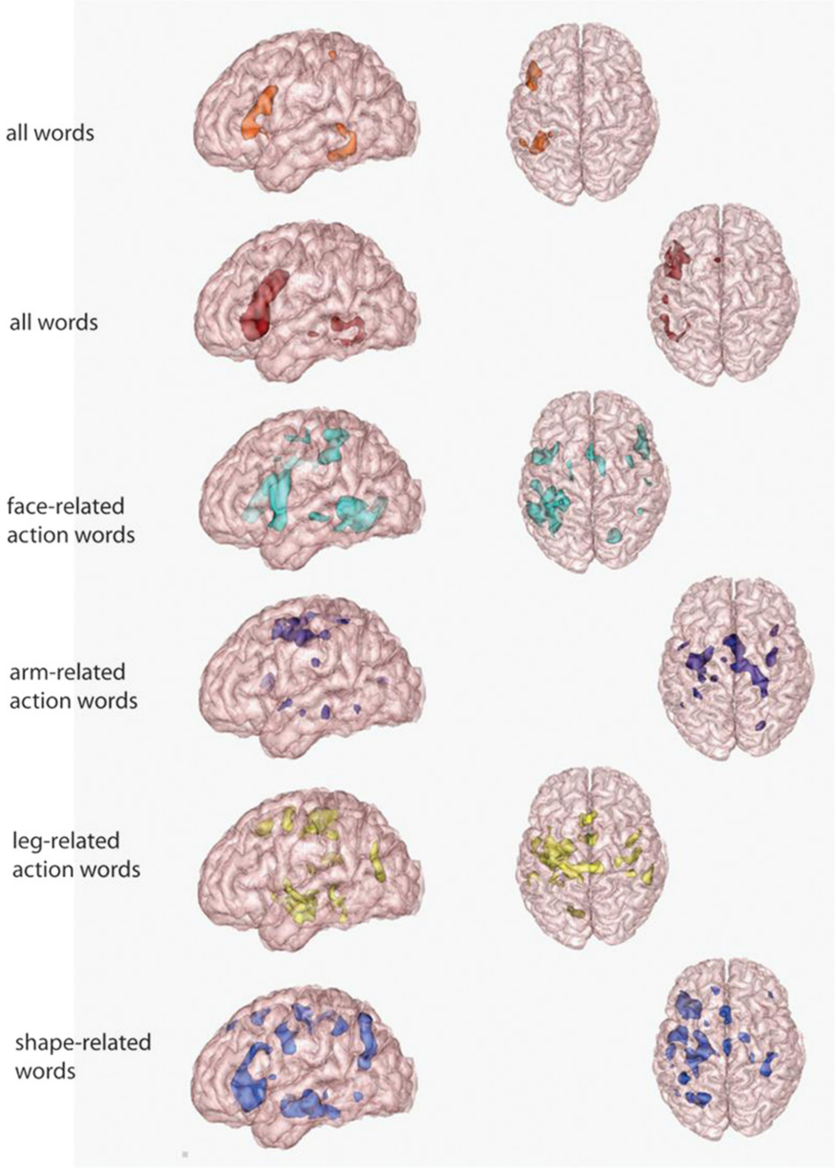

Fig. 5. Distributed activation patterns for general lexical and category-specific semantic processing as revealed by fMRI cluster analysis. Voxel clusters found active to most written word stimuli (non-specific clusters at the top, in orange and brown) included foci in perisylvian and inferior-temporal cortex. These were strongly lateralized to the language-dominant left hemisphere. Four clusters were primarily active to one semantic word type only, to words related to face (in cyan), arm (purple), and leg action (yellow), and to visual shape (blue). Category-specific semantic clusters were distributed over both hemispheres and included local foci in frontal and temporal lobes. For each distributed cluster, a lateral view of the left hemisphere and a dorsal view of the entire brain are shown (after Pulvermüller, Kherif et al., 2009). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

long-term neurosemantic research goal is to link a broad spectrum of semantic and pragmatic features, distinctions and categories to brain mechanisms, to spell these out in terms of neuronal circuits, and to explain their distribution and functional characteristics based on neuroscience principles. Although a brain-based systematic of semantic kinds is outside the focus of this present paper, additional semantic category distinctions will be discussed in Section 11 (see also Barsalou, 1999; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Feldman, 2006; Fischer & Zwaan, 2008; Gärdenfors & Warglien, in press; Glenberg & Kaschak, 2002; Kemmerer & Gonzalez-Castillo, 2010; Kiefer & Pulvermüller, in press; Pulvermüller, 1999; Pulvermüller & Fadiga, 2010).

9. Action perception circuits carry semantic processes

Although language-related sematotopic cortical activation, and similarly other brain signatures of semantic word categories, could be demonstrated, the low temporal resolution of haemodynamic imaging with fMRI makes it impossible to decide between two interpretations of these findings: One possibility is that the activation of specific action-related networks directly reflects word recognition and comprehension, as the somatotopy-of-action-word model would suggest. An alternative possibility has been pointed out by Glenberg and Kaschak in the context of behavioural work on semantic embodiment (Glenberg & Kaschak, 2002). It is possible that thoughts about actions actually follow the comprehension process and behavioural, but also brain-physiological, effects relate to such "post-understanding inference". *Others have spoken of "epiphenomenal" processes (Mahon & Caramazza, 2008).* Such secondary inferences would be triggered by the comprehension of a word or sentence, but would not necessarily reflect processes intrinsically linked to language comprehension. Importantly, earlier fMRI research has shown that observation of action-related pictures, but also mere voluntary mental imagery of actions, can activate motor and premotor cortex in a somatotopic fashion (Buccino et al., 2001; Jeannerod & Frak, 1999). Therefore, it is important to clarify whether motor system activation to action-related language processing reflects the comprehension process *per se* or rather a later stage following language comprehension. Apart from mental imagery of actions, scenes or objects, possible post-comprehension processes include planning of action execution, recalling an action performed earlier, and reprocessing the meaning of the language stimulus.

How is it possible to separate comprehension processes from subsequent inferences and other mental activities? In one view, brain processes reflecting comprehension can be characterized as (1) *immediate*, (2) *automatic*, and (3) *functionally relevant* (see also Pulvermüller, 2005).

(1) *Immediacy:* Early effects of lexical and semantic processing are known to occur around 100–200 ms after critical stimulus information comes in (Pulvermüller, 1996; Pulvermüller, Shtyrov, & Hauk, 2009; Sereno, Rayner, & Posner, 1998). In contrast, late postlexical meaning-related processes are reflected by late components of the event-related potential and field, which are maximal around 400 ms after word onset (Holcomb & Neville, 1990). If activations of motor areas and other word-kind-specific effects index semantic processes intrinsically tied to word form access, they should emerge within ~200 ms after stimulus information allows for the unique identification of an incoming word.

(2) *Automaticity:* When seeing or hearing a word, it is hardly possible to avoid understanding its content, and comprehension might even occur without intentionally attending to the stimuli (Boulenger et al., 2006; Gentilucci, Benuzzi, Bertolani, Daprati, & Gangitano, 2000; Stroop, 1935). Therefore, brain processes reflecting comprehension are expected to persist under distraction, when the subjects' attention is directed away from the critical language stimuli.

(3) *Functional relevance:* If one semantic kind of word elicits specific activation in a cortical area and this area contributes to semantic processing, a change of the functional state of this area may even lead to a measurable and specific effect on the processing of the semantic word kind. Such functional interaction can work both ways: Lesion or under-activation of the area may impair the category-specific processes as an additional activation of the area may benefit them. Having said this, it should be added that the prediction on specific lesion effects only holds true if no other redundant semantic processes are available to jump in for the deficient ones.

However, if a category-specific activation effect, as the semantic somatotopic activation of motor systems, did reflect a post-comprehension process, it should occur late (latency substantially greater than 200 ms), be absent under distraction, and its alteration should be without effect on word processing. A series of experiments was conducted to investigate these three issues.

9.1. Immediacy

To reveal the time course of cortical activation in action word recognition and find out whether specific motor areas are sparked immediately or after some delay, neurophysiological experiments were conducted. Experiments using event-related brain potentials looking at silent reading of face, arm and leg words showed category-specific differential activation already ∼200 ms after written word onset (Hauk & Pulvermüller, 2004). Consistent with the fMRI results, distributed source localization performed on event-related brain potentials revealed an inferior-frontal source – close to the motor representation of the face and mouth – that was strongest for face-related words and a superior-central source - close to the leg representation – maximal for leg-related items (Hauk & Pulvermüller, 2004). This dissociation in brain activity patterns supports the notion of stimulus-triggered early lexico-semantic processes. To investigate whether motor preparation processes co-determined this effect, experiments were performed in which the same response – a button press with the left index finger – was required to all words. The early activation difference between face- and leg-related words persisted, indicating that lexico-semantic processes rather than post-lexical motor preparation were reflected (Pulvermüller, Hummel, & Härle, 2001).[6]

In sum, the somatotopic activation indexing word meaning aspects appeared about ¼ of a second after information about the identity of stimulus words was available. Similar results were obtained for comparisons between other word kinds (Kiefer, 2001; Kiefer et al., 2008; Moscoso Del Prado Martin et al., 2006; Pulvermüller, Lutzenberger et al., 1999). As physiological studies of psycholinguistic processes had shown previously that the first brain responses reflecting comprehension and psycholinguistic information access at higher lexical and semantic levels first appeared around this point in time (Pulvermüller, 1996; Pulvermüller, Shtyrov et al., 2009; Sereno & Rayner, 2003), the earliness of the mapping of meaning aspects on different brain areas argues in favour of a reflection of comprehension processes *per se*.

9.2. Automaticity

The earliness of word category-specific semantic activation along the sensorimotor cortex in passive reading tasks suggests that this feature is automatic. To further investigate this possibility, subjects were actively distracted while action words were being presented and brain responses were measured (Pulvermüller, Shtyrov, & Ilmoniemi, 2005; Shtyrov, Hauk, & Pulvermüller, 2004). Subjects were instructed to watch a silent video film and ignore the language input while spoken face-/arm- and leg-related action words were presented. Care was taken to exactly control for physical and psycholinguistic features of the word material. For example, the Finnish words “hotki” (eat) and “potki” (kick) — which included the same recording of the syllable [kI] spliced to the end of each word’s first syllable — were compared. In this way, any differential activation elicited by the critical final syllable [kI] in the context of [hot] or [pot] can be uniquely attributed to its lexico-semantic context. Magnetoencephalography (MEG) results showed that a mismatch negativity (Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001) maximal at 100–200 ms after onset of the critical syllable was elicited by face/arm and leg word contexts. Relatively stronger activation was present in the left inferior-frontal cortex for the face/arm-related word, but, in contrast, for the leg-related words significantly stronger activation was seen in superior-central areas, close to the cortical leg representation (Pulvermüller, Shtyrov et al., 2005). These MEG results were confirmed with a different method, electroencephalography (EEG), using words from different languages, including, for example, the English word pair *pick* versus *kick* (Shtyrov et al., 2004). It is remarkable that the activation peak of the superior central source followed that of the inferior frontal source with an average delay of only 30 ms,

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[6] Motor systems activation was absent for arm words in this study requiring finger responses, possibly due to the engagement of motor systems in response preparation. A recent fMRI study also failed to detect arm area activation during lexical decision tasks on hand-action-related words (Willems, Toni, Hagoort, & Casasanto, 2010), possibly also due to preparatory and execution processes keeping the motor system active. Semantic links to effectors seem to be best documented in experiments avoiding responses with these same effectors.

consistent with the spread of activation being mediated by fast-conducting cortico–cortical fibres between the perisylvian and dorsal sensorimotor cortex. This speaks in favour of automatic activation of motor areas in action word recognition and therefore further strengthens the view that this activation reflects comprehension. Differential activation of body-part representations in sensorimotor cortex to action word subcategories was seen across a range of cognitive paradigm, including lexical decision, attentive silent reading, and oddball paradigm under distraction. This further supports the position that word-related semantic mechanisms, rather than task or strategy-dependent ones, are reflected.[7]

9.3. Functional relevance

If action word processing sparks the motor system in a specific somatotopic fashion, and even if this activation is fast and automatic, this does not necessarily imply that the motor and premotor cortex is relevant or even necessary for the processing of action words. To find out, different parts of the motor system were stimulated with weak magnetic pulses while subjects had to process action words in a lexical decision task (Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005). To minimize interference between word-related activation of the motor system and response execution processes (cf. footnote 6), lip movements were required while arm- and leg-related words were presented. Sub-threshold TMS applied to the arm representation in the left hemisphere, where strong magnetic pulses elicited muscle contractions in the right hand, led to faster processing of arm words relative to leg words, whereas the opposite pattern of faster leg than arm word responses emerged when TMS was applied to the cortical leg area (see Fig. 3, bottom left diagram) (Pulvermüller, Hauk et al., 2005). Processing speed did not differ between stimulus word groups in control conditions in which ineffective "sham" stimulation or TMS to the right hemisphere was applied. This result shows a specific influence of activity in the motor system on the processing of action-related words.

Whether action-perception circuits are crucial and necessary for semantic processing can be investigated using neuropsychological methods exploring the effect of functional changes in cortex on behaviour. Some neuropsychological work reporting category-specific semantic deficits have already been mentioned in previous sections (e.g., Gainotti, 2004; Warrington & McCarthy, 1987). Data from stroke patients with lesions in inferior frontal or temporal lobes indicate a double dissociation between processing action verbs and object-related nouns (A. R. Damasio & Tranel, 1993; Daniele et al., 1994; Fazio et al., 2009; Gainotti, 2004; Miceli, Mazzucchi, Menn, & Goodglass, 1983; Neininger & Pulvermüller, 2003). Action verbs processing is also impaired specifically in patients with degenerative brain diseases affecting the motor system or its direct vicinity, including motor neuron disease (Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001), Parkinson's disease (Boulenger et al., 2008; Cotelli et al., 2007) and the frontal variant of frontotemporal dementia (Cotelli et al., 2006). Similar to findings about subgroups of nouns, these selective noun/verb deficits can be interpreted in the context of an action-perception model: most verbs are semantically related to actions, whereas most nouns relate to object information available through the visual modality (Pulvermüller, Lutzenberger et al., 1999). Interestingly, patients with Motor Neuron Disease or lesions in left-inferior frontal cortex show parallel impairments in processing verbs and action concepts (Bak et al., 2001; Kemmerer et al., in press; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003). These results demonstrate that inferior frontal cortex is necessary for the processing of action concepts and action-related verbs.[8]

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[7] Recently, Tomasino et al. (2007) confirmed body part specificity of motor cortex activation to action words presented in a semantic task, but not in a phonological task. As phonological processing induces patterns of motor system activation, which may overlay and interfere with semantically-induced activation (Pulvermüller et al., 2006), these results do not provide evidence against the automaticity of semantic motor mapping, which has been documented in a range of tasks (including semantic and lexical decision, passive reading, passive and distracted listening).

[8] Differential activation to noun and verb processing has even been observed for pseudowords presented in contexts that bias comprehension towards a noun or verb reading (Shapiro et al., 2005) and, interestingly, for *identical* inflectional affixes appearing on noun and verb stems (such as the word-final [t] in Finnish, which can function either as an inflectional noun or verb affix) (Pulvermüller & Shtyrov, 2009). These results have been interpreted in the sense that brain circuits of grammatical morphemes and grammatical processing units may link, respectively, with fractions of the action-perception circuits of the object nouns or action verbs with which they correlate (Pulvermüller & Shtyrov, 2009).

More fine-grained category dissociations have been reported in a different form of dementia, called Semantic Dementia (Patterson, Nestor & Rogers 2007). In this massive general semantic deficit, anterior-temporal areas are most severely affected initially, with lesions progressing to orbito-frontal areas. Consistent with this lesion pattern, semantic category-dissociations were found for face- vs. arm-related action words and for colour- vs. form-words (Pulvermüller et al., 2010). Together, these magnetic stimulation and patient studies show that the action-perception circuits found active in the processing of semantic word categories are also critical and necessary for the processing of words of specific semantic kinds.

Overall, the experiments show that the activation of motor systems of the cortex occurs early in action word processing, is automatic to some degree, and has a specific functional influence on the processing of semantic word kinds, especially action word types. This provides brain-based support for the idea that motor area activation reflects the comprehension of the semantic meaning of words regularly used to speak about actions. In the wider context of semantic theory, experimental results indicate that comprehension processes for specific kinds of words include the access to information about actions and perceptions that systematically relate to word meaning. It is noteworthy that neuroscience evidence was crucial in revealing this (Barsalou, 2008; Martin, 2007; Pulvermüller, 2005). However, it is equally true that behavioural experimental results are consistent with these conclusions and further strengthen the embodiment of language in action-perception mechanisms (Borghi, Glenberg, & Kaschak, 2004; Boulenger et al., 2006; de Vega, Robertson, Glenberg, Kaschak, & Rinck, 2004; Fischer & Zwaan, 2008; Gentilucci et al., 2000; Glenberg & Kaschak, 2002; Richter & Zwaan, 2009). *In general, the brain-mechansistic differences between word types seem to show a relationship to their different roles in language use (*Section 2*).*

10. Neuroscience and semantics: some crucial questions

Much of this article focused on the question of whether there are brain manifestations of meaning, whether these reflect semantic kinds of words and which mechanisms might underlie them. The results are important for clarifying the brain basis of meaning. They are also consistent with, and therefore support, a certain view on semantic differences between “word kinds”, the nature of meaning and a view of language as being tightly interwoven with action.[9] Therefore, this research may constitute a reason to discuss the possibility that neuroscience evidence might potentially be a useful complement of semantic theory. Are neuroscience theory and data relevant for answering questions in the field of semantics? This and the following section will now highlight selected questions for which neuro-semantic interaction might be beneficial.

10.1. Is sentence meaning derived compositionally from word meanings?

In the context of brain imaging work on sentence processing, semantic compositionality had been touched upon: Is sentence meaning, especially the meaning of abstract sentences, computed compositionally from the meanings of composite words? A potentially relevant finding was that the *meaning of words* included in abstract idiomatic sentences, whose semantics is not easily deduced from their constituent parts, became manifest when subjects understand the meaning of *the abstract sentences* (Boulenger et al., 2009). Keeping in mind all limitations and the preliminary character of any initial finding, this result is consistent with the view that the constituent words’ meanings are accessed in the comprehension of abstract and opaque sentence meaning.

10.2. Are form and meaning of signs processed in encapsulated systems?

A different type of question receives a clear answer on the basis of the results reported. In linguistics, core language processes have been conceptualised as modular and encapsulated (Hauser,

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[9] The results on action words are more difficult to reconcile, for example, with semantic theories defining meaning as object relationship only or with linguistic models envisaging word form (lexeme or lemma) processing as encapsulated from semantics.

Chomsky, & Fitch, 2002). One may therefore ask whether the processing systems for phonological and word form on the one hand and semantics on the other are modular, so that each of them computes an output without being influenced by the other. The fact that magnetic pulses and lesions to the motor system influence the recognition of specific kinds of action words constitutes evidence that the symbol processing system is not encapsulated from the action system viewed as a contributor to semantic processes (Pulvermüller, Hauk et al., 2005). A range of highlighted results suggest that semantic action systems of the brain interact with perisylvian lexical circuits in the recognition of words; a similar point can be made for interactions with perceptual systems. The neuroscience perspective offered by a principled approach to the brain theory of lexico-semantic circuits equally advocates the position that linguistic and semantic systems are tightly interwoven and interdependent functionally. This confirms that, at the level of the brain, language is "woven into action" (§ 7, Wittgenstein, 1953) in a neuromechanistic sense.

10.3. Are semantic categories inborn?

Is it necessary to postulate semantic distinctions at a symbolic level, possibly *predetermined by genetically fixed mechanisms (Caramazza & Mahon, 2003), or do they rather emerge naturally, in the learning of perceptual differences and action types (Elman et al., 1996)?* The close relationship between cortical systems for perception and action, even their specific subsections, as in the case of motor representations of body parts or types of visual information, and corresponding areas activated during, and contributing to, semantic category processing, strongly suggests a tight link, possibly even shared neuronal circuits, between sensorimotor and semantic processes (Kiefer & Pulvermüller, in press; Pulvermüller & Fadiga, 2010). The arbitrary relationship between symbols and their specific meaning and usage can only be established by learning (for a neuronal model, see Wermter et al., 2004). However, equally important for this kind of learning is the fact that the brain separates sensory and motor information topographically, and motor and perceptual systems are in themselves pre-structured in relevant ways, for example into areas dedicated to specific parts of the body and types of visual information. The relevant learning mechanisms are therefore effective in a highly prestructured neuronal engine. *The interplay between inborn factors and learning in determining the brain correlates of semantic processing is an important target for future research.*

10.4. Can action knowledge be semantic knowledge?

From a principled theoretical perspective, one may question the idea that activity in sensorimotor systems might actually reflect semantic processes. In neuroscience, the idea sometimes emerged that there is a main centre for semantic binding far removed from primary cortices, which most researchers envisage to lie in inferior-temporal lobe, where language and visual systems interface with each other, and a location for word-meaning binding is therefore plausible given meaning is conceptualised as object-reference (for discussion, see, for example, Hickok & Poeppel, 2007; Price, 2000; Pulvermüller, 1999). *In contrast with this position, analyses of brain imaging studies show that brain regions distributed over the entire left hemisphere (and partly in the right) are active in semantic processing (Binder, Desai, Graves, & Conant, 2009; Pulvermüller, 1999; Vigneau et al., 2006), with some of this distributed semantic activation being systematically linked to word meaning type (Fig. 5, Pulvermüller, Kherif et al., 2009). Along with* the belief in a single meaning centre, areas that deal with the trivialities of motor movements, and equally those involved in elementary visual feature processing, are sometimes thought to be incapable of contributing to higher cognitive processes including meaning understanding. Even though there is significant correlation between local source strengths in inferior arm-/face-related and dorsal leg-related areas of sensorimotor cortex and the semantic ratings of individual words obtained from study participants (Pulvermüller, Shtyrov et al., 2005), one may, in theory, question whether action features are excluded from semantics by definition.

However, such a position would not be reasonable. Crocodiles and alligators are defined by certain properties, including form and colour features, in the very same way as the concepts of walking or ambulating are crucially linked *to specific motor programmes (or schemata) for movements of the legs. The perceptual and conceptual similarity in colour and form features corresponds to the similarities between* *movement trajectories, muscle participations and patterns of motor coordination. Semantic features and similarities can be defined in the very same way in the perceptual domain as they apply in the domain of actions.* Certainly, there is room for derived, including metaphorical, usage. As a big fish might be called the crocodile of its fish tank (even if it is not green), one may speak of walking on one's hands or a stroll through the mind (thus ignoring the feature of body-part relatedness). One may even tell a story about a crocodile with artificial heart and kidneys, although it had generally been agreed upon, following Frege, that these ingredients are part of the definition of an animal (or, more appropriately, a higher vertebrate) (Frege, 1966). That walking is related to the legs may therefore be considered an analytical truth, in the same way as a crocodile is defined as having a heart, and in spite of the fact that one can use the hands for an activity analogous to walking. This may simply be considered a modified type of walking, as the post-surgery crocodile is a modified crocodile. Instances of heartless crocodiles and hand-supported walking are possible, but probably not in the range of typical uses of these words. It seems safe to include both perceptual properties such as green-ness and action aspects such as leg-relatedness in the set of possible semantic features. Generally, this discussion above is an illustration of the usefulness of another concept coined by Wittgenstein, that of family resemblance as the basis of word usage and meaning (Wittgenstein, 1953). It is, in fact, not correct to stipulate a defining set of common feature of all instances of reptiles, locomotion, or games, but the different entities these words are being used to talk about show family resemblance instead. And semantic family resemblance can apply to object words ("crocodile", "alligator") as it applies to action words ("ambulate", "walk").

In essence, there do not seem to be strong conceptual arguments against the view that knowledge about how to act and interact should be excluded from semantic knowledge. In view of the strong arguments that action and interaction play a prominent role in semantic learning, it is necessary to consider action semantics.

10.5. Do all action words have underlying semantic action circuits?

It should be noted that not all action-related words can be conceived as being related to semantic action circuits in the brain's motor system (for discussion, see Pulvermüller, 1999). For actions outside the repertoire of the perceiver, it is questionable whether action-perception circuits exist. A barking dog waggling its tail will not spark action-related neurons in humans (cf. ref., Buccino et al., 2004) and similarly the semantics of the corresponding words and phrases would therefore be unlikely to involve semantic action circuits. Nevertheless, humans can recognize these actions and understand the words, presumably on the basis of visual information processed in inferior-temporal cortex and corresponding perceptual-semantic systems. However, if a given action is part of the action repertoire of the acting individual, semantic action-perception circuits are being established in that individual's brain, which can be linked up with linguistic circuits. Within the resultant higher-order circuits, neurons located in motor systems can exert facilitation on the circuits' neurons in perceptual areas, thus improving perception and language understanding (see Garagnani et al., 2008). For language related to the action repertoire established in a community, there should therefore be a role of semantic action circuits in both language perception and semantic comprehension processes.

10.6. And finally: what about abstract words?

"Abstract concepts such as "freedom" and "ethics", or logical concepts such as "if" and "not" have a conceptual structure only. It is hard to see how their meaning could be derived from motor system properties" (Toni, de Lange, Noordzij, & Hagoort, 2008). Clearly, there are highly abstract concepts for which a deduction from sensory input or action features would be very difficult to construe. One proposal therefore complements an embodied action-perception system for semantically simple action- and object-related symbols with an abstract symbolic system, in which all meanings are stored, and which thus also takes care of the difficult cases, the abstract terms (Mahon & Caramazza, 2008). This proposal does not appeal because of the redundancies it implies. Why should motor concepts be stored redundantly, both in motor and symbolic systems (Kiefer, Sim, Helbig, & Graf, in press)? Barsalou proposed grounding abstract meaning in embodied mechanisms, for example of the meaning of the word "or" in the alteration of the visual simulations of objects (Barsalou, 1999). However, if this view is correct, the disjunction concept would, in fact, be realized as the mechanism allowing the brain to switch on and off specific representations alternatingly. A brain mechanistic underpinning of abstract meaning is still missing.

It is evident that every brain, even every primitive nervous system, is equipped with mechanisms for disjunction, conjunction, negation and other logical operations. *Let me qualify this statement. Assume that there are two neural elements each of which becomes active when the individual sees one specific object, called A and B. A third neuron receives input from both and can be activated by either input. Now, activity of the third neuron signals that A or B is present. If the third neuron has a high threshold for becoming active, it may need both inputs to be active, in which case its activation would index "A and B", that both objects are present. In this sense, a neuron can be said to mechanistically realise, or "calculate", logical operations, "or", "and", "not" and, with slightly more elaborate wiring, "either-or", identity and temporal statements such as "always" or "once". The examples illustrate that our brain is equipped with built-in mechanisms relevant for logical operations. This was proposed in an early article by McCulloch and Pitts entitled "A logical calculus of ideas immanent in nervous activity" (McCulloch & Pitts, 1943) and has since inspired work in the theory of automata (Kleene, 1956) and language (e.g., Braitenberg & Pulvermüller, 1992; Schnelle, 2010)*. Main points of this logical calculus theory of neuronal function still hold true although neuron models have significantly improved since the proposal was first made (e.g., Bussey, Saksida, & Murray, 2005). Therefore, considering again the statement cited at the beginning of this subsection, there is no need to construe the semantics of "and" and "or" and other highly abstract words or deduce them from sensorimotor information. *It rather appears that mechanisms for logical relationships are built-in in nerve cell circuits, thus enabling us to abstract away from the sensory input to more and more general concepts.*

Integration of logical circuits with sensorimotor circuits can provide a mechanism for abstract concepts. At the theoretical level, the relationship between an abstract word such as "to free" or "freedom" and patterns of concrete actions and experiences is complex. In one view, the class of "freeing" actions includes a range of very different basic activities (unlocking door, opening hand cuffs etc.) that typically remove a constraint from an entity. The actions and perception involved can vary greatly and it would be a mistake to search for the common semantic feature of all cases; the relationship that holds between them is (once again) best described as family resemblance. In brain terms, a mechanism that "calculates" an either-or function over a wide range of action-perception circuits provides a candidate mechanism for realising such abstract semantic concepts. The abstract semantic circuits that "calculate" either-or functions over semantic action-perception circuits should be expected to emerge close to the motor, visual and other perceptual areas, that is, in prefrontal and anterior-temporal cortex (Pulvermüller, 2008). This suggestion is in good agreement with empirical evidence. Brain systems activated by abstract word and sentence processing overlap with language areas, but involve additional areas, especially dorso-lateral prefrontal cortex, angular gyrus and temporal pole (Binder, Westbury, McKiernan, Possing, & Medler, 2005; Boulenger et al., 2009; Lauro, Tettamanti, Cappa, & Papagno, 2008). Extending the mechanistic brain perspective outlined above offers tentative circuit models of abstract word meaning which may eventually lead to a better understanding of the abstract semantics of sentences (Feldman, 2006, 2011; Lakoff, 1987).

11. Brain basis of combinatorial semantics

Word meaning can be learned from context. This crucial fact is frequently raised as an argument against approaches that relate semantic learning to object and action contingencies of words. *The Augustinian and Wittgensteinian word learning paradigms discussed in* Section 2 *represent two examples of situations relevant for semantic learning at very early stages of language acquisition in children.* In fact, only a minority of words is being learned in the context of reference object perception and action execution (see, e.g., Kintsch, 1974; Kintsch, 1998). The word-object and word–action learning paradigms are therefore insufficient as a full account of semantic learning. What are the neurobiological mechanisms that could support semantic learning from context?

After action-perception learning of aspects of word meaning has taken place for a sufficiently large set of words, it becomes possible to learn semantic properties "parasitically" when words occur together in strings, sentences or texts (Pulvermüller, 2002). When new and therefore still meaningless word forms are being encountered by the learner together with known meaningful words, widely distributed lexico-semantic circuits are active together with the perisylvian circuits of the unknown items. Correlated activation of the perisylvian word form circuit of the new item with semantic feature neurons of already known words can account for context-induced binding of semantic information to the new word form (Pulvermüller, 2002). This off-line mechanism provides a basis of second order, context-based, or "parasitic", semantic learning and provides a putative neuroscience explanation for why word-word correlation approaches to meaning are successful in modelling semantic relationships between words (Kintsch, 2002; Landauer & Dumais, 1997). *Semantic learning from context can more easily account for the fast acquisition of a large vocabulary seen at advanced stages of lexical learning, especially during the so-called vocabulary spurt (Tomasello, 2005).* It is important, however, to note that this neurobiological mechanism of learning semantics based on word-word correlations requires that a sufficiently large set of semantic features and words has already been learned *by way of linkage of information about perceived objects, performed action and utterances used.* Otherwise, what Searle called the Chinese room argument – *that correlation patterns between symbols not grounded in objects and actions are insufficient for semantic information* – cannot be overcome (Searle, 1990). Along with word-object and word–action mapping, word-word correlation learning is indispensable for semantic learning of large vocabularies (Gleitman, 1990, 1994).

Still, such indirect, "parasitic" semantic learning is not plausible for words semantically unrelated to experiences or activities, for example function words and affixes primarily playing a grammatical role. Their usage seems to be linked to the occurrence of other word forms, rather than to semantic features. It is also essential to consider that Chinese-room type learning of semantics is evident, especially in learners suffering from sensory deprivation. Blind children are able to acquiring important aspects of the usage of colour words (Landau & Gleitman, 1985), even though the role colour information plays for their semantic system slightly differs from that in sighted individuals (Connolly, Gleitman, & Thompson-Schill, 2007). In their colour word learning, semantic information about colour could not possibly be extracted from sensory information but must be combinatorial in nature. An argument for the role of combinatorial mechanisms in semantics is also based on the documented links between syntactic structure of verbs and their semantic relatedness, as, for example, between verbs taking noun phrases or full complementizer phrases as their object complements ("He starts his …" vs. "He states that …", Fisher, Gleitman, & Gleitman, 1991; Gleitman, 1994). How would such combinatorial information be manifest in a neurobiological model of language?[10]

Nerve cells are not only especially responsive to simultaneous stimulation, they can also be selective to sequential input. Neuronal sensitivity to sequential input is the basis of movement detection, a process present in many animals' nervous systems (Barlow & Levick, 1965; Hubel, 1995; Reichardt & Varju, 1959). A similar mechanism may be crucial for processing linguistic sequences. If neurons or populations of neurons are sensitive to specific sequences of words, such elementary sequence detectors can contribute to a grammar mechanism at the neuronal level (Pulvermüller, 2003). Assume that the entire vocabulary of a language is listed at the top of a table and the same vocabulary also appears on its left; the individual cells of the table can then be taken to represent all possible ordered combinations of word pairs. The table can be filled by listing the number of occurrences of given word pair sequences (within a local context of a few items) obtained from a corpus. Fig. 6 shows results for 20 words obtained for pair sequences taken from the 100 Mio words of the British National Corpus. Neuronal networks that mimic the high connectivity within areas can now be fed with these data. Such neurocomputational studies make it possible to study putative neuronal learning processes induced by combinatorial information.

In such simulation studies, strings with shared constituents led to the correlated activation of sequence detectors for these similar strings and to tightening of connections between them. This

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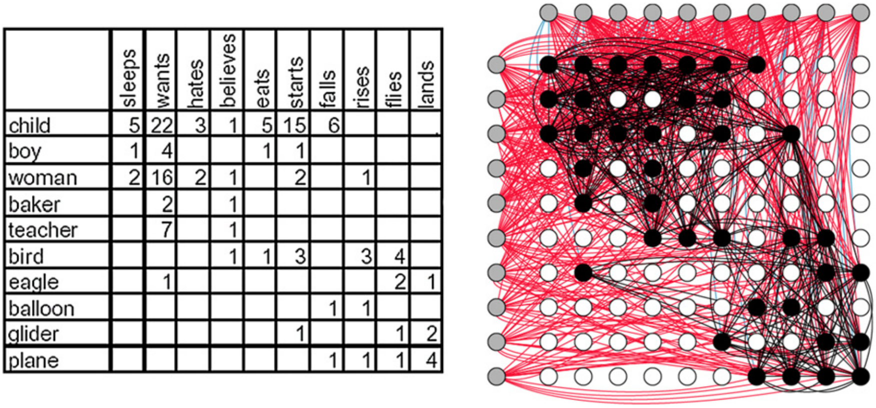
[10] To note, a number of problems pointed out by Gleitman (e.g., in Gleitman, 1990) can be solved using the action approach and word–action learning paradigm. Especially, a distinction between *give* and *take* is implicit in the action context, as the actor is taking only one of the two roles and the commenter/caretaker can refer to that role. In addition, as pointed out in Section 4, relatively abstract inner state can be taught insofar as these inner states have reliable outer criteria in infants (who do not yet know how to cheat and fake). However, Gleitman's general point about meaning-structure correspondence and its usefulness in aiding language learning is an important one and needs to be addressed within a neurobiological approach to language.



	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

Fig. 6. Combinatorial information immanent to noun-verb sequences and network result of storage of this information in an auto-associative memory which includes sequence detectors for word pairs. The diagram on the left presents the matrix of co-occurrences of 20 nouns and verbs obtained from the British National Corpus, BNC (in number of noun-verb pair occurrences per 100 million words of text). The diagram on the right shows the network of lexical circuits and sequence detectors and the connections strengthened by learning the string set obtained from the BNC. Grey circles in the periphery represent neural units corresponding to the words in the diagram on the left. The central matrix shows sequence detectors corresponding to word pair sequences. Filled black circles indicate sequence detectors whose respective word pair was in the input, leading to strengthening of connections between sequence detector and word-related neuronal units (in red). Black lines show strengthened auto-associative links between pairs of sequence detectors. At the top left and bottom right, two discrete combinatorial neuronal assemblies, DCNAs, have formed. Depending on the threshold of activation, these DCNAs either bind all nouns to verbs, or provide specific syntactic-semantic linkage of action verbs and nouns related to living entities, and of flight-related verbs and flying-object nouns (after Pulvermüller & Knoblauch, 2009). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

association process between combinatorial units resulted in neuronal aggregates of sequence detectors with surprising properties. The neuronal aggregates, or *discrete combinatorial neuronal assemblies*, connected classes of lexical elements, such as nouns and verbs, and supported syntactic generalisation, suggesting a similarity to grammatical rules (Knoblauch & Pulvermüller, 2005; Pulvermüller & Knoblauch, 2009). Important in the present context is that the combinatorial information extracted from text corpora led to a stronger association of lexical category members with similar semantic features. For example, Fig. 6 shows a subdivision of the noun group into words for living beings – which are strongly linked to action and mental verbs – and words for flying entities – which are linked to movement-related verbs. Note that the semantic categories are overlapping and so are the combinatorial assemblies. The co-occurrence statistics of words in strings is long known to include a wealth of grammatical-syntactic information (Brent, 1993; Brent and Cartwright, 1996), including sub-categorizations of lexical word categories reflecting semantic features (Briscoe & Carroll, 1997; Lin, 1998). Similar lexico-semantic classification can be obtained for untagged text using neuronal network architectures, for example simple recurrent networks (Elman, 1990) or Kohonen maps (Honkela, Pulkki, & Kohonen, 1995), and mathematical techniques, for example Independent Component Analysis (Väyrynen & Honkela, 2005). Statistical and neural network approaches therefore seem to extract combinatorial information immanent to sentences. The present approach maps this information on a neuronal architecture consistent with the human brain. This research suggests that the learning of this combinatorial information entails the emergence of discrete combinatorial neuronal assemblies underlying the rule-like connection between syntactic-semantic word categories (e.g. nouns related to living entities – N [+living], verbs related to actions of living being – V [+action]; Fig. 6, Pulvermüller, 2010; Pulvermüller & Knoblauch, 2009).

Realistic neuronal circuits taking into account combinatorial information therefore classify lexical items into semantic categories. Other structural information, for example the number of noun complements and the linkage of complementizers to verbs, can be included in this type of neurobiological model (Pulvermüller, 2003). As combinatorial neuronal processes mapping word-word correlation are distinct from the mechanisms of word-world learning discussed in detail in previous sections, the neurobiological theory of language accounts for both major facets of semantics. In contrast to word-object and word–action semantic learning, which critically depend on neuronal links between the perisylvian language cortex and sensory and motor systems of the brain, the word-word correlation machinery seems to draw upon left-perisylvian cortex where all words have parts of their circuits localised (Fig. 5, see also Hagoort, 2005).

12. Summary and outlook

This paper focused on a range of different facets of semantics. Based on the models discussed and evidence reported, these facets and their brain basis can be described as follows:

- *Object- and action-semantics:* Semantic knowledge also manifest in correlations between symbols and action execution or object perception are stored in widely dispersed cortical action-perception circuits involving cortical motor, sensory and multimodal areas (Sections 2, 5, 7 and 8).
- *Affective-emotional semantics:* Emotional-affective information immanent to the meaning of words is stored in links between perisylvian cortical circuits and their "limbic tails", involving a range of cortical areas (oribtofrontal, insular, cingulate, and anterior-temporal cortex) and subcortical nuclei of the limbic system. These links vary between more and less affective-emotional words and may develop differently in well- and not-so-well-acculturated second language learners (Section 6).
- *Abstract semantics:* The meaning of abstract words related to classes of actions and events is computed by logical circuits operating on action-perception circuits, which draw upon prefrontal, anterior-temporal and parieto-temporo-occipital cortex (Section 10).
- *Combinatorial semantics:* The knowledge immanent to the co-occurrence of classes of structurally and semantically related words is stored by discrete combinatorial neuronal assemblies linking syntactic-semantic classes of word-related circuits to each other; perisylvian cortex is a likely brain locus for these combinatorial neuronal assemblies (Section 11).

There is support from brain-theoretical considerations, neuronal modelling and neuroscience experiments for distinct semantic mechanisms for different kinds of words. Brain activation patterns distinguished between semantic word categories and suggest distributed semantic circuits with different cortical topographies for

- Action words related to actions typically performed with the face, arm and leg words in fronto-central cortex,
- Object words related to animals or tools, and to objects with typical colour or form features in inferior-temporal cortex,
- Sound words in auditory system,
- Emotion and odour words in the limbic system.

In language comprehension, activation of these semantic action-perception circuits emerges early and even in tasks where subjects do not attend to language stimuli. Similar category-specific action patterns also emerge during sentence processing. The category-specific semantic circuits for words inferred from brain activation studies predict *functional contributions of category-specific focal areas,* which could be confirmed by neuropsychological TMS and patient studies. Especially noteworthy are

- Category effects of motor cortex TMS on lexical decision,
- Deficits in action verb processing in patients with focal lesions in the motor system, Motor Neuron Disease and Parkinson's Disease, and
- Processing differences between semantic word categories in patients with language and conceptual deficits due to stroke, dementia and other neurological diseases.

Finally, there were several lines of influence from language philosophy and linguistics that led to fruitful neuroscience research and, in return, a confirmation of some earlier suggestions:

- Word kinds differ between each other – semantically and in terms of brain mechanisms.
- Language is “woven into action” in a very concrete sense: by way of semantic links between language and motor cortex.
- Action-perception mechanisms are a necessary component of semantic learning, but combinatorial information is an important complement. Brain-wise, neurocomputational studies indicate that combinatorial knowledge becomes manifest in syntactic-semantic categories of lexical items.

Sections 10 and 11 highlighted further semantic issues to which neuroscience research can contribute, including neuromechanistic aspects of combinatorial and abstract semantics, the brain basis of a priori semantic distinctions, and questions of modularity and compositionality.

These results underscore the importance of linking semantics and neuroscience research even more closely in the future. Neurosemantics as the study of brain circuits of meaning opens a new way of addressing old questions and eventually reach a state where semantic theory can be underpinned by mechanistic neuronal circuit models that predict, explain and, if implemented appropriately, may eventually partly complement or even replace and assist semantic capacities of humans. Open questions still left to address are ample, not least in the domain of word category processing and the processing of these word categories when they are embedded in sentences, discourse and communication.

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