 <p>What it means to Communicate</p>	<p>NESTCOM</p> <p>What it Means to Communicate</p> <p>Project reference Contract No: 043374 (NEST)</p>
---	--

Brain Embodiment Of Category-Specific Semantic Memory Circuits (WP1)

NESTCOM Report 2

Deliverable 1

Friedemann Pulvermuller

Report Version: 1

Report Preparation Date: 29 June 2007

Classification: Public

Contract Start Date: 1st January 2007

Duration: Two Years

Project Co-ordinator: Professor Stefan Wermter

Project Co-ordinator Organisation: University of Sunderland

Partners: University of Sunderland, Medical Research Council, Universita degli Studi di Parma



Project funded by the European Community under the Sixth Framework Programme NEST - New and emerging science and technology

At present, abstract and embodied theories of semantic and conceptual processing compete for the minds of cognitive scientists. Are concepts built in interaction with the world, from perceptual information? Or are they inborn and only in a very distant relationship with the “reality”, which contacts the thinking organs (if at all!) only via long axons and unreliable sensory organs? Can an abstract thought be built from sensory experience – or would there rather be need for other ingredients to construct abstraction? These are questions that heated the debate in ancient Greece – cf. Plato’s and Aristotle’s positions – and are being warmed up in contemporary cognitive and brain science. Can we add anything new? Well, we have a vast number of nice brain pictures to show – pictures that indicate brain parts active when people think, speak, listen and understand. But a colored picture is not always easily converted into a new insight. Here, the embodiment question will be addressed on the basis of new evidence from cognitive neuroscience, in the hope that the brain pictures, especially the dynamic ones, might be telling – or, more modestly, somehow helpful in contributing to the debate.

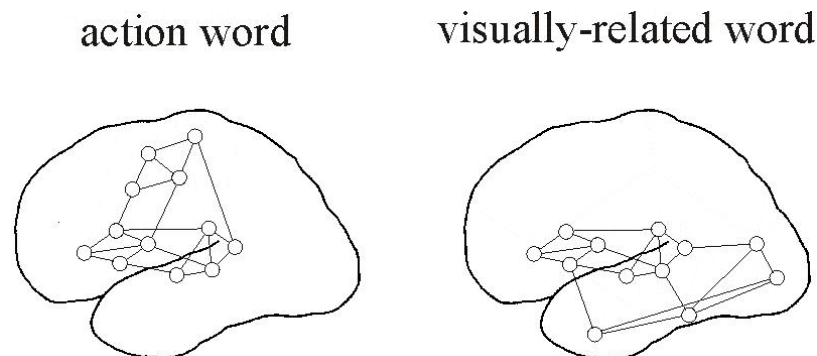
Embodied action-perception networks for storing semantic information: The case of category-specificity

Where is word meaning represented and processed in the human brain? This question has been discussed controversially since 19th Century neurologists postulated a “concept center” in the brain that was thought to store the meanings of words (Lichtheim, 1885). Today, the cortical loci proposed for a center uniquely devoted to

semantic processing range from inferior frontal cortex (Bookheimer, 2002; Posner & Pavese, 1998) to anterior, inferior, superior, or posterior left temporal cortex (Hickok & Poeppel, 2004; Patterson & Hodges, 2001; Price, 2000; Scott & Johnsrude, 2003). Others have proposed that the entire left fronto-temporal cortex is a region equally devoted to semantics (Tyler & Moss, 2001), or that the parahippocampal gyrus (Tyler et al., 2004) or the occipital cortex (Skrandies, 1999) are particularly relevant. As there is hardly any area in the left language-dominant hemisphere for which there is no statement that it should house the semantic binding center, these views are difficult to reconcile with each other (see Pulvermüller, 1999). Is there a way to resolve this unfortunate diversity of opinions?

A way out might be pointed by approaches to category-specific semantic processes (Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; Humphreys & Forde, 2001; Warrington & McCarthy, 1983; Warrington & Shallice, 1984). The idea here is that different kinds of concepts, and different kinds of word meaning, draw upon different parts of the brain. Hearing the word “crocodile” frequently together with certain visual perceptions may lead to strengthening of connections between the activated visual and language-related neurons. Specific form and color detectors in primary cortex and further neurons responding to more complex features of the perceived gestalt higher up in the inferior temporal stream of visual object processing will become active together with neurons in the perisylvian language areas that process the word form. These neurons would bind into distributed networks now implementing word forms together with aspects of their referential semantics. In contrast, learning of an action word, such as “ambulate”, critically involves linking an

action type to a word form. In many cases, action words are learned in infancy when the child performs an action and the caretaker uses a sentence including an action word describing the action (Tomasello & Kruger, 1992). As the brain circuits for



controlling actions are in motor, premotor and prefrontal cortex, it is clear that, in this case, correlated activation should bind perisylvian language networks to frontocentral circuits processing actions.

Figure 1 A brain-based model of category-specific processing of words with different semantics. Words semantically related to actions may be cortically processed by distributed neuron ensembles linking together word forms and action programs. Words referring to objects that are perceived through the visual modality may be processing by neuron sets distributed over language areas and the visual system (Pulvermüller, 1996).

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 (Figure 1, Pulvermüller, 1996, 1999). Many nouns refer to visually perceivable objects and are therefore characterized by strong semantic links to visual information, whereas most verbs are action verbs and link semantically to action knowledge. Like action verbs, nouns that refer to tools are usually also rated

by subjects to be semantically linked to actions, and a large number of animal names are rated to be primarily related to visual information (Preissl, Pulvermüller, Lutzenberger, & Birbaumer, 1995; Pulvermüller, Lutzenberger, & Preissl, 1999; Pulvermüller, Mohr, & Schleichert, 1999). 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. 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 or premotor areas, more strongly than words without strong semantic action links. The same was found for temporo-occipital areas involved in motion perception. On the other hand, words with visual semantics tended to activate visual and inferior temporal cortex or temporal pole more strongly than action-related words. This differential activation was interpreted as evidence for semantic category-specificity in the human brain (Martin & Chao, 2001; Pulvermüller, 1999).

Some problems with semantic category-specificity

Indeed, the 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. However, it has

been asked whether the reason for the differential activation observed would necessarily be semantic or conceptual in nature. Could there be alternative explanations?

Although the broad majority of the imaging studies of category-specificity support the idea that semantic factors are crucial, there is work that could not provide converging evidence (Devlin et al., 2002; Tyler, Russell, Fadili, & Moss, 2001). These studies used particularly well-matched stimuli, so that word length, frequency and other psycholinguistic factors could not account for any possible differences in brain activation. Therefore, these authors argued that these factors might account for differences between “semantic” categories reported previously. Although some earlier studies reporting semantic category differences performed meticulous stimulus matching for a range of psycholinguistic factors, 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 did not control for these factors. 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. Any difference in brain activation, and also any differential vulnerability to cortical lesion, could thus be explained 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 could contribute to the explanation of category dissociations (Humphreys & Riddoch, 1987; Rogers et al., 2004; Tyler, Moss, Durrant-Peatfield, & Levy, 2000).

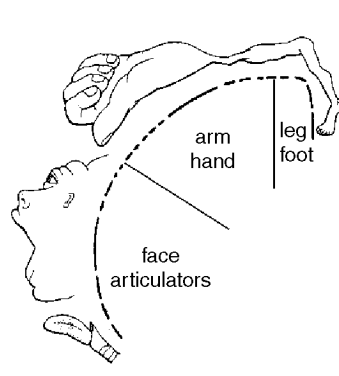
On these grounds, at least some evidence for category-specificity has therefore been criticized as being not fully convincing.

What makes things worse is that predictions on where category-specific activation should occur in the brain have not always been very precise. Whereas rough estimates, such as the prediction that action semantics should involve frontal areas and visual semantics temporo-occipital ones, could be provided and actually confirmed, the more precise localization was sometimes surprising and not a-priori predictable. For example, semantic information related to processing of color and motion information semantically linked to words and pictures was reported to occur ~2cm anterior to the areas known to respond maximally to color or motion, respectively (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). 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 is opened by looking at subtypes of action words.

Cortical embodiment of semantics: the case of action words

Action words are defined by abstract semantic links between language elements and information about actions. These words refer to actions and the neurons that process the word forms are likely interwoven with neurons controlling actions. The motor cortex is organized in a somatotopic fashion with the mouth and articulators represented close to the sylvian fissure, the arms and hand at dorsolateral sites and the foot and leg projected to the vertex and interhemispheric sulcus (Figure 2, Penfield & Rasmussen, 1950). Additional somatotopic maps exist in the

frontocentral 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 refer to movements of the face or articulators, arm or hand, or leg or foot, the distributed neuronal ensembles would therefore include semantic neurons in perisylvian (face words), lateral (arm words) or dorsal (leg words) motor and premotor cortex (Pulvermüller, 1999). This is the essence of the somatotopy-of-action-word model, which implies differently distributed networks for the English words *lick*, *pick* and *kick* (Figure 2). The 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-centered workspace suggested by recent work (Graziano, Taylor, & Moore, 2002).



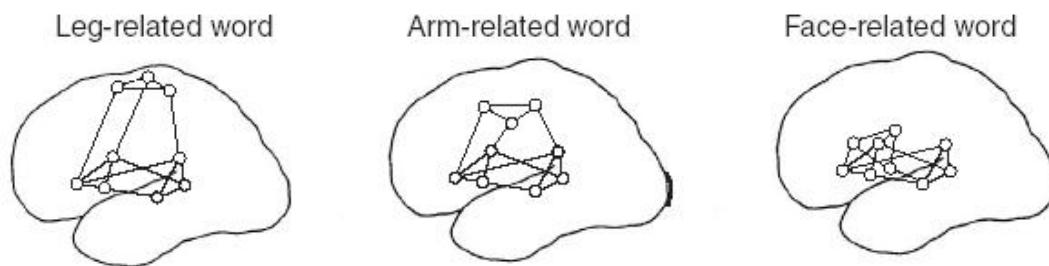


Figure 2 Semantic somatotopy model of action word processing: Distributed neuronal assemblies bind information about word forms and the actions they refer to semantically. Because action words can relate to different parts of the body (examples: lick, pick, lick), the cortical distributions of their perception-action networks differ between each other (Pulvermüller, 2001). The inset shows the somatotopy of the primary motor cortex as revealed by Penfield and colleagues (Penfield & Boldrey, 1937).

Crucial predictions of the semantic somatotopy model is that perception of spoken or written action words should activate cortical areas involved in action control and execution in a category-specific somatotopic fashion, depending on the semantics of the action words. As the cortical areas of action control and execution can be defined experimentally, one could in principle use such action localizer experiments to predict exactly where semantic activation should occur for different aspects of action-related meaning.

In functional imaging experiments, elementary repetitive movements of single body parts activate motor and premotor cortex. For example, Hauk *et al.* reported functional MRI data showing that tongue, finger and foot movements lead to the somatotopic activation pattern illustrated in Figure 3 (diagram on the left, Hauk, Johnsrude, & Pulvermüller, 2004). 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 (Figure 3,

diagram on the right, Hauk et al., 2004). Consistent with earlier findings, all words equally activated areas in the temporal cortex and also in the inferior frontal cortex (Pulvermüller, Shtyrov, & Ilmoniemi, 2003; Wilson, Saygin, Sereno, & Iacoboni, 2004; Zatorre, Evans, Meyer, & Gjedde, 1992). 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 perception-action networks, provides strong evidence for this theory in particular and for the embodiment of aspects of semantics in action mechanisms in general.

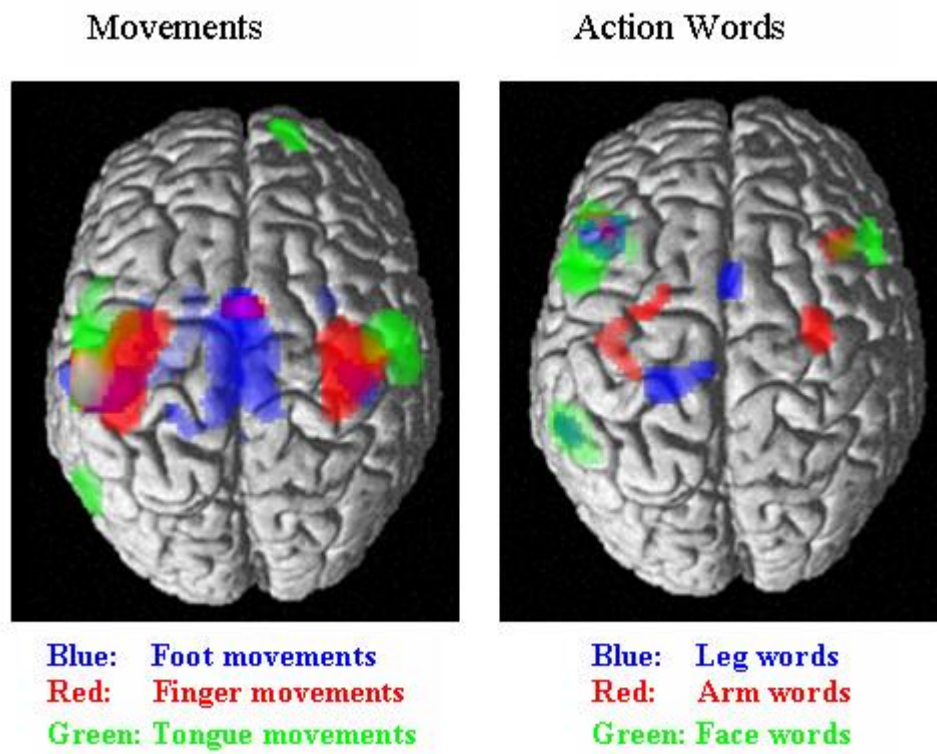


Figure 3 Cortical activation (fMRI) during motor movements and during passive reading of action words. Overlapping activation is elicited by both leg- (blue), arm- (red), and face-related (green) movements and words, indicating a common neural substrate for the processing of actions and the meaning of action words (after Hauk et al., 2004).

A similar experiment 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 was monitored (Tettamanti et al., 2005). Specific premotor areas reflecting the differential involvement of body part information in the semantic analysis of the language input were again found active. Taken together, these fMRI results indicate that somatotopic activation of motor circuits reflects aspects of word and sentence meaning, and that such activation can be elicited by spoken and by written language.

Somatotopic semantic activation: Comprehension or post-comprehension inference?

Although language-related somatotopic cortical activation could be demonstrated, the low temporal resolution of haemodynamic imaging makes it impossible to decide between two interpretations of this finding: One possibility is that the activation of specific action-related networks directly reflects action 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 behavioral work on embodiment (Glenberg & Kaschak, 2002). It is possible that thoughts about actions actually follow the comprehension process and behavioral, but also brain-physiological, effects relate to such “post-understanding inference”. 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, 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? Let me propose that brain processes reflecting comprehension can be characterized as (1) *immediate*, (2) *automatic*, and (3) *functionally relevant*.

- (1) *Immediacy*: Early effects of lexical and semantic processing are known to occur around 100-200 ms after critical stimulus information comes in (Pulvermüller & Shtyrov, 2006; Sereno, 1998 #3564). In contrast, late postlexical meaning-related processes are reflected by late components of the event-related potential (ERP) and field, which are maximal around 400 ms after word onset (Holcomb & Neville, 1990). If the activation of motor areas is related to semantic processes intrinsically tied to word form access, it should take place within the first 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. So brain processes reflecting comprehension might be expected to persist under distraction, when the subjects' attention is directed away from the critical language stimuli.
- (3) *Functional relevance*: If action words presentation leads to specific activation of motor systems relevant to word processing, one may even expect that a change of the functional state of these motor systems leads to

a measurable effect on the processing of words semantically related to actions.

However, if somatotopic activation of motor systems did reflect a post-comprehension process, it can be late (substantially greater than 200 ms) and absent under distraction, and function state changes in the motor system would be without effect on word processing.

A series of experiments was conducted to investigate these three issues. 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 (ERPs) looking at silent reading of face, arm and leg words showed that category-specific differential activation was present ~200 ms after word onset (Hauk & Pulvermüller, 2004). Consistent with the fMRI results, distributed source localization performed on stimulus-triggered ERPs revealed an inferior frontal source that was strongest for face-related words and a superior central source that was 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 postlexical motor preparation were reflected (Pulvermüller,

Härle, & Hummel, 2000). This speaks in favor of an interpretation of motor activation in terms of comprehension processes.

The earliness of word category-specific semantic activation along the sensorimotor cortex in passive reading tasks might suggest that this feature might be 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 (Figure 4). Relatively stronger activation was present in the left inferior frontal cortex for the face/arm-related word, but, significantly stronger activation was seen in superior central areas, close to the cortical leg representation, for the leg-related word (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, consistent with the spread of activation being mediated by fast-conducting cortico-cortical fibers between the perisylvian and dorsal sensorimotor cortex. This speaks in favor of automatic activation of motor areas in action word recognition and therefore further strengthens the view that this activation reflects comprehension. It appears striking that 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 idea that word-related, rather than task or strategy-dependent, mechanisms are being tapped into.

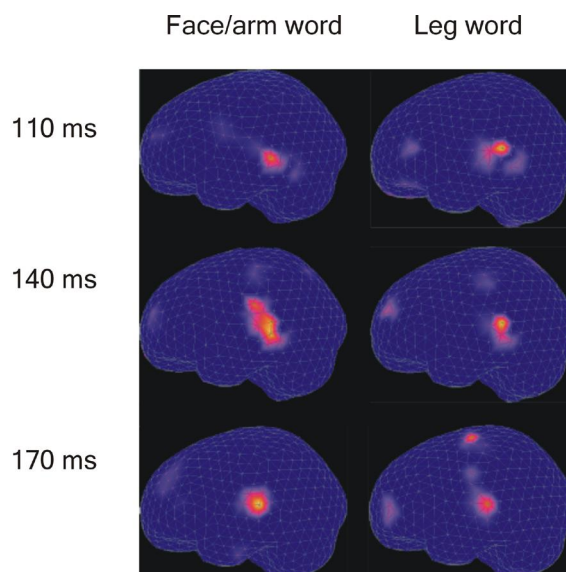


Figure 4 Cortical activation (MEG) elicited by face/arm (left) and leg-related words (right) at different times after spoken action words could be uniquely recognized. Note the slight upward movement of the inferior central source for the face/arm word and the delayed appearance of the superior central source for the leg word. These activation time courses may reflect the travelling

of neuronal activity in distributed neuronal assemblies that represent and process words with different action-related meanings (after Pulvermüller, Shtyrov et al., 2005)

Even if action word processing sparks the motor system in a specific somatotopic fashion, this still does not necessarily imply that the motor and premotor cortex influence the processing of action words. Different parts of the motor system were therefore 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, 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 (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 shows a specific influence of activity in the motor system on the processing of action-related words.

Further evidence for specific functional links between the cortical language and action systems comes from TMS-induced motor responses (Fadiga, Craighero, Buccino, & Rizzolatti, 2002). Listening to Italian sentences describing actions performed with the arm or leg differentially modulates the motor responses brought about by magnetic stimulation of the hand and leg motor cortex (Buccino et al., 2005). It appears that effective specific connections of language and action systems can be

documented for spoken or written language, at the word and sentence levels, and for a variety of languages (English, Italian, German, Finnish) using a variety of neuroscience methods (fMRI, MEG, EEG, TMS).

These 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 semantically specific functional influence on the processing of action words. This provides brain-based support for the idea that motor area activation is related to comprehension of the referential semantic meaning of action words. In the wider context of a theory of embodiment of conceptual and semantic processing, the conclusion is that comprehension processes are related to, or embodied in, access to action information. It is noteworthy that neuroscience evidence was crucial in revealing this (Pulvermüller, 2005). However, it is equally true that behavioral results are consistent with these conclusions and further strengthen the embodiment of language in action-perception mechanisms (Borghetti, Glenberg, & Kaschak, 2004; Boulenger, Paulignan, Roy, Jeannerod, & Nazir, 2006; de Vega, Robertson, Glenberg, Kaschak, & Rinck, 2004; Gentilucci, Benuzzi, Bertolani, Daprati, & Gangitano, 2000; Glenberg & Kaschak, 2002).

Does motor cortex map aspects of semantics?

One may question the idea that activity in the motor system might actually reflect semantic processes. The idea that there should be a specific center for semantics is still dominating (although there is little agreement between researchers about where the semantics area is situated, see paragraph on one or many semantics centers below). Areas that deal with the trivialities of motor movements, and equally

those involved in elementary visual feature processing, are therefore, by some, thought to be incapable of contributing also to the higher processes one might be inclined to reserve for humans. In this context, it is important to point to the strong evidence that activation in motor systems directly reflects aspects of semantics. Evidence that semantic features of words are reflected in the focal brain activation in different parts of sensorimotor cortex comes from MEG work on action words: There was a 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). This means that the subjects' semantic ratings were reflected by local activation strength and leaves little room for interpretations of other than a semantic nature.

Even though the action-related and visually-related features discussed, and the associative learning mechanisms binding them to language materials, may not account for all semantic features of relevant word-related concepts, it appears clear that they reflect critical aspects of word meaning (Pulvermüller, 1999): Crocodiles are defined by certain properties, including form and color features, in the same way as the concepts of walking or ambulating are crucially linked to moving one's legs. 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 is generally agreed upon, following Frege, that these

ingredients are part of the definition of an animal (or, more appropriately, a higher vertebrate) (Frege, 1966). That writing is related to the hand 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 it is possible to write in the sand with one's foot. This may simply be considered a modified type of writing, as the post-surgery crocodile is a modified crocodile. An instance of a heartless crocodile and leg-related writing is possible, but probably closer to metaphorical usage of these words than to their regular application. It seems safe to include perceptual properties such as greenness and action aspects such as hand-relatedness in the set of possible semantic and conceptual features.

A further point has sometimes been mentioned in the context of embodied approaches to semantics, the cell assembly model included. The idea that word-world correlation provides a significant explanation of the acquisition of word meanings has been criticized, because it is well known that only a minority of words are actually being learned in the context of reference object perception and action execution (Kintsch, 1974, 1998). However, after action-perception learning of aspects of word meaning has taken place for a sufficiently large set of words, it becomes feasible to learn semantic properties "parasitically" when words occur together in strings, sentences or texts. A neuroscientific basis for this "parasitic semantic learning" might lie in the overlap of word-related cell assemblies in the perisylvian language areas and the lack of semantic neurons related to action and perception information outside perisylvian space of the networks processing new words with unknown semantic features (Pulvermüller, 2002). In this case, a new word would activate its form-

related perisylvian cell assembly, while neurons outside perisylvian space processing aspects of the semantic of context words are still active. The correlated activation of the semantic neurons of context words and the form-related perisylvian neurons of the new word may lead to linkage of semantic features to the new word form. This provides a potential basis of second order semantic learning and provides a putative neuroscience explanation for why correlation approaches to word meaning are successful in modeling semantic relationships between words (Kintsch, 2002; Landauer & Dumais, 1997). It is important, however, to note that this mechanism can only succeed if a sufficiently large set of semantic features and words is learned through correlation of perception, action and language-form features in the first place. Otherwise, what Searle called the Chinese room argument, implying that semantic information cannot emerge from correlation patterns between symbols, cannot be overcome (Searle, 1990). Action-perception correlation learning and word-word correlation learning are both indispensable for semantic learning of large vocabularies.

The time course of semantic activation in action word recognition was on a rather short scale. Relevant areas were seen to be active already within 200 ms after critical stimulus information came in (Pulvermüller, Shtyrov et al., 2005; Shtyrov et al., 2004). This suggests early semantic activation, as early as the earliest processes reflecting phonological or lexical information access (Hauk, Davis, Ford, Pulvermüller, & Marslen-Wilson, 2006; Obleser, Lahiri, & Eulitz, 2003; Shtyrov, Pihko, & Pulvermüller, 2005). The early neurophysiological reflection of semantic brain processes does not imply that meaning processing is restricted to the first 200

ms after a word can be identified. There is ample evidence for neurophysiological correlates of semantic processes that take place later-on (Coles & Rugg, 1995). These later processes may follow upon the early semantic access processes and may reflect reinterpretation, which is especially important in circumstances where the context or other factors make comprehension difficult.

Abstraction from a brain perspective

Although these results demonstrate that action words activate the cortical system for action processing in a somatotopic fashion and that this somatotopy reflects word meaning, they do not imply that all aspects of the meaning of a word are necessarily reflected in the brain activation pattern that it elicits. It is possible to separate brain correlates of semantic features specifying face-, arm-, and leg-relatedness, or, in the visual domain, of color and form features (Moscoso Del Prado Martin, Hauk, & Pulvermüller, 2006; Pulvermüller & Hauk, 2006). It became even possible to provide brain support for the grounding of words referring to odors in olfactory sensation and evaluation mechanisms in brain areas processing olfactory and emotion-related information (González et al., 2006). However, for other semantic features, the idea that their meaning can be extracted from sensory input, or deduced from output patterns, is more difficult to maintain. Although the question how an embodiment perspective would explain abstraction processes has frequently been addressed (Barsalou, 1999, 2003; Lakoff, 1987), it is still not clear whether all semantic feature can – and have to – be extracted from input-output patterns.

A brain perspective might help to solve aspects of this issue. There are highly abstract concepts for which a deduction from sensory input is difficult to construe. Barsalou tried to ground the meaning of the word “or” in the alteration of the visual simulations of objects (Barsalou, 1999). However, if this view is correct, one might rightly claim that the disjunction concept would, in fact, be grounded in the alteration mechanism, which would allow the brain to switch on and off alternative representations alternately. Looking at the brain theory literature, it is actually very clear that any brain, even every primitive nervous system, is equipped with mechanisms for calculating disjunction, conjunction, negation and other logical operation. This was the content of an early article by McCulloch and Pitts entitled “A logical calculus of ideas immanent in nervous activity” (McCulloch & Pitts, 1943) and has since inspired much subsequent work (e.g., Kleene, 1956; Schnelle, 1996). Its main points still hold true although neuron models have significantly improved since the proposal was first made. These authors pointed out that, by wiring two neurons onto a third one and by adjusting the activation threshold of number three, conjunction and disjunction can be computed. Negation, identity and either-or computations would be equally straightforward (requiring slightly more or less neuronal material; Figure 5). These examples demonstrate that our brain comes with built-in mechanisms relevant for abstract semantic processing. There is no need to construe the semantics of “and” and “or” and other highly abstract words *exclusively* from sensory or motor information. It rather appears, that the very fact that these mechanisms are built-in in our brain enables us to abstract away from the sensory input to more and more general concepts.

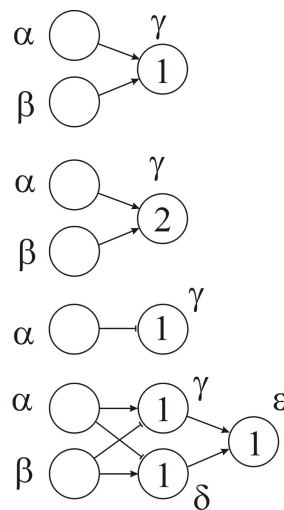


Figure 5 Logical circuits immanent to a network of neurons as discussed by McCulloch and Pitts (McCulloch & Pitts, 1943). If two neurons project to a third neuron, the activation threshold of the third neuron will determine whether it acts like a logical element symbolizing “or” (uppermost diagram) or “and” (second from top). Circuits symbolizing “not” and “either-or” can also be implemented. Arrows stand for excitatory and t-shaped line endings for inhibitory connections. Numbers indicate activation thresholds (after Pulvermüller, 2003).

Such enabling might apply to the computation of actions at different levels of the action description, corresponding to different levels of abstractness. Moving one arm in such and such a way is a basic action, opening a door could imply exactly the same movement but with characteristic somatosensory and possibly auditory input, and freeing somebody could also be realized by performing the same basic action. To implement the aspects of the action semantics of “open”, it is possible to connect disjunction neurons with a range of action control neurons coordinating alternative action sequences that would allow one to open doors, boxes, and other objects. Similarly, in order to implement action semantics of the word “free”, higher order disjunction neurons would be needed that look at a range of different movement programs one could perform in the context of setting somebody or something free. Again, additional conditions would, of course, need to be met too. For example, the

performer would need to assume that someone or something is captured, locked in, or contained in something else. Disjunction neurons looking at different concrete action representations may be located adjacent to motor and premotor sites and would be ideally placed in prefrontal cortex (see Pulvermüller, 1999). This hypothesis, that more abstract action-related word meanings are processed in areas adjacent to motor and premotor cortex, in prefrontal areas, receives strong support from recent imaging work (Binder, Westbury, McKiernan, Possing, & Medler, 2005; Pulvermüller & Hauk, 2006).

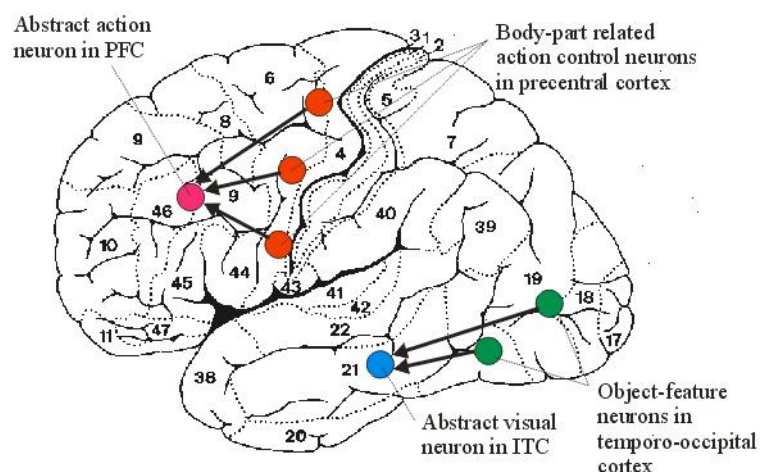


Figure 6 A model of modality specific abstraction processes in the human brain. Abstract words that can refer to a range of actions (e.g., “free”) have cell assemblies including neurons that act as disjunction units with input from a range of neurons controlling concrete body-related actions. These abstract action neurons are in prefrontal cortex. Similar abstract visual semantic neurons performing disjunction computations on visual input are in anterior areas of the inferior temporal “what” stream of visual processing, for example in parahippocampal gyrus (for a discussion of experimental evidence, see Pulvermüller & Hauk, 2006).

These hints towards abstraction mechanisms of different types might suffice here to point out some perspectives of a brain-based approach to embodied semantics.

Language processes in the brain – distributed and discrete

Similar to most current theories postulating distributed processing of language and concepts in the mind and brain (Rogers et al., 2004; Seidenberg, Plaut, Petersen, McClelland, & McRae, 1994), the current proposal puts that the cell assemblies processing words are widely distributed. This means that the neuronal ensembles are spread out over different areas of the brain or over different compartments of a neuronal model simulating these brain mechanism (Braitenberg & Pulvermüller, 1992; Pulvermüller, 1999; Pulvermüller & Preissl, 1991). However, in contrast to most distributed processing accounts, the cell assemblies are conceptualized as functionally coherent networks that respond in a discrete fashion. This implies that the networks representing words, the “word webs”, are either active or inactive and that the full activation of one word’s representation is in competition with that of other word-related networks. In this sense, cell assemblies are similar to the localist representations postulated by psycholinguistic theories (Dell, 1986; Page, 2000). Still, as each of the distributed cell assemblies includes neurons processing features related to form or semantics, there can be overlap between cell assemblies representing similar words or concepts. This leads to an interplay of facilitatory and inhibitory mechanisms when word webs become fully active in a sequence. The full activation, or ignition, of a word-related cell assembly can be considered a possible cortical correlate of word recognition – or of the spontaneous pop-up of a word together with its meaning in the mind.

If word webs can become active in a discrete fashion, this does not imply that each ignition is exactly identical to all other full activations of the network. As word

webs are linked to each other through the grammar network and also exhibit semantic and form overlap, the context of brain states and other cognitive network activations primes and therefore influences the way in which a given word web ignites. This may provide a mechanism for context-related focussing on semantic features.

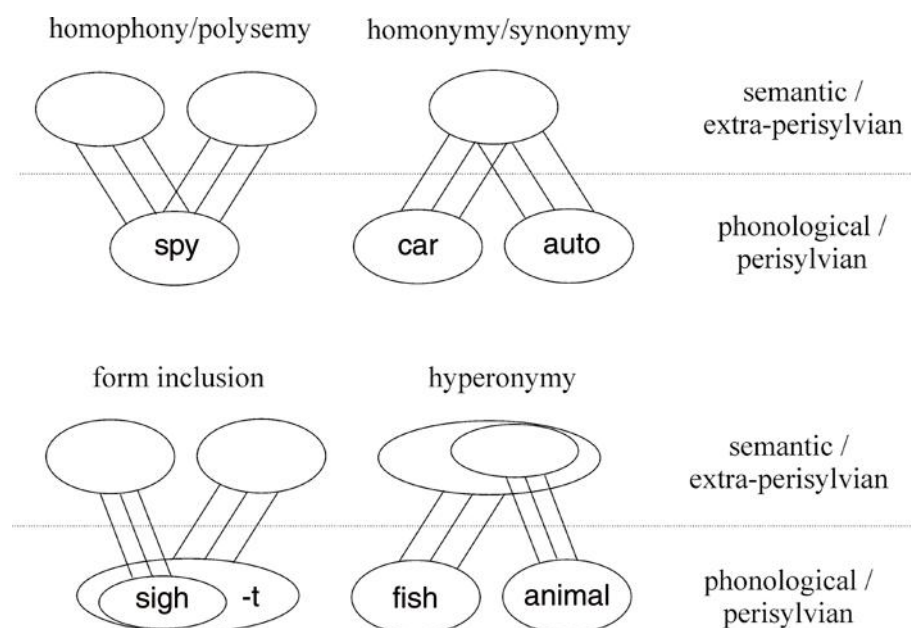


Figure 7 Word forms and semantics are proposed to be processed in different parts of the distributed word-related cell assembly. Most semantic information is stored outside the perisylvian language areas, whereas most information related to the phonological word form is in perisylvian space. Words related to each other phonologically or semantically would overlap in their perisylvian or extra-perisylvian sub-assemblies. Homophones

A further example is the contextual disambiguation of a semantically ambiguous word. The brain basis of an ambiguous word has been conceptualized as a set of two word webs overlapping in their form-related assembly part (Figure 7). Semantic context can, in this case, disambiguate by priming one of the semantic

subassemblies of the two overlapping word representations. The two overlapping cell assemblies would be in both facilitatory (due to form overlap) and inhibitory (due to competition between cell assemblies) interaction. Most likely, the facilitatory effects would precede the inhibitory ones (Pulvermüller, 2003).

One or more semantic-conceptual binding site?

Although the results on the cortical correlates of semantic word groups cannot be explained if all semantic processes are restricted to one cortical area, they might still be compatible with the general idea of a central semantic binding site. This system would be thought to manage dynamic functional links between multiple cortical areas processing word forms and conceptual-semantic information. The idea of such a central “concept area” or “convergence zone” has a long tradition in the neuroscience of language and seems to be motivated by the belief that a central locus must exist, at which concepts are related to each other and abstract information is extracted from them. As I have tried to make clear, it may be possible to implement semantic binding by distributed cell assemblies which, as a whole, function as binding networks. In this case, the binding would not be attributable to one specific brain area but rather to a set of areas, those over which the assembly is distributed. Still, there are certainly more peripheral areas, for example primary motor and sensory cortices, where correlated activation patterns occur in the first place, and areas connecting between these “peripheral” ones, with the major task of linking the correlation patterns together in a most effective manner. These higher or connection areas might naturally be more important for the binding of information from different modalities. Whether or not all these route for multimodal information linkage necessarily go

through the same convergence zone or rather through a range of different areas of association cortex, as neuroanatomical studies might suggest (e.g., Braitenberg & Schüz, 1998; Young, Scannell, Burns, & Blakemore, 1994), remains a matter of future research.

A possible route to answering the question of a center for semantic and conceptual binding is offered by patient studies. Here it is remarkable that patients with semantic dementia usually have a lesion in the temporal pole and this region was therefore suggested as the areas most important for semantic binding (Patterson & Hodges, 2001). However, the *bilateral* nature of neural degeneration usually seen in semantic dementia may suggest that one focal lesion is not enough to cause general semantic deficits (Patterson & Hodges, 2001). Multiple semantic binding sites are also supported by the specific semantic deficit in action word processing seen in patients with Motor Neuron Disease (Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001). More evidence for multiple semantic binding sites came from double dissociations between semantic word categories arising from lesions in *right-hemispheric* fronto-parietal versus temporo-occipital areas (Neininger & Pulvermüller, 2003), which complement similar observations made earlier for lesions to the left language-dominant hemisphere (Damasio & Tranel, 1993; Daniele et al., 1994). Some of these lesions were so focal that they only affected motor and premotor cortex, but nevertheless specifically degraded the processing of action words in psychological experiments (Neininger & Pulvermüller, 2001). Dissociations of these types are consistent with the existence of multiple semantic integration systems in both cerebral hemispheres (Pulvermüller & Mohr, 1996).

Summary and Outlook

Information about actions and perceptions relevant in the explanation of the meaning of referential words appear to be linked to the word forms at the level of the brain. The relevant links may be established by correlation of neuronal activation in perisylvian word form circuits and semantic circuits in action- and perception-related brain regions. Semantic category differences may be based on the differential involvement of neuronal sets in inferior-temporal visual cortex, fronto-central action-related cortex, and other brain parts. Precise predictions on the cortical locus of specific semantic brain processes could be generated for subtypes of action words referring to face-, arm- and leg-movements, such as “lick”, “pick” and “kick”. Processing of these words lights up the motor system in a similar way as the respective actions would. Specific activation of the motor systems takes place rapidly during speech and written language processing, is automatic and makes a functional contribution to word processing. The results provide brain support that language is grounded in, and embodied by, action and perception mechanisms. The rapidness, automaticity and functional significance of semantically-specific sensorimotor processes sparked by word forms argues against an epiphenomenal character and supports the position that “embodied” action-perception circuits contribute to, and are essential for, semantic-conceptual processing.

The data summarized show that it is fruitful to model the brain basis of meaningful words as distributed cell assemblies binding phonological and semantic information about actions and perceptions at an abstract or cross-modal level. These distributed neuronal ensembles may function as discrete word specific processors including neuron sets in different cortical areas. Different sets may overlap, thereby reflecting shared semantic or phonological features between words, and they may compete for full activation in the perception process. In word recognition, activation of the distributed areas, over which these neuronal assemblies are spread out, is near-simultaneous, thereby binding information from different modalities (e.g., articulatory and acoustic) and linguistic functions (e.g., phonological and semantic). Apart from their role in language, these networks may play a role in conceptual processing.

These proposals and the reviewed neuroscience evidence backing them have important implications for constructing life-like perception-action systems and robots with brain like control systems (Knoblauch, Markert, & Palm, 2005; Roy, 2005; Shastri, Grannes, Narayana, & Feldman, 2005; Wermter, Weber, Elshaw, Gallese, & Pulvermüller, 2005; Wermter et al., 2004). A major conclusion here is that there are good reasons to link brain based language models to the body-related motor and perception systems. Such embodied artificial models might succeed for the same reason why the biological originals they copy were successful in evolution: A main point here might be the possibility to process crossmodal information exchange in an extremely rapid manner.

Still, wouldn't all of the results discussed here be compatible with abstract modular models postulating that aspects of semantics are mapped on different

cognitive processors, without a-priori prediction on the exact cortical loci where they are located (for discussion, see Caramazza & Mahon, 2003)? It must be admitted that this is certainly the case. However, it is a difference between models that are compatible with a range of brain facts – as any abstract modular theory that does not specify brain correlates necessarily is – and brain-based models that do imply specific loci for – for example – semantic and conceptual brain processes. The advance that has been achieved is in this dimension. Some semantic brain activations in the brain can now be understood and explained on the basis of neuroscientific knowledge. Rather than looking at brain activation pictures, seeing the activations and therefore stipulating that meaning is sitting here and there, we can now come up with precise a priori predictions and neuroscientifically grounded post-hoc explanation attempt. This brings us closer to an answer to the Why-question: Why is it conceptual-semantic brain activation occurring here and not there? Even if these explanation attempts are preliminary, they may propel cognitive neuroscience from a science describing phenomena to an explanatory science grounding findings, also about concepts and thought, in the laws of nature.

Acknowledgements: This work was supported by the Medical Research Council (UK) and by the European Community under the “Information Society Technologies Programme” (IST-2001-35282) and in the context of the Nestcom grant.

References

- Bak, T. H., O'Donovan, D.G., Xuereb, J. H., Boniface, S., & Hodges, J. R. (2001). Selective impairment of verb processing associated with pathological changes in Brodmann areas 44 and 45 in the Motor Neurone Disease-Dementia-Aphasia syndrome. *Brain, 124*, 103-120.
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behav Brain Sci, 22*(4), 577-609; discussion 610-560.
- Barsalou, L. W. (2003). Abstraction in perceptual symbol systems. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 358*(1435), 1177-1187.
- Binder, J. R., Westbury, C. F., McKiernan, K. A., Possing, E. T., & Medler, D. A. (2005). Distinct brain systems for processing concrete and abstract concepts. *J Cogn Neurosci, 17*(6), 905-917.
- Bird, H., Lambon-Ralph, M. A., Patterson, K., & Hodges, J. R. (2000). The rise and fall of frequency and imageability: noun and verb production in semantic dementia. *Brain and Language, 73*(1), 17-49.
- Bookheimer, S. (2002). Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annu Rev Neurosci, 25*, 151-188.
- Borghetti, A. M., Glenberg, A. M., & Kaschak, M. P. (2004). Putting words in perspective. *Mem Cognit, 32*(6), 863-873.
- Boulenger, V., Paulignan, Y., Roy, A. C., Jeannerod, M., & Nazir, T. A. (2006). Seeing

action words interferes with the concurrent execution of a reaching movement.

Journal of Cognitive Neuroscience, in press.

Braitenberg, V., & Pulvermüller, F. (1992). Entwurf einer neurologischen Theorie der Sprache. *Naturwissenschaften, 79*, 103-117.

Braitenberg, V., & Schüz, A. (1998). *Cortex: statistics and geometry of neuronal connectivity* (2 ed.). Berlin: Springer.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G., & Freund, H. J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European Journal of Neuroscience, 13*(2), 400-404.

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. *Brain Res Cogn Brain Res, 24*(3), 355-363.

Cappa, S. F., Perani, D., Schnur, T., Tettamanti, M., & Fazio, F. (1998). The effects of semantic category and knowledge type on lexical-semantic access: a PET study. *Neuroimage, 8*(4), 350-359.

Caramazza, A., & Mahon, B. Z. (2003). The organization of conceptual knowledge: the evidence from category-specific semantic deficits. *Trends Cogn Sci, 7*(8), 354-361.

Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience, 2*(10), 913-919.

- Coles, M. G. H., & Rugg, M. D. (1995). Event-related brain potentials. In M. D. Rugg & M. G. H. Coles (Eds.), *Electrophysiology of mind. Event-related brain potentials and cognition* (pp. 1-26). Oxford: Oxford University Press.
- Damasio, A. R., & Tranel, D. (1993). Nouns and verbs are retrieved with differently distributed neural systems. *Proceedings of the National Academy of Sciences, USA*, *90*, 4957-4960.
- Daniele, A., Giustolisi, L., Silveri, M. C., Colosimo, C., & Gainotti, G. (1994). Evidence for a possible neuroanatomical basis for lexical processing of nouns and verbs. *Neuropsychologia*, *32*, 1325-1341.
- de Vega, M., Robertson, D. A., Glenberg, A. M., Kaschak, M. P., & Rinck, M. (2004). On doing two things at once: temporal constraints on actions in language comprehension. *Mem Cognit*, *32*(7), 1033-1043.
- Dell, G. S. (1986). A spreading-activation theory of retrieval in sentence production. *Psychological Review*, *93*, 283-321.
- Devlin, J. T., Russell, R. P., Davis, M. H., Price, C. J., Moss, H. E., Fadili, M. J., & Tyler, L. K. (2002). Is there an anatomical basis for category-specificity? Semantic memory studies in PET and fMRI. *Neuropsychologia*, *40*(1), 54-75.
- Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science*, *270*(5234), 305-307.
- Fadiga, L., Craighero, L., Buccino, G., & Rizzolatti, G. (2002). Speech listening specifically modulates the excitability of tongue muscles: a TMS study. *European Journal of Neuroscience*, *15*(2), 399-402.

- Frege, G. (1966). Der Gedanke (first published 1918-1920). In G. Patzig (Ed.), *Logische Untersuchungen* (pp. 30-53). Göttingen: Huber.
- Gentilucci, M., Benuzzi, F., Bertolani, L., Daprati, E., & Gangitano, M. (2000). Language and motor control. *Exp Brain Res*, *133*(4), 468-490.
- Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychon Bull Rev*, *9*(3), 558-565.
- González, J., Barros-Loscertales, A., Pulvermüller, F., Meseguer, V., Sanjuán, A., Belloch, V., & Ávila, C. (2006). Reading cinnamon activates olfactory brain regions. *Neuroimage*, *in press*.
- Graziano, M. S., Taylor, C. S., & Moore, T. (2002). Complex movements evoked by microstimulation of precentral cortex. *Neuron*, *34*(5), 841-851.
- Hauk, O., Davis, M. H., Ford, M., Pulvermüller, F., & Marslen-Wilson, W. D. (2006). The time course of visual word recognition as revealed by linear regression analysis of ERP data. *Neuroimage*, *30*(4), 1383-1400.
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in the motor and premotor cortex. *Neuron*, *41*, 301-307.
- Hauk, O., & Pulvermüller, F. (2004). Neurophysiological distinction of action words in the fronto-central cortex. *Human Brain Mapping*, *21*(3), 191-201.
- He, S. Q., Dum, R. P., & Strick, P. L. (1993). Topographic organization of corticospinal projections from the frontal lobe: motor areas on the lateral surface of the hemisphere. *Journal of Neuroscience*, *13*(3), 952-980.

- Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition*, 92(1-2), 67-99.
- Holcomb, P. J., & Neville, H. J. (1990). Auditory and visual semantic priming in lexical decision: a comparison using event-related brain potentials. *Language and Cognitive Processes*, 5, 281-312.
- Humphreys, G. W., & Forde, E. M. (2001). Hierarchies, similarity, and interactivity in object recognition: "category-specific" neuropsychological deficits. *Behavioral and Brain Sciences*, 24(3), 453-509.
- Humphreys, G. W., & Riddoch, M. J. (1987). On telling your fruit from your vegetables - a consideration of category-specific deficits after brain-damage. *Trends in Neurosciences*, 10, 145-148.
- Jeannerod, M., & Frak, V. (1999). Mental imaging of motor activity in humans. *Curr Opin Neurobiol*, 9(6), 735-739.
- Kiefer, M. (2001). Perceptual and semantic sources of category-specific effects: Event-related potentials during picture and word categorization. *Memory and Cognition*, 29, 100-116.
- Kintsch, W. (1974). *The representation of meaning in memory*. Hillsdale, NJ: Erlbaum.
- Kintsch, W. (1998). *Comprehension: A paradigm for cognition*. New York: Cambridge University Press.
- Kintsch, W. (2002). The potential of latent semantic analysis for machine grading of clinical case summaries. *J Biomed Inform*, 35(1), 3-7.

- Kleene, S. C. (1956). Representation of events in nerve nets and finite automata. In C. E. Shannon & J. McCarthy (Eds.), *Automata studies* (pp. 3-41). Princeton, NJ: Princeton University Press.
- Knoblauch, A., Markert, H., & Palm, G. (2005). An associative cortical model of language understanding and action planning. In J. Mira & J. R. Alvarez (Eds.), *International work-conference on the interplay between natural and artificial computation 2005* (Vol. 3562, pp. 405-414). Berlin: Springer.
- Lakoff, G. (1987). *Women, fire, and dangerous things. What categories reveal about the mind*. Chicago: University of Chicago Press.
- Landauer, T. K., & Dumais, S. T. (1997). A solution to Plato's problem: the Latent Semantic Analysis theory of acquisition, induction, and representation of knowledge. *Psychological Review*, *104*, 211-240.
- Lichtheim, L. (1885). On aphasia. *Brain*, *7*, 433-484.
- Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: structure and processes. *Current Opinion in Neurobiology*, *11*(2), 194-201.
- Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, *270*, 102-105.
- Matelli, M., Camarda, R., Glickstein, M., & Rizzolatti, G. (1986). Afferent and efferent projections of the inferior area 6 in the macaque monkey. *J Comp Neurol*, *251*(3), 281-298.
- McCulloch, W. S., & Pitts, W. H. (1943). A logical calculus of ideas immanent in nervous activity. *Bulletin of Mathematical Biophysics*, *5*, 115-133.

- Moscoso Del Prado Martin, F., Hauk, O., & Pulvermüller, F. (2006). Category specificity in the processing of color-related and form-related words: An ERP study. *Neuroimage*, *29*(1), 29-37.
- Näätänen, R., Tervaniemi, M., Sussman, E., Paavilainen, P., & Winkler, I. (2001). 'Primitive intelligence' in the auditory cortex. *Trends in Neurosciences*, *24*(5), 283-288.
- Neininger, B., & Pulvermüller, F. (2001). The right hemisphere's role in action word processing: a double case study. *Neurocase*, *7*(4), 303-317.
- Neininger, B., & Pulvermüller, F. (2003). Word-category specific deficits after lesions in the right hemisphere. *Neuropsychologia*, *41*(1), 53-70.
- Obleser, J., Lahiri, A., & Eulitz, C. (2003). Auditory-evoked magnetic field codes place of articulation in timing and topography around 100 milliseconds post syllable onset. *Neuroimage*, *20*(3), 1839-1847.
- Page, M. (2000). Connectionist modelling in psychology: a localist manifesto. *Behav Brain Sci*, *23*(4), 443-467; discussion 467-512.
- Patterson, K., & Hodges, J. R. (2001). Semantic dementia. In R. F. Thompson & J. L. McClelland (Eds.), *International encyclopaedia of the social and behavioural sciences. Behavioral and cognitive neuroscience section* (pp. 3401-3405). New York: Pergamon Press.
- Penfield, W., & Boldrey, E. (1937). Somatic sensory and motor representation in the cerebral cortex as studied by electrical stimulation. *Brain*, *60*, 389-443.
- Penfield, W., & Rasmussen, T. (1950). *The cerebral cortex of man*. New York: Macmillan.

- Posner, M. I., & Pavese, A. (1998). Anatomy of word and sentence meaning. *Proceedings of the National Academy of Sciences, USA*, 95, 899-905.
- Preissl, H., Pulvermüller, F., Lutzenberger, W., & Birbaumer, N. (1995). Evoked potentials distinguish nouns from verbs. *Neuroscience Letters*, 197, 81-83.
- Price, C. J. (2000). The anatomy of language: contributions from functional neuroimaging. *Journal of Anatomy*, 197 Pt 3, 335-359.
- Pulvermüller, F. (1996). Hebb's concept of cell assemblies and the psychophysiology of word processing. *Psychophysiology*, 33, 317-333.
- Pulvermüller, F. (1999). Words in the brain's language. *Behavioral and Brain Sciences*, 22, 253-336.
- Pulvermüller, F. (2001). Brain reflections of words and their meaning. *Trends in Cognitive Sciences*, 5(12), 517-524.
- Pulvermüller, F. (2002). A brain perspective on language mechanisms: from discrete neuronal ensembles to serial order. *Progress in Neurobiology*, 67, 85-111.
- Pulvermüller, F. (2003). *The neuroscience of language*. Cambridge: Cambridge University Press.
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6(7), 576-582.
- Pulvermüller, F., Härle, M., & Hummel, F. (2000). Neurophysiological distinction of verb categories. *Neuroreport*, 11(12), 2789-2793.
- Pulvermüller, F., & Hauk, O. (2006). Category-specific processing of color and form words in left fronto-temporal cortex. *Cerebral Cortex*, 16(8), 1193-1201.

- Pulvermüller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *European Journal of Neuroscience*, *21*(3), 793-797.
- Pulvermüller, F., Lutzenberger, W., & Preissl, H. (1999). Nouns and verbs in the intact brain: evidence from event-related potentials and high-frequency cortical responses. *Cerebral Cortex*, *9*, 498-508.
- Pulvermüller, F., & Mohr, B. (1996). The concept of transcortical cell assemblies: a key to the understanding of cortical lateralization and interhemispheric interaction. *Neuroscience and Biobehavioral Reviews*, *20*, 557-566.
- Pulvermüller, F., Mohr, B., & Schleichert, H. (1999). Semantic or lexico-syntactic factors: What determines word-class specific activity in the human brain? *Neuroscience Letters*, *275*, 81-84.
- Pulvermüller, F., & Preissl, H. (1991). A cell assembly model of language. *Network: Computation in Neural Systems*, *2*, 455-468.
- Pulvermüller, F., & Shtyrov, Y. (2006). Language outside the focus of attention: the mismatch negativity as a tool for studying higher cognitive processes. *Progress in Neurobiology*, *79*(1), 49-71.
- Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. J. (2003). Spatio-temporal patterns of neural language processing: an MEG study using Minimum-Norm Current Estimates. *Neuroimage*, *20*, 1020-1025.
- Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. J. (2005). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience*, *17*(6), 884-892.

- Rizzolatti, G., & Luppino, G. (2001). The cortical motor system. *Neuron*, 31(6), 889-901.
- Rogers, T. T., Lambon Ralph, M. A., Garrard, P., Bozeat, S., McClelland, J. L., Hodges, J. R., & Patterson, K. (2004). Structure and deterioration of semantic memory: a neuropsychological and computational investigation. *Psychol Rev*, 111(1), 205-235.
- Roy, D. (2005). Grounding words in perception and action: computational insights. *Trends Cogn Sci*, 9(8), 389-396.
- Schnelle, H. (1996). Approaches to computational brain theories of language - a review of recent proposals. *Theoretical Linguistics*, 22, 49-104.
- Scott, S. K., & Johnsrude, I. S. (2003). The neuroanatomical and functional organization of speech perception. *Trends in Neurosciences*, 26(2), 100-107.
- Searle, J. R. (1990). Minds, brains, and programs. *Behavioral and Brain Sciences*, 3(3), 417-457.
- Seidenberg, M. S., Plaut, D. C., Petersen, A. S., McClelland, J. L., & McRae, K. (1994). Nonword pronunciation and models of word recognition. *J Exp Psychol Hum Percept Perform*, 20(6), 1177-1196.
- Shastri, L., Grannes, D., Narayana, S., & Feldman, J. (2005). A connectionist encoding of parameterized schemas and reactive plans. In G. K. Kraetzschmar & G. Palm (Eds.), *Hybrid information processing in adaptive autonomous vehicles*. Berlin: Springer.

- Shtyrov, Y., Hauk, O., & Pulvermüller, F. (2004). Distributed neuronal networks for encoding category-specific semantic information: the mismatch negativity to action words. *European Journal of Neuroscience*, *19*(4), 1083-1092.
- Shtyrov, Y., Pihko, E., & Pulvermüller, F. (2005). Determinants of dominance: Is language laterality explained by physical or linguistic features of speech? *Neuroimage*, *27*(1), 37-47.
- Skrandies, W. (1999). Early effects of semantic meaning on electrical brain activity. *Behavioral and Brain Sciences*, *22*, 301.
- Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., Fazio, F., Rizzolatti, G., Cappa, S. F., & Perani, D. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, *17*(2), 273-281.
- Tomasello, M., & Kruger, A. C. (1992). Joint attention on actions: acquiring verbs in ostensive and non-ostensive contexts. *Journal of Child Language*, *19*, 311-333.
- Tyler, L. K., & Moss, H. E. (2001). Towards a distributed account of conceptual knowledge. *Trends in Cognitive Sciences*, *5*(6), 244-252.
- Tyler, L. K., Moss, H. E., Durrant-Peatfield, M. R., & Levy, J. P. (2000). Conceptual structure and the structure of concepts: a distributed account of category-specific deficits. *Brain Lang*, *75*(2), 195-231.
- Tyler, L. K., Russell, R., Fadili, J., & Moss, H. E. (2001). The neural representation of nouns and verbs: PET studies. *Brain*, *124*(Pt 8), 1619-1634.

- Tyler, L. K., Stamatakis, E. A., Bright, P., Acres, K., Abdallah, S., Rodd, J. M., & Moss, H. E. (2004). Processing objects at different levels of specificity. *J Cogn Neurosci*, *16*(3), 351-362.
- Warrington, E. K., & McCarthy, R. A. (1983). Category specific access dysphasia. *Brain*, *106*, 859-878.
- Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain*, *107*, 829-854.
- Wermter, S., Weber, C., Elshaw, M., Gallese, V., & Pulvermüller, F. (2005). Neural grounding of robot language in action. In S. Wermter & G. Palm & M. Elshaw (Eds.), *Biomimetic neural learning for intelligent robots* (pp. 162-181). Berlin: Springer.
- Wermter, S., Weber, C., Elshaw, M., Panchev, C., Erwin, H., & Pulvermüller, F. (2004). Towards multimodal neural network robot learning. *Robotics and Autonomous Systems*, *47*, 171-175.
- Wilson, S. M., Saygin, A. P., Sereno, M. I., & Iacoboni, M. (2004). Listening to speech activates motor areas involved in speech production. *Nat Neurosci*, *7*(7), 701-702.
- Young, M. P., Scannell, J. W., Burns, G., & Blakemore, C. (1994). Analysis of connectivity: neural systems in the cerebral cortex. *Review in Neuroscience*, *5*, 227-249.
- Zatorre, R. J., Evans, A. C., Meyer, E., & Gjedde, A. (1992). Lateralization of phonetic and pitch discrimination in speech processing. *Science*, *256*, 846-849.

