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Neuroimaging and brain lesion patient investigations on the role of neural motor systems for processing concrete and abstract semantics

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Felix R. Dreyer

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Erstgutachter: Prof. Dr. Dr. Friedemann Pulvermüller

Zweitgutachterin: Prof. Dr. Gisela Klann-Delius

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To Armin. In the stars.

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Abbreviations

AAT - Aachener Aphasie Test

ADEM - Acute Disseminated Encephalomyelitis

ANOVA - Analysis Of Variance

BA - Brodmann Area

CIAT - Constrained Induced Language Action Therapy

DTI - Diffusion Tensor Imaging

EEG - Electroencephalography

EPI - Echo-Planar Imaging

FDR - False Discovery Rate

fMRI - functional Magnetic Resonance Imaging

FWE - Family-wise Error

IF - Inferior Frontal

ILAT - Intensive Language Action Therapy

LDT - Lexical Decision Task

LQ - Laterality Quotient

M – Mean

MEG - Magnetoencephalography

MEP - Motor Evoked Potential

MND - Motor Neurone Disease

MNI - Montreal Neurological Institute

MPRAGE - Magnetization Prepared Rapid Acquisition Gradient Echo

MRI - Magnetic Resonance Imaging

MT - Middle Temporal

MVPA - Multivariate Pattern Analysis

PET - Positron Emission Tomography

rACC - rostral Anterior Cingulate Cortex

RCT - Randomized Controlled Trial

RM - Repeated Measures

ROI - Region Of Interest

RSDT - Revised Standardized Difference Tests

RT - Reaction Time

SD - Standard Deviation

SE – Standard Error of the Mean

SMA – Supplementary Motor Area

SPM - Statistical Parametric Mapping

TMS - Transcranial Magnetic Stimulation

VLSM - voxel-based lesion symptom mapping

WHO - World Health Organization

1. Introduction

The capacity to relate seemingly arbitrary linguistic symbols and words to their meaning and apply them successfully in linguistic contexts is one of the hallmarks of human cognitive function. Not surprisingly, the nature of these word meanings, their semantics, has been subject to long standing philosophical and empirical debates, regarding their origin (from an ontogenical and evolutionary perspective), their contents and in recent decades also the nature of their neural substrates. With the three empirical projects presented in this dissertation, this work aims to contribute to the discussion from an empirical perspective by investigating neural substrates involved in semantic processing, by exploring the necessity of modality-preferential semantic system contributions to semantics and by discussing the respective observations in the context of previous evidence and theoretical models of semantics and their neural foundations. To do so, I will briefly introduce different cognitive and neural models of semantics in this chapter and elaborate on their predictions regarding the neural substrates of linguistic semantics, before I turn to reviewing previous empirical evidence relevant in context of these predictions. I will put the spotlight also on specific kinds of semantics, namely the meaning of abstract words, as those words have previously been argued to pose a specific challenge to some of the presented models of semantics.

1.1 Cognitivist models of semantic representation and the symbol grounding problem

Motivated by advancements in artificial intelligence and computer science, traditional cognitivist models of semantics assume word meaning to be represented in a homogeneous, uniform format, either in form of symbol systems, manipulated by syntactic rules (Fodor, 1983), or in semantic networks, storing the meaning of words and the semantic relations between words (Quillian, 1969; Collins and Loftus, 1975). Semantics were assumed to be handled by a dedicated semantic system, independent from other cognitive modules, like those related to basal sensory or motor processing (Fodor, 1983; Ellis and Young, 1988). Cognitive modules in general were seen to be encapsulated from another, i.e. when processing inputs from another module, a cognitive module cannot access information that is stored in other modules, but has to rely on the information that is stored in itself. Hence, a dysfunction in one module is assumed to have no influence on the quality of representation and processing in another module. It should be noted though that these cognitive theories indeed assume the semantic system to receive input from other, non-semantic modules, like perceptual systems, and to send its output e.g. to systems for the execution of a response action, once semantic processing is complete, but the role of these systems is merely “subsidiary” for the “central” semantic system (Fodor, 1983).

This view however has an important caveat, as pointed out by Harnad (1990) (and acknowledged already by Quillian, 1969): based on Searle’s Chinese Room thought experiment (Searle, 1980) it is exemplified that a purely symbolic system cannot convey meaning on its own. If symbol meaning is exclusively represented via references to other atomic or molecular symbolic meanings, such a system becomes inherently circular, as the respective referenced symbols have their meaning in turn again defined by references to other symbols. This circularity renders purely symbolic systems entirely meaningless, as they fail to relate a symbol (or linguistic sign) to its referent in the world, so that the symbols of a purely symbolic system are in fact not interpretable.

Again it should be noted that amodal symbol systems do not deny in- and output from and to sensory or motor systems, but any mapping of external to central semantic information is assumed to occur in an entirely arbitrary fashion.

1.2 Cognitive and neural approaches towards a grounding of semantics

A solution is to the symbol grounding problem is to ground at least some symbols directly in sensory (and by extension also motor) experience. These grounded symbols of semantic representation can then serve as basis of the grounding of other symbols via combinatorial processes (Harnad, 1990). Critically, such a system would contradict the modularity and functional independence of the semantic system to systems for basal perceptual and motoric functions.

In contrast to the aforementioned symbolic accounts, grounded or embodied theories propose that semantics are, in part, directly represented and grounded in sensory and motor knowledge (e.g. Barsalou, 1999, 2008). Here, semantics is thought to be represented in a distributed fashion, rather than in a single separate, distinct and autonomous module. Importantly, semantics are here assumed to be represented in modality specific format, contrasting with the assumed amodality of symbol system approaches. In this view, sensorimotor information is not believed to be “subsidiary”, but indeed constitutive for semantic representation. If one assumes cognitive processes in general, or also specifically the processing of semantics to be in some way realized in the brain, it may appear worthwhile to not only focus on a purely cognitive level but to also investigate the respective underlying neural architecture and mechanisms. This approach allows to derive theories on the neural mechanisms underlying semantics, which can be tested empirically using psycholinguistic and neuroscientific methodology.

Under the assumption that overlaps in neural substrates of cognitive functions are informative about overlaps of the nature of the respective representational formats, grounded and embodied theories on the neural underpinnings of semantics (e.g. Pulvermüller, 1999, 2005; Barsalou *et al.*, 2003; Pulvermüller and Fadiga, 2010; Glenberg and Gallese, 2012) propose that semantic processing is, at least in part, realized in brain systems involved in direct sensory perception or motor action. If semantics are indeed represented in a modality specific format, the respective neural correlates should not only involve amodal- or multi-modal systems but also modality specific motor and sensory systems in the brain. Crucially, the mapping of sensorimotor information to a word form is believed to not occur in an arbitrary fashion, but to follow a pattern of sensorimotor somatotopy, involving those modality specific systems that are specifically crucial for a words meaning. As a consequence, any change in the functional state of a sensorimotor system should be reflected in changes of those semantic representations that were based on the respective sensorimotor representation. At the same time other semantic representations that do not contain any information of said altered sensorimotor system are hypothesized to remain unaffected. As a further consequence of the constitutive role of sensorimotor information for semantic representation, the respective modality specific systems should become active automatically and instantaneously once the semantics of a words are being accessed.

1.3 Hebbian learning and Neural Cell Assemblies

In addition to hypotheses on the spatial properties and temporal dynamics, any neural theory on the nature of semantic representations should also explain or model, how and why these specific spatio-temporal attributes of the neural correlates of semantic representations come to be. A neurobiological mechanism that would potentially allow a semantic grounding in modality-preferential systems of the brain, as described above, is Hebbian learning. The Hebbian learning principle proposes that cells strengthen their mutual connections when they become active in synchrony (Hebb, 1949) and can be seen to be biologically realized in long term potentiation (Bliss and Lømo, 1973). This basic principle allows for correlational or associative learning, which would in turn allow to learn the relation between a linguistic sign and its sensory motor referents. In neural terms, this process results in groups of neurons that are strongly connected with excitatory links, called cell assemblies (Hebb, 1949; Braitenberg, 1978).

For example, when one learns the reference of the word ‘hammer’, this linguistic sign would be, among others, related to the perceptual sensations of seeing a hammer and the motor activity related to using it. In neural terms this correlation of sign and reference in the world would be reflected in connections of neuronal cell assemblies, representing the word-form, to neurons handling the respective sensory or motor information. The resulting cell assembly would directly speak against a localistic and encapsulated account of semantics. Given their excitatory mutual connections, activations of only specific cell assembly components can result in widespread ignition, or at least facilitated activation, of the entire cell assembly. In the context of the ‘hammer’ example, the perception of the word ‘hammer’ would be expected to result in (facilitated) sensorimotor activity and vice versa sensorimotor experiences related to situations the sign ‘hammer’ is used, would result in (facilitated) activations of the sign components in the cell assembly.

However, the physical referents of the sign ‘hammer’ would, at least in a naturalistic setting, vary to a large degree between situations this sign occurs and it used, i.e. due to different people using the hammer, different intentions to use a hammer or simply due to different kinds of hammers being used. This large variety in physical referents would result in a strengthening of word form cell assemblies with very widespread and heterogeneous sensorimotor referents, as informational content that is not actually relevant to understand the meaning of the sign ‘hammer’ is associated with its usage. Such a cell assembly could over time lose a great deal of its entropy (in an information theory sense, i.e. information content), and would make differentiations of semantics between individual signs more difficult (Sejnowski, 1977). Therefore, another learning principle must be considered in addition to Hebbian learning, which is Anti-Hebbian learning. According to this learning rule, neurons that fire in a-synchrony weaken their mutual connections (Bienenstock *et al.*, 1982). The biological equivalent of Anti-Hebbian learning would be synaptic long term depression (Lynch *et al.*, 1977; Linden and Connor, 1995).

Both learning rules in concert allow to relate the sign ‘hammer’ to the sensorimotor experience that is common between situations, informative about its meaning and importantly it also allows to differentiate between meanings of different words. Simulation approaches applying those learning rules under neurobiological constrains indicate that this principle can indeed be successfully applied to model language learning and semantic representations (Wennekers *et al.*, 2006; Garagnani *et al.*, 2008; Tomasello *et al.*, 2017).

Once the meaning of a sign (or word) has been learned it can also provide a basis for learning the meaning of novel signs by linguistic description and context alone. In this scenario, words appearing with each other in linguistic cortex would result in correlated patterns of activation between their respective cell assemblies. These correlated cell assembly activations can then strengthen their mutual connections to another using the same principles of Hebbian and Anti-Hebbian learning in a similar vein as previously described to occur within cell assemblies. This mechanism provides means to hand over previously grounded semantics between signs via word-word, rather than just word-world learning (Cangelosi *et al.*, 2002; Pulvermüller, 2002). Thus it is possible that a words meaning is not grounded directly in experiential references, but via the proxy of a “grounding kernel” of previously learned word meanings (Cangelosi, 2010; Pulvermüller, 2013a).

1.4 Semantics in the brain

The question whether modality specific knowledge is of relevance for semantic representations, as proposed by embodied and grounded approaches towards semantics and as denied by proponents of entirely amodal symbolic semantic representations, can be addressed empirically using methods established in the fields of psycholinguistics and neuroscience. In order to do so, one first needs to make the assumption that in general the cognitive faculty of semantic representation and processing is realized in neural architecture and biological mechanism in the brain. Furthermore, one needs to assume the localization of the neural underpinnings of semantics (and their correlates) within the brain to be informative about the representational format of semantics, at least to a degree that allows to infer overlaps in representational format from overlaps in neural substrates between cognitive functions.

Advances in neuroimaging methods in the past decades allowed to test for the hypotheses of grounded and ungrounded approaches towards the neural basis of semantic processing in the brain in vivo on a large number of participants. For example, a large-scale meta-analysis summarized the results of 120 of those neuroimaging investigations on semantic processing (Binder *et al.*, 2009). This analysis revealed a widespread (modality unspecific) network covering inferior frontal gyrus, the middle temporal and fusiform gyrus, posterior inferior parietal lobe, dorsomedial prefrontal cortex, ventromedial prefrontal cortex and posterior cingulate gyrus, thus speaking against a single area being exclusively involved in semantic processing and representation. At the same time, also a specific contribution of modality-preferential areas was not reported.

However, this latter observation can be attributed to the design of the meta-analysis and the summarized studies, rather than to an absence of sensorimotor area involvement in semantic processing. Here, it appears to be problematic that the majority of the summarized studies used tasks that required an active motor response, which could have masked motor activations related to perception of linguistic input.

Furthermore, the majority of neuroimaging approaches included in the meta-analysis presented results on contrasts between meaningful stimuli, to stimuli devoid of meaning. Any semantic system however should be capable to achieve more than just telling apart meaningful from meaningless stimuli. Instead the actual word meanings have to be considered. From a localistic, amodal symbolic perspective on semantics this would not be necessary, as the neural substrates would be assumed to remain homogenous between semantics of different words. In contrast, grounded or embodied frameworks on the neural underpinning of semantics explicitly predict differential neural substrates, depending on exact word meaning. In case word semantics are not being controlled for, it is likely that those modality specific activations cancel each other out when averaged across all meaning types applied, thus revealing merely the modality unspecific contributors to semantics, as reported in meta-analysis results. Therefore approaches that control for explicit semantic content should be considered in order to test hypothesis of grounded approaches towards semantics. This is not to say that Binder and coworkers were not aware of this issue. In fact they presented also data on a very limited set of 10 studies on a controlled, though broad, semantic categories of ‘artifacts’ and ‘living things’. However the aforementioned motor response caveat still applied. In the following paragraphs I will specifically review those approaches that provide a very fine grained control of exact word semantics, in order to test predictions of grounded neural theories of semantics. In doing so, I will focus predominantly on the contribution of motor systems to action-related semantics, especially as some theoretical approaches (Wittgenstein, 1953) in particular highlight the relevance of (social) action contexts of language usage for linguistic meaning.

Investigations of category specific semantic processing

In an early positron emission tomography (PET) approach, Martin and colleagues (1996) presented pictures of animals and tools in a silent object naming paradigm. For both object categories, ventral temporal and inferior frontal areas showed increased cerebral blood flow when compared to the presentation of non-sense objects. At the same time, direct contrasts between both picture categories revealed stronger signal for animals than for tools in occipital areas, related to the processing of visual features. The reverse direction for this comparison revealed pronounced activation in primary and premotoric areas, related to direct tool manipulation. These observations lead to the conclusion that semantic representations are represented in distributed networks, covering perisylvian/ventral temporal and extrasylvian sensorimotor regions, depending on the exact word semantics. Similar findings in terms of category specific involvement in category specific semantics were also reported in a PET study by Damasio *et al.* (1996). Unfortunately, the authors of both studies did not present any matching characteristics between the different word- and object classes applied in both studies on neither psycholinguistic nor basal perceptual stimulus characteristics. While a post hoc test reported by Martin *et al.* (1996) confirmed that the observed category specific activations were not a consequence of confounds in visual complexity, a similar control for psycholinguistic variables was not reported, thus rendering it difficult to directly relate the observed results to differences in their semantic properties rather than to differences on non-semantic properties like e.g. word length or word frequency. In a passive reading functional magnetic resonance imaging (fMRI) paradigm that explicitly controlled for those psycholinguistic differences between semantic word categories, Hauk and coworkers (2004) could show an involvement of inferior temporal and inferior frontal cortex in addition to precentral motor areas in the processing of action words. Over and above this replication of previously reported involvement of motor systems in processing action-related semantics in a domain general fashion, the exact action word type, i.e. the related effector was reflected in the corresponding activation patterns in a somatotopic fashion. Hand action verbs like ‘pick’ were shown to specifically involve motor areas that were also active when performing actual hand movements. Likewise face action words like ‘lick’ were demonstrated to elicit activations in close proximity to motor areas involved in tongue movements and leg action words, like ‘kick’ were shown to elicit activations in the motor system specifically in those areas that are involved in actual leg movements. This pattern of effector specific semantic somatotopy in the motor system was replicated in further fMRI studies on single verb (Rüschemeyer *et al.*, 2007; Raposo *et al.*, 2009; Moseley and Pulvermüller, 2014) and noun stimuli (Rüschemeyer *et al.*, 2010; Carota *et al.*, 2012; Moseley and Pulvermüller, 2014). Similar results were also obtained when using whole sentence stimuli describing effector specific (Tettamanti *et al.*, 2005; Aziz-Zadeh *et al.*, 2006; Boulenger *et al.*, 2008a; Pulvermüller *et al.*,2009; Raposo *et al.*, 2009; Desai *et al.*, 2009; de Grauwe *et al.*, 2014) or effector unspecific actions (Tomasino *et al.*, 2007). Although some researchers see some of these effects to be difficult to replicate (Postle *et al.*, 2008; Caramazza *et al.*, 2014), systematic comparison of corresponding studies demonstrated good reproducibility (Carota *et al.*, 2012; Kemmerer *et al.*, 2012).

Furthermore, such semantic-specific fMRI activations of extrasylvian areas was shown to be not reduced to the motor system, but to involve primarily sensation-related systems as well. Here, nouns that relate to objects with strong auditory semantics, like 'telephone' or 'bell' were shown to elicit activity also in posterior superior and middle temporal gyri, areas normally involved in actual processing of object-related sounds (Kiefer *et al.*, 2008), whereas passive reading of nouns with strong taste-related semantics, like 'salt' resulted in specific contributions of gustatory systems (Barrós-Loscertales, 2012). Likewise passive reading of nouns strongly associated to smells, like 'cinnamon', was reflected in olfactory systems, in addition to activations in classical perisylvian areas (González *et al.*, 2006).

In light of these results an involvement of the motor system in semantic processing can soundly be concluded to occur in a somatotopic fashion with a high degree of spatial resolution.

Investigations of temporal dynamics of sensorimotor involvement in processing semantics

Apart from the question of the spatial properties of semantic processing, answering the question, *where* semantics are being processed, it is furthermore imperative to investigate also the temporal dynamics of sensorimotor area involvement, in order to make precise statements on their role for language processing (Hauk, 2016). This is necessary to exclude the possibility that recorded fMRI signals in sensorimotor areas actually merely reflect confounded cognitive processes, like word related, secondary imaginary-, episodic memory-, or task-related executive processes, rather than genuine semantic processing. Any temporal disentanglement of semantic and possibly confounded processes can however not be achieved by fMRI, as it provides just a very limited temporal resolution, ranging in the domain of seconds. In contrast, electrophysiological measures like electroencephalography (EEG) or magnetoencephalography (MEG) allow to make statements on correlates of general cognitive or specific semantic processes with millisecond precision. Here, EEG results by Hauk and Pulvermüller (2004) indicate somatotopic contributions of the motor system for effector specific action verbs in a passive reading paradigm to occur already 250 ms after word presentation. Similar findings were obtained using MEG mismatch negativity paradigms on words relating to either leg or face movements and showing effects specifically in dorsal or ventral motor areas already 200 ms (Pulvermüller *et al.*, 2005b) or even around 90 ms (Shtyrov *et al.*, 2014) after presentation of word final syllables which define the respective word semantics. As for the aforementioned fMRI findings on the spatial properties of extrasylvian contributions for semantics, such early somatotopic effects were not observed for action words exclusively, but were also reported for words with strong relation to sensory experience (Kiefer *et al.*, 2008).

Despite these early involvement of extrasylvian areas it has been argued that it could still be the case that these contributions are actually secondary to genuine semantic processing, occurring solely in amodal/not modality specific perisylvian areas, as there is no objective time threshold that would rule out the presence of even earlier semantic processes (Mahon and Caramazza, 2008). At best, the aforementioned EEG and MEG results can therefore only show that interpretations in terms of non-semantic processes are merely less likely to hold true (Hauk, 2016). Despite the plethora of evidence of a somatotopic and early involvement mentioned in this and the above paragraphs, both measures cannot provide direct proof for an actual behavioural relevance of sensorimotor systems for semantic processing. To achieve that, behavioural approaches have to be considered, especially those that relate changes in behaviour to changes or lesions in the brain, like neurostimulation paradigms or systematic investigations of neurological patient populations.

Behavioural evidence for an interplay of sensorimotor and conceptual systems

If the aforementioned grounded and embodied approaches towards semantic representations hold true, an influence of sensorimotor activations on semantic processing would be predicted and vice versa an influence of semantics processing on sensorimotor activity. With regards to the former prediction, behavioral evidence presented by Glenberg and Kaschak (2002) indicates a general influence of motor actions on semantic processing. In their study, participants were asked to judge the sensibility of sentences, with target sentences describing movements either towards or away from the body. Responses were given either via pressing a lever (away from the body) or pulling it (towards the body) and reaction times in this setup resulted in specific interference effects in case the necessary lever movement to give the response did not match the direction of movement described in the target sentence.

Furthermore, Witt and coworkers (2010) demonstrated that pressing a softball during object naming specifically affects naming latencies for pictures of tools, whereas responses for psycholinguistically matched animals where not influenced, thus hinting effector specificity in the interaction between actual movements and semantic processing. A direct behavioural demonstration of such somatotopy was provided by Shebani and Pulvermüller (2013), who asked participants to perform complex tapping patterns with their hands or feet while remembering a list of action verbs referring to either hand or face actions. Error patterns showed a cross-over double dissociation between experimental conditions, despite the word categories being matched in terms of their psycholinguistic properties, thus indicating directly a somatotopic overlap of semantic specific memory and motor systems and likewise a causal role of the latter for the former. Reverse effects, from semantic processing to (motor) behavior where reported as well, as hand movements were observed to be directly manipulated by presentation of hand action verbs (Boulenger *et al.*, 2006) and also hand-grip force was reported to increase in a passive reading paradigm specifically for hand action verbs (Frak *et al.*, 2010). Furthermore, as in the previous paragraphs, those behavioural findings were not unique to the motor system and its activation by action, but where also observed to occur in the context of sensory stimulation for words related to respective sensory information (Connell *et al.*, 2012).

Neurostimulation evidence

Neurostimulation methods can be used in two different ways to investigate the neural basis of semantic processing, depending on the exact stimulation protocol: Either by stimulating motor areas in context of semantic processing, to elicit motor evoked potentials (MEP), rendering correlative measures of the motor systems activation state, or by affecting activity in parts of the brain directly, resulting in either an increase or inhibition of neural activity for short periods of time. Both approaches are therefore relevant in context of the hypothesis of grounded semantic models, whereas latter approach specifically allows to infer a causal role of the stimulated area for semantic processing, in case neurostimulation results in semantic specific differences in behavior. Using the first approach outlined above, Oliveri and coworkers (2004) showed hand MEPs to be affected specifically when action-related words had to be read aloud, while words from matched non-action-related categories exhibited no such effect. Following the same rationale Buccino and colleagues (2005) demonstrated that passive listening to effector specific action-related sentences leads to effector specific changes in MEPs, as hand MEPs were modulated by sentences describing hand actions, while foot MEPs remained unchanged and vice versa foot MEPs were modulated by foot action sentences. The latter result directly reflect a semantic-somatotopy pattern of motor system involvement in semantic processing, corresponding to electrophysiological and neuroimaging findings summarized above.

With regards to the alternative approach that uses transcranial magnetic stimulation (TMS) as an independent, instead of a dependent variable in experimental design, Willems and coworkers (2011) applied constant theta burst TMS on left hemispheric premotor areas, to temporarily inhibit neural activity in this areas thus creating virtual lesions. Results of a subsequent lexical decision paradigm indicated reduction of response speed specifically for manual, hand action-related, but not for non-manual verbs. Results are interpreted in terms of reduced inhibition of primary motor areas (by inhibiting premotor areas) causing facilitation of behavioral performance. This interpretation fits to results of a similar virtual lesion approach (Gerfo *et al.*, 2008) that targeted the hand motor cortex directly. Here, the authors reported hand action words (nouns and verbs) to be processed more slowly in an active reading paradigm, whereas non-action controls did not exhibit such a TMS induced behavioural impairment. Comparable results were also obtained after virtual lesions of the hand motor areas, specifically for hand action verbs in a semantic decision paradigm (Repetto *et al.*, 2013). TMS induced virtual lesions of motor areas were furthermore shown to affect also non-behavioural, electrophysiological indexes of semantic processing (Kuipers *et al.*, 2013). In this study, rTMS on hand motor areas was applied previous to word pair presentation in a semantic priming EEG paradigm. Here stimulation was shown to increase the amplitudes of N400 event related potential components, interpreted in terms of reduced semantic priming, specifically for hand action-related verb prime and target pairs, whereas N400 amplitudes for mouth action-related prime and target pairs where not affected and also a sham-stimulation control condition had no effect on the N400 amplitudes. The aforementioned virtual lesion approaches confirmed earlier observations by Pulvermüller and coworkers (2005b) on a functional role of motor areas for semantic processing. In this study, a different stimulation setup was applied, to facilitate neural activity directly, using single TMS pulses were applied to either the hand or the foot motor cortex while presenting hand- or foot-related action verbs in a lexical decision paradigm. Here an interaction between TMS stimulation site and action verb semantics was observed in reaction times, again suggesting a somatotopic involvement of motor areas in processing action word semantics.

In sum, these approaches that directly manipulate neural activity of the motor system strongly support a notion of a causal involvement of motor areas in processing of semantics.

Although these different approaches provide consistent conclusions it has been argued by some authors (Mahon & Caramazza, 2008; Mahon, 2015) that even these findings do not present evidence unambiguously in favor of the motor system actually holding semantic representations of action words. Instead, the reported effects could occur as the result of spreading of the induced neuronal activity back from the motor system into an entirely amodal or multimodal semantic system that stores the actual representations of a words meaning and would thus be compatible with entirely disembodied or ungrounded approaches towards semantics. In addition, the effects reported above in this section were only found for response speed and not for response accuracy. This may be merely the result of the non-invasiveness of neurostimulation approaches, which can only induce small changes in neuronal activity and hence also only small behavioural effects, but it also allows the interpretation that merely the processing of semantics was disturbed or facilitated, while issue of the representational format of semantics remains untouched by those approaches (Mahon, 2015).

Patient evidence

From a theoretical perspective, behavioural impairments in patient populations with neurological lesions however could paint a different picture than the aforementioned neurostimulation approaches. In the case a patient with lesions in the sensory or motor systems exhibits behavioural deficits in processing of action- or sense-related semantics, any interpretation in terms of (neurostimulation induced surplus) activity spreading back from basal sensory and motor areas to an amodal conceptual system cannot be applied, as in this case brain activity is missing (as a consequence of the lesion) and not induced via external stimulation. Furthermore, the investigations of neurological patients would allow to apply standard inference schemes in neuropsychology, that is investigations of single and double dissociations (Crawford *et al.*, 2003), to derive conclusions on the necessity of specific brain areas for specific cognitive functions.

Early evidence on such semantic category specific impairments was presented by Warrington and McCarthy (1983, 1987). In two single patients, each suffering from an infarction of their middle cerebral artery and global aphasic symptoms performance on manipulable objects was impaired more severely than that for animals, flowers and foods in a range of matching to sample tests. At the same time, a cohort of patients with herpes simplex encephalitis presented the opposite pattern in a similar series of tasks, with animals and foods being impaired while (mostly manipulable) objects being less affected in comparison

(Warrington and Shallice, 1984). This double dissociation demonstrates that semantic processing is not realized in one unitary semantic system, but different semantics must – at least in part – be realized in differing neural substrates. Unfortunately the authors of those patient reports present only limited details concerning the exact lesioned brain areas, so that conclusions about the specific contributions of extrasylvian sensory and motor are difficult to derive. However, it should be noted that a herpes simplex encephalitis is normally characterized by a spread from peripheral nerves, like the olfactory nerve into the brain (Dinn, 1980) that leads to predominantly temporal lesions, including parts of the ventral visual stream, involved in visual object recognition (Goodale and Milner, 1992). A lesion in these areas would correspond to the reported selective deficits for foods and animals, as they are strongly associated to visual and (in case of foods) olfactory information. Likewise, one of the presented stroke patients (Warrington and McCarthy, 1983) was reported to have a right hemiparesis that was strongest for arm movements, indicating lesions in arm motor systems. This would correspond, at least in a grounded cognition framework, to the specific impairment for small manipulable objects, which are characterized by arm and hand action-related semantics.

Impairments of the motor system

In order to make more fine grained statements of the functional involvement of sensory or motor systems in semantic processing, neurological patients with deficits specifically in their motor or sensory function should be considered. One clinical population that appears to be well suited in this respect are those of motor neurone disease (MND) patients, who show specific impairments of their motor functions. In a seminal study by Bak and coworkers (2001) a word to picture matching task was performed on a group of six MND patients, who were shown to have task accuracy impairments more pronounced for action verbs than for non-action nouns. Bak and Hodges (2004) were able to extend on this issue by reporting results in a picture-to-picture semantic similarity matching paradigm on three MND patients for noun (Pyramids and Palm Trees Test; Howard & Patterson, 1992) and verb (Kissing and Dancing Test; Bak and Hodges, 2003) targets. In alignment to the earlier findings, MND patients made more errors for semantic evaluation of action verbs, than for non-action nouns. Grossman and coworkers (2008) were able to investigate a whole cohort of MND patient in a similar fashion, by applying a description-to-target matching paradigm on object and action targets. Again, performance for action verbs was more impaired than that for objects, but the authors were also able to show that especially atrophies in bilateral premotor areas correlated with errors in action verb processing, whereas correlations of inferior-frontal areas where observed for performance for both, action and object words.

Another disease that is related to specific motor impairment of motor functions is Parkinson's disease (PD). As for MND, also PD patients were shown to exhibit specific impairments for processing action semantics, compared to non-action controls for single verbs (Boulenger *et al.*, 2008b; Silveri *et al.*, 2012; Fernandino *et al.*, 2013a) and whole action-related sentences (Fernandino *et al.*, 2013b). Strikingly, the processing difference between action verbs and control verbs was observed to disappear during treatment of PD symptoms to restore motor functionality. Boulenger and coworkers (2008b) showed semantic priming effects in response time of ten non-demented PD patients off medication, but not on medication, for action verbs to be significantly decreased compared to that for object nouns, indicating impaired semantic processing for action verbs. Similar evidence for a tight coupling of motor and semantic functions in PD was furthermore reported by Silveri and coworkers (2012) who investigated 12 PD patients during and without deep brain stimulation of the subthalamic nucleus, which reduces motor impairments. In the absence of stimulation, PD patients performed significantly worse than controls in a verb naming paradigm, in terms of task accuracy and latency, whereas there was no such difference to controls during stimulation. In contrast, non-action object controls again showed no such difference in either stimulation condition. To conclude, evidence from both, MD and PD patients therefore strongly suggests a causal role of the motor system in processing action-related semantics.

However, both etiologies are of rather diffuse nature, rendering it difficult to identify the exact neural substrates of the selectively impoverished performances on action verbs, mentioned above. While PD is prominent for motor impairments, it is also related to overall cerebral atrophy (Backer *et al.*, 1979), thus rendering it difficult to attribute the observed effects exclusively on motor system impairment. In addition, effects of both dopaminergic treatment (Boulenger *et al.*, 2008b) and deep brain stimulation (Silveri *et al.*, 2012) could, like it was the case for the neurostimulation effects in healthy participants mentioned above, be attributed to global effects or network specific backwards spreading of activity, possibly affecting an entirely amodal or multimodal semantic system and thus causing the observed deficits. Likewise, lesions of PD patients were not exclusive to their motor system. Post mortem analysis performed on four of the six patients in (Bak *et al.*, 2001) revealed lesions also in Broca's area in three of these subsample-patients and this observation was replicated in morphometric analysis of a larger patient sample (Grossman *et al.*, 2008). Again, this renders it difficult to disentangle contributions of classical perisylvian language- and extrasylvian motor areas, as it was also the case for the patient reports mentioned at the beginning of this section.

Evidence from stroke patients

To cope with these issues, it is beneficial to consider lesions that allow a better identification of lesioned and non-lesioned neural substrates, as it is the case for strokes. In turn, strokes however have the disadvantage that they rarely affect sensory or motor systems in isolation, due to the vascular architecture of the brain, where infarctions or hemorrhages in the arteries often result in large rather than focal lesions. It is therefore difficult to acquire large numbers of patients for spatially fine grained investigations. Despite these difficulties, Neininger and Pulvermüller (2001) were able to test one stroke patient with a very focal lesion in the somatosensory, pre- and primary motor cortex who exhibited selective slowing of responses for action verbs in a speeded lexical decision task, compared to matched non-action control nouns. This observation was replicated for lexical decision accuracy in a larger group of stroke patients with frontal motor lesions, though in this case lesions were often also covering inferior frontal and/or superior temporal lesions. A different angle to investigate category specific neural substrates in stroke patients was chosen by Arevalo and coworkers (2012) and Kemmerer and coworkers (2012; though including also some patients of other lesion etiologies in analysis). Both studies used voxel-based lesion symptom mapping to analyze semantic deficits in large patient groups on a voxel-by-voxel basis. Here, results indicated lesions in motor areas, in addition to lesions in perisylvian systems, to be predictive for impairments on action semantics in a spoken-word-to-picture-matching paradigm (Arevalo *et al.*, 2012), as well as in an extensive test battery consisting of tasks for picture naming, spoken-word-to-picture-matching, attribute judgments of words or pictures, and associative comparisons involving words or pictures (Kemmerer *et al.*, 2012). Arevalo and coworkers (2012) tested nouns and verbs of effector specific action semantics, but did not report any somatotopy in their results. Instead, both, foot and hand action-related stimuli, were shown to be impaired following lesions in premotor areas, inferior frontal gyrus, middle and/or superior temporal cortex. Results on stroke patients therefore seem to merely support the domain general contribution of the motor system to sensory motor semantics. This latter observation might be driven by the aforementioned wide-spread lesion nature in stroke patients, covering more than just the motor areas related of one specific effector, as also in voxel-based lesion symptom mapping approaches such confounds in lesion patterns cannot be overcome (Kimberg *et al.*, 2007; Rorden *et al.*, 2009).

Evidence for non-motor semantics

As for the neuroimaging and electrophysiological approaches, also patient reports were not limited to the action domain in presenting category specific deficits. For example, Bonner and Grossman (2012) investigated a cohort of primary progressive aphasia patients with grey matter atrophies in their temporal auditory with an auditory lexical decision task and found accuracies to be decreased especially for nouns related to sounds. Unfortunately, as for most of the above patient reports on action semantic deficits, atrophies were not exclusive to auditory cortex, but included in addition further perisylvian and extrasylvian frontal and angular areas. Again, this renders it difficult to attribute a selective causal involvement in processing and representation of auditory semantics specifically to basal auditory systems. Trumpp and coworkers (2013) overcame this objection by presenting a patient suffering from a very focal (just .9 cm in diameter) abscess in the temporal auditory cortex. In a (visual) lexical decision paradigm, this patient was observed to make more errors for nouns with auditory semantics and also showed impoverished category fluency specifically for auditory nouns, compared to nouns without strong relations to sounds. This finding demonstrates directly a link between and a necessary role of the neural substrates for hearing for the processing of sound-related semantics.

Further evidence for a somatotopic contribution of sensory systems comes from patients with lesions in their visual systems. Here, Neininger and Pulvermüller (2003) showed that patients with lesions in visual temporal-occipital cortex perform worse on nouns with strong visual semantics compared to matched control words without such prominent visual features in a visual lexical decision paradigm. In addition Pulvermüller and coworkers (2010) demonstrated that semantic dementia patients, characterized by lesions in the anterior temporal lobes, show selective deficits for the processing of words related to specific colors compared to control words that relate to specific words. As perceptual processing of object-related color has previously been shown to involve anterior temporal regions whereas object-related form is represented in more posterior fusiform areas, the observed pattern in semantic dementia patients even support a somatotopy within the visual system in terms of their causal role for processing semantics related to visual information. But, as explained above, also here the lesions do not allow to clearly tell apart contributions of specific visual areas and multimodal perisylvian areas in a fine grained fashion. Again, this leaves the possibility that the observed effects are in fact not genuine to lesions in modality specific visual systems, but merely results of lesion pattern confounds.

Summary of patient results and caveats

Summarizing the aforementioned evidence on category specific impairments in patients it can be concluded that lesions in the sensorimotor system are indeed specifically associated with behavioural impairments in processing of action or sensory related stimuli, though lack of lesion focality often does not warrant a high spatial resolution of inferences. Effects for action semantics were frequently observed for verbs, often in direct comparison to non-action noun controls (see Warrington and McCarthy, 1983, 1987 for results of comparisons within noun categories, as described in previous paragraphs). A notable exception in this respect was the study by Arevalo *et al.* (2012), as they applied both, nouns and verbs, but unfortunately noun and verb occurrences were not equally distributed between different categories. Although matched to another in terms of psycholinguistic features in the large majority of the aforementioned patient approaches, nouns and verbs do still differ in their grammatical class, thus leaving the possibility of the observed selective impairments being grammatical class specific, rather than being specific for semantics.

1.5 The issue of abstract concepts

Apart from the methodological concerns regarding the evidence for grounded semantic representations, as summarized above, grounded approaches are furthermore criticized for their apparent inability to explain representations of abstract words. Whereas abstract symbolic systems do not see any special challenge by abstract words, as concepts, grounded theories appear difficult to apply in this case as there is no transparent mapping of sensory or motor information to their semantics (Mahon and Caramazza, 2008; Dove, 2016). These authors conclude that grounded theories must therefore be inherently limited in their potential scope and could not be applied as a theory for semantic representations in general. However, even if abstract words were entirely amodal, symbolic approaches would need to account for the general processing differences between abstract and concrete verbs, as represented in the classical concreteness effect (e.g. James, 1975; Kroll and Merves, 1986). Here, concrete words were shown to have better results in lexical decision paradigms than words of abstract semantics, even when other psycholinguistic features are being controlled for. Similar processing differences between abstract and concrete stimuli were furthermore also highlighted in concreteness effects in comprehension and memory (Moeser, 1974; Holmes and Langford, 1976).

Classical accounts to explain differences between abstract and concrete concepts

One of the classical models proposed to explain this concreteness effect is the dual coding theory (Paivio, 1969; 1986). This model proposes that concrete words are represented in a verbal code format, thought to be situated on the left hemisphere, and in a sensory image-based format, assumed to extend over the right hemisphere. In contrast, abstract words are assumed to be represented in the verbal code exclusively, without any particular involvement of sensory coded information. Hence, the crucial difference between abstract and concrete words could be attributed to differences in their imageability. This proposal was put in question by results of Schwanenflugel and Shoben (1983), as well as by Schwanenflugel and Stowe (1989) who demonstrated that the concreteness effect disappears, once associative contextual information of abstract and concrete words has been controlled for. In conclusion, the context availability model (Kieras, 1978; Schwanenflugel and Shoben, 1983) proposes that the processing advantage for concrete nouns stems from the fact that they typically have more contextual linguistic or general semantic information available than their abstract counterparts. A distinct sensory code is therefore assumed to be not needed in semantic representation to explain processing differences between abstract and concrete words.

Reviewing the evidence in favor of grounded models of semantics for concrete words, as presented in the first half of this Introduction, it becomes apparent that neither of these classical approaches appears to be strongly supported. The observed modality-preferential activations for semantic category specific stimuli speak against entirely “verbal”, i.e. amodal representations, as proposed by the context availability theory. At the same time, the cortical distribution over left (and right) hemisphere of these contrasts go against the prediction of exclusive right hemisphere involvement for the representation of modality specific content in the dual coding approach.

Previous investigations on abstract words

Still, these models and the concreteness effect in general are influential also for current research, as they motivate the general principle on how abstract semantics are investigated, i.e.

in comparison to concrete words, which one could assume to be of importance in order to answer the question, whether or not modality specific representations are also of relevance for abstract concepts. In this context, two recent meta-analyses of neuroimaging investigations of abstract semantics are of special relevance (Binder *et al.,* 2009; Wang *et al.,* 2010). Together, both studies summarized 25 individual PET and fMRI studies on abstract words and sentences and revealed the inferior frontal and medial temporal areas to be activate more strongly to abstract than to concrete stimuli. Modality specific sensorimotor areas however were, at least in the majority of studies, not highlighted. It may appear to be tempting to take these systematic meta-analyses as evidence in favor of disembodied accounts on abstract word semantics, but instead it could also be argued that the individual studies (and hence also the two meta-analyses) do not allow this conclusion by design. Some of the reasons for this are similar to the ones previously mentioned for meta-analyses on concrete words (Binder *et al.*, 2009):

1) Many of the studies analyzed required active motor responses from the participants. As for concrete words, this setup makes it likely that task-specific motor activity and its anticipation or preparation masks motor activity that is genuine to semantic processing and representation.
2) Both meta-analyses focus on contrasts of abstract against concrete words or sentences, thus revealing activity that is greater in one condition than in the other. Any activity that is possibly shared between abstract and concrete stimuli however is lost in this comparison. Hence individual contrasts, separately for abstract and concrete stimuli would be needed to reveal neural substrates that are involved in both kinds of semantics.
3) All of the studies summarized treated abstract words as one monolithic category, without paying tribute to the exact abstract word meanings. Taking the category specificity results for concrete words as an example, it may appear likely that also different subclasses of abstract words are related to different neural substrates, which would cancel each other out when many semantically heterogeneous abstract stimuli are averaged together in analysis. As these category specific activations could potentially involve also modality-preferential sensorimotor areas their contribution to semantic processing could potentially not be revealed in neither meta-analysis by design.

As a consequence, any approach (not only those relying on neuroimaging measures) that tries to answer the question whether or not modality-preferential motor or sensory systems are also involved in handling abstract semantics should not attempt to merely contrast abstract to concrete contrasts, but to compare both abstract and concrete words to a common baseline. Furthermore, abstract words should not be treated as one monolithic category, but more fine grained subclasses of abstract words should be considered instead, to pay tribute to exact semantic content of words under investigation.

And indeed, although scarce, previous behavioural and neuroimaging approaches that investigated specific subclasses of abstract stimuli found evidence of modality specific motor systems to be also involved when abstract semantics are being processed. Here, Glenberg and coworkers (2008a) could demonstrate that hand movements previous to a sensibility judgment task can affect performance for abstract sentences which describe the passing of abstract information (like ‘Anna delegates the responsibilities to you’). Furthermore, hand motor evoked potentials were shown to be manipulated by such sentences (Glenberg *et al.*, 2008b), again pointing to a tight coupling of motor systems and the processing of abstract semantics. With regards to abstract emotion concepts Casasanto (2009), as well as Casasanto and Chrysikou (2011) showed that motor experience and handedness play a role in processing abstract emotion concepts, using a series of behavioural implicit association tasks. Evidence for a grounding of abstract emotion words in the motor system was presented even with a more fine grained somatotopy by Moseley and coworkers (2012). Their study applied concrete but also abstract emotion words, like ‘love’ or ‘hate’, in a passive reading paradigm, similar to the one applied by Hauk and colleagues (2004). Results indicated activity not only in left frontal gyrus and limbic system, but also in precentral motor areas related to hand and face movements, thus pointing directly to a grounding of abstract emotion semantics in those motor systems relevant for expressing emotions and perceiving emotions in others. Wilson-Mendenhall and coworkers (2013) revealed activation preferences for the abstract word ‘convince’ in a word-picture matching paradigm in modality-general areas which were previously identified to be involved in social cognition and mentalizing processes.

For another group of abstract words, referring to mathematical number concepts, anterior parietal cortex in addition to (hand) motor areas were reported to activate in a passive reading fMRI paradigm (Tschentscher *et al.*, 2012). Furthermore, also the processing of abstract quantifiers was shown to be influenced by changes in the motor system due to action preparation (Guan *et al.*, 2013).

To summarize, it appears that just like for their concrete counterparts, also for abstract words the exact neural substrates depend, at least in part, on their specific semantic content, i.e. there is more to their semantics than just their mere abstractness. Characteristics of this content and how exactly it could be grounded have been considered by a range of theoretical approaches (see Dove, 2016 and Borghi *et al.*, 2016 for recent reviews). As I will point out in the following paragraphs, it remains questionable however, whether any of these approaches could really be taken as a general principle for grounding of abstract terms.

Embodied accounts towards abstract semantics

Conceptual Metaphor Theory

One of the earliest approaches to explain abstract semantics in grounding terms is the conceptual metaphor theory (Lakoff and Johnson, 1980). The core hypothesis of the conceptual metaphor theory is that abstract meaning is carried via a mapping from an (abstract) target domain into concrete source domains via usage of metaphorical expressions. For example, with the metaphorical expression “boiling with anger”, the abstract domain of anger is mapped to a more concrete domain of a hot fluid. In this framework, abstract concepts can be grounded via mappings to whole sets of concrete domains and metaphorical expression, which are not mutually exclusive to another. Empirical evidence for such a mapping between domains can for example be seen in work by Casasanto and Bottini (2014), who provided behavioural evidence for a mapping of abstract words into the concrete/physical domain of space, realized via expressions like “top of the class” or “low price”. Similarly the aforementioned findings of Casasanto (2009) and Casasanto and Chrysikou (2011) can also be interpreted of a mapping of abstract emotion semantics into the motor domain. However, it could be argued these findings may also be explained by alternative grounding mechanisms without the need to underlying metaphorical mappings (for such alternatives see the paragraphs below). Furthermore, it remains questionable, whether metaphorical mappings and related expression can indeed be found for all abstract words, or whether they are only found for a specific subset. Any systematic investigation of this issue is complicated by the mostly introspective methods used to define those metaphors, although alternative empirical procedures, like metaphorical pattern analysis, have been developed in recent years from the domain of corpus linguistics (Stefanowitsch, 2006), which would allow to test the scope of the conceptual metaphor approach directly. Some authors (Galton, 2011; Borghi *et al.*, 2017) argue however that even if an abstract term like ‘anger’ might be mapped to the concrete domain of a liquid (via “boiling with anger”), it remains unclear in the conceptual metaphor theory what properties of liquids exactly constitute this mapping or how relevant properties are being identified. For example, the property of liquids to not run uphill or to have their boiling point altered as a function of atmospheric pressure do not appear to be relevant for understanding the meaning of *anger*.

Grounding in Emotion

In recent years, work by the group around Vigliocco (Vigliocco *et al.*, 2009, 2014; Kousta *et al.*, 2011) proposed abstract semantics to be primarily grounded via emotion-related affective information and corresponding neural substrates in anterior cingulate cortex and limbic systems, rather than in basal sensory and motor areas. According to this view, not only abstract emotion words but the entire domain of abstract words would be characterized by (latent) affective semantics that allows to ground their meaning in experience. Evidence in favor of this proposal is derived from a series of lexical decision paradigms which found performance differences between abstract and concrete words, even when both imageability and context availability where matched between two classes, thus showing that neither of the classical dual coding or context availability approaches could account for this difference (Kousta *et al.*, 2011). Instead, their analysis found differences in emotionality (i.e. emotional valence independent of polarity) to be predictive for the processing differences between abstract and concrete words. In a large scale analysis of over 1400 abstract words it was furthermore revealed that abstract words have stronger affective semantics than concrete words (Vigliocco *et al.*, 2014), thus leading to the conclusion that emotional neural systems have to be involved in general when abstract semantics are being processed. And indeed, the rostral part of the anterior cingulate cortex, which has previously been shown to be involved in processing emotions, to stronger engagement in processing abstract over concrete words, even when differences in context availability and imageability were being controlled for (Vigliocco *et al.*, 2014). However, it has been argued whether emotionality indeed can be taken as a general principle for grounding of abstract semantics. Here, concerns have been raised, whether a grounding in emotions can account for the representation of all kinds of semantics, even those that do not possess emotional connotation (Shallice and Cooper, 2013; Dove, 2016; Borghi, 2017). The observed differences in affective semantics between concrete and abstract words could be driven by either a bias in stimulus selection for analysis or a general bias for abstract emotion words in the lexicon of abstract words. Whether the processing of a non-emotional abstract word like ‘thought’ or ‘logic’ also involves affective information and related neural substrates of emotion processing however remains to be clarified (see Chapter 5).

Multiple representations approaches

Borghi (2017) and Dove (2016) identify some theories to extend on the classical dual coding approach in order to explain a grounding of abstract semantics (e.g. language-and-situated-simulation theory: Barsalou *et al.*, 2008; the words-as-tools approach: Borghi and Cimatti, 2009; Borghi and Binkofski, 2014; Representational pluralism: Dove, 2011). These theories assume action/perceptual information derived from direct action/perceptual experience, but also from linguistic experience to be constitutive for the representation of both, abstract and concrete words. The linguistic experience can, at least in principle, represent also information on relations between words and their co-occurrences, similar to what symbol systems (Fodor, 1983) or distributional/stochastic models of semantics (Landauer and Dumais, 1997) are capable of. The degree of involvement from each domain is modified by word semantics (with concrete concepts relying more on action/perceptual information) and situational context. Predictions regarding the corresponding neural substrates are arguably spelt out with the highest specificity in the words-as-tools approach. Here, linguistic information is seen specifically to be related to mouth actions, leading to a greater contribution of face/mouth/articulator effectors to the processing of abstract semantics compared to other effectors. A reason for this is seen in differences in the mode of acquisition between abstract and concrete words in native language learning during childhood. Concrete words have predominantly sensorimotor input of their referents available during learning, whereas abstract words are learned via linguistic input in a social discourse context, thus leading to an increased sensorimotor grounding in related face motor and social cognition systems. Evidence for the words-as-tools proposal can be seen in recent behavioural results of Borghi and Zarcone (2016) who demonstrated an interaction in response time of a semantic decision task between abstract and concrete words and responses given via the mouth or hand, pointing to an increased involvement of mouth-motor systems for abstract over concrete words. Further evidence in favor of this view can be seen in semantic rating results (Ghio *et al.*, 2013). As for the other approaches it remains to be investigated however, whether such a selective grounding in face motor systems can be generalized over all kinds of abstract words or whether there are also differences in the relevance of linguistic experience and hence the face motor system between different kinds of abstract words.

Grounding in distributed neural cell assemblies

Intuitively the apparent lack of consistent transparent sensorimotor referents for abstract words should make it difficult to form stable cell assemblies relating their word-form to meaning in terms of sensorimotor experience using the aforementioned principles of Hebbian and Anti-Hebbian learning. However, it has been argued that even if there is indeed no sensorimotor feature shared between all situations an abstract (or even concrete) word is being used, partial overlaps between individual instantiations and hence partial overlaps in sensorimotor experience could be present, a pattern referred to as "family resemblance" (Wittgenstein, 1953). Crucially this "family resemblance" could be sufficient for establishing cell assemblies linking the word form of an abstract word to its meaning represented by those partially overlapping neurons in modality-preferential sensorimotor systems (Pulvermüller, 2013a). This linkage to sensorimotor experience based on "family resemblance" in the cell assembly might be weaker than those for words with transparent physical referents which could provide physical features that are indeed present in all (or the large majority of) situations a word is being used, thus providing a potential explanation for processing differences between abstract and concrete words. Nevertheless, this mechanism would still be able to provide a grounding in experience even for abstract words, as preliminary results of a recent (Anti-) Hebbian learning based cell assembly simulation approach indicate (Schomers and Pulvermüller, 2017).

In addition to such a grounding via family resemblance, also the aforementioned alternative approaches towards a grounding of abstract words could be realized in cell assembly terms and could, at least in theory, be combined with the aforementioned grounding via "family resemblances".

A grounding in emotion could be realized by adding respective affective systems to the orchestra of sensorimotor experience representing a words meaning. Given the feature of semantic transfer between signs as well as the compositionality and generativity between different cell assemblies, also proposals favoring multiple representations for abstract (and concrete) word semantics can be realized in neural cell assembly terms. Here it is important to note that also word co-occurrences or the general stochastic properties between words can modify respective cell assemblies as well, thus allowing for word-word learning in addition to the aforementioned word-world learning mechanisms. With regards to the words-as-tools proposal it should furthermore be mentioned that in a cell assembly framework linguistic input can easily be treated as source of sensorimotor experiential information to base a grounding of abstract semantics on. Given the feature of combining symbols (and their grounded cell assemblies), even the aforementioned proposal of a grounding of abstract semantics via the proxy of metaphorical expressions could potentially be realized in terms of neural cell assemblies, though keeping in mind the caveats of the conceptual metaphor theory. Importantly, in a cell assembly approach all these different approaches do not exclude another and in contrast to the individual proposals summarized above, there is no defined characteristic of abstract words that must be assumed for all kinds of abstract words in order to allow semantic grounding. In contrast to the alternative proposals, there no specific contribution of modality-preferential (sensorimotor) is predicted to occur for all kinds of abstract words, but different types of abstract words are assumed to be reflected by different patterns of sensorimotor/affective contributions, corresponding to previous evidence summarized in the sections above.

1.6 Objectives of the dissertation

The overall aim of this dissertation is to elaborate on the issue on whether or not the motor system is involved in and of functional relevance for the processing of concrete, as well as of abstract word semantics. With regards to abstract semantics the first two dissertation projects (Chapters 3 and 4) relate directly to previous observations on specific hand and face motor area contributions to the abstract subclass of abstract emotion words (Moseley *et al.*, 2012). As these findings presented merely correlational measures of an involvement of motor systems in processing of abstract semantics, these dissertation projects aimed directly at the investigation of their functional role for abstract semantics, by testing neurological patients. To make inferences with a high spatial resolution, only patients with discrete lesion patterns in preselected neural systems were considered for analysis of single cases (Chapter 3) or whole groups of patients (Chapter 4). The third dissertation project (Chapter 5) aimed to investigate, whether abstract emotion nouns are the exception in the domain of abstract semantics, when it comes to a motor system involvement in their processing, or whether motor system activity is also informative about the processing of abstract words that are even more disembodied and do not possess emotion semantics. Both approaches should help to resolve the issue, whether or not the motor system is informative about processing of also abstract words, or whether grounded theories of semantics can indeed only be applied in the context of concrete words.

2. Material preparations

2.1 Working definition of abstractness

As the term “abstractness” is used with different meanings in the literature, I would like to clarify my working definition of abstractness for the context of this dissertation. Here, abstractness, is meant to resemble the absence of transparent concrete physical referents, which could be perceived by the senses, could be interacted with or be directly related transparently to motor actions. Therefore, words denoting superordinate categories of concrete objects, like ‘furniture’ are not considered to be abstract, even if these words provide a higher degree of abstraction than their direct concrete, subordinate instantiations (e.g. ‘chair’ or ‘desk’). As long as their concrete subordinate members are objectively identifiable, these words would be considered to be concrete in this definition. Whether or not a word was seen as concrete or abstract in this sense was determined using extensive semantic ratings to rule out any strong sensorimotor semantics in abstract stimuli (see details below).

2.2 Lexicon creation and stimulus selection

Choice of method to measure stimulus semantics

To investigate semantic processing, the meaning of linguistic symbols, words or phrases needs to be controlled when selecting experimental stimuli. The endeavor poses a particular challenge if processing of specific semantics or semantic subtypes is considered, rather than merely contrasting meaningful to meaningless stimuli. In the case of the current dissertation projects, especially semantics that relate to sensory or motor experience are of relevance and should be objectively controlled in experimental stimuli. As the meaning of a word cannot be defined directly, indirect measures have to be applied instead. One instance of such an indirect semantics measure are semantic feature lists, which frequently have been used before as a dependent measure to investigate differences or similarities between different words or concepts (e.g. Rosch and Mervis, 1975; Wiemer-Hastings and Xu, 2005). For example, the meaning of ‘magpie’ could be represented by the features ‘black’, ‘white’, ‘wings’, ‘can fly’, ‘feathers’ and ‘steals shiny things’. As this list could easily be extended by further features (‘beak’, ‘builds nest’, ‘lays eggs’, ‘nest predator’, etc.) it becomes apparent with this example alone that it is very difficult, if not entirely impossible, to generate an exhaustive list of features, especially in any time constrained experimental setting. Furthermore, this example also shows that features can vary greatly in their level of specificity both within and between different subjects. While I do not want to doubt the validity and interpretability of feature lists as a dependent measure in general, these attributes make feature lists not well suited for the purpose of stimulus generation and validation in my dissertation projects. It is likely that feature lists turn out to be rather heterogeneous for different individuals and most importantly it would not be guaranteed that the sensorimotor attributes would appear in an individual's feature list for a word, even if they were intuitively relevant. Likewise the mere absence of particular features in an individual feature list provides no evidence that the corresponding word is indeed devoid of such semantic characteristics.

An alternative measure which does not suffer from those disadvantages is that of semantic ratings and was hence chosen for stimulus selection of my dissertation paradigm. Here, semantic relations of a stimulus to a set of predefined features are evaluated on Likert-scales. This procedure has previously been applied in a wide range of studies on semantic processing and is especially popular in approaches that target a possible grounding of word semantics in sensorimotor systems (e.g. Hauk *et al.*, 2004; Connell and Lynott, 2009, 2013). Semantic relatedness judgements might rely heavily, if not in entirely, on individual subjective experience with a word or concept and may therefore vary significantly between individual subjects. A professional basketball player for example might give the word 'ball' very high scores on a scale for the semantic attribute of hand action-relatedness and lower scores in comparison to its leg action-relatedness, whereas this pattern is likely reversed in professional football players. To cope with this issue, a whole group of individual raters have to be applied and individual ratings should be combined for further analysis. Resulting measures of central tendency, like the arithmetical mean, could then be used to derive the average semantic relatedness of a word to specific features. While such central tendency scores cannot predict the semantic representation in each individual to be tested in the experimental paradigms the rated stimuli are designed for with 100% accuracy, it gives at least a good idea what the average general semantic connotations could look like. In addition, the shape of rating distributions can already provide evidence on the homogeneity of semantic evaluations for the corresponding stimuli, allowing to exclude those words from the final selection which show a too extreme variance of ratings between raters. With those arguments in favor of semantic ratings in mind, I will now turn to the description of the exact procedures applied to generate the ratings for my set of stimuli.

Preselection of stimuli for semantic rating

The aim of the semantic rating procedure was to collect words that fall into predefined semantic categories, with high within category homogeneity and simultaneous dissimilarity in relevant features to other category. Due to pragmatic considerations in experimental and rating session design, a preselection of items to be rated had to be generated. Instead of collecting semantic ratings for arbitrary lists of words, the preselection was motivated by the planned paradigms purposes, as words selected for the rating procedure were chosen to likely fall in specific, predefined semantic categories. In addition to intuitive selections of words, two other methods were used to generate this initial list of words to be rated: 1) Consideration of stimuli used in previous studies and 2) a systematic review of text corpus results. For 1) a set of previous studies on modality specific contributions to semantic processing of nouns and verbs was reviewed (Pulvermüller *et al.*, 1999; Hauk *et al.*, 2004; Carota *et al.*, 2012; Moseley *et al.*, 2012) and translated to German, if necessary. For 2) two queries in the dlex text corpus (Heister *et al.*, 2011) were being performed, generating lists of 1924 nouns and 3312 verbs with the selection criteria of a lemma frequency of at least one per million and a maximum number of three syllables. In a first step, all words from these lists were excluded that did not fall in any of six predefined semantic categories of interest (arm, face, leg action-related, abstract emotion or abstract mental, for nouns and verbs and animals for nouns only), according to judgements from two raters. Resulting sets of 1239 nouns and 676 verbs were given to seven further participants who were asked to also categorize all words into the aforementioned five (for verbs) or six (for nouns) semantic categories and only those words were considered for the later word rating paradigm that had an consistent categorization in at least eight raters (out of nine) in total.

Selection of semantic scales

Ratings were collected on 21 different semantic dimensions in total, with twelve being of direct relevance for the dissertation project, whereas the other semantic features were evaluated for future research purposes. As the motivation of the dissertation projects was to investigate the meaning of concrete, action-related words, as well as words referring to abstract concepts, semantic scales were selected to cover effector specific action-relatedness features (i.e. face/mouth-, hand/arm- and foot/leg action-relatedness), relation to mental processes, to emotions and for abstractness/concreteness. To control for sensory information and validate the abstractness of abstract word stimuli, ratings for relatedness to gustatory, olfactory, haptic-tactile and auditory information were included, too. In addition, word knowledge measures were achieved for all stimuli.

Rating procedure and participants

For the current dissertation projects, it was critical to assure that different semantic categories of interest in the experimental paradigms were matched on non-semantic psycholinguistic properties, so that any between category performance or neuroimaging difference can indeed be attributed to word semantics rather than other psycholinguistic stimulus features (like word length, number of syllables, word frequency etc.). As the exact ratings of a word could not be predicted a priori, the set of words for the initial semantic ratings was selected to be significantly larger than needed for the actual experimental paradigms, to allow for the aforementioned matching post hoc by removing stimuli from selection that do not fit in terms of their basal psycholinguistic or semantic characteristics. To this end a set of 526 nouns and 471 verbs was selected for the rating procedure. The rating paradigm was implemented in E-prime (Version 2.0.8.90) and presented all words individually in randomized order for each semantic scale on a computer screen. Participants were instructed to provide semantic ratings according to their first intuitive response, without using excessive or strategic exploration of potential relations to the semantic feature in question.

Ratings were given via mouse-clicks on a Likert scale ranging from 1 (no semantic relation to the semantic feature in question) to 7 (very high relation to the semantic feature in question), with the exception of the concreteness scale, which was designed with the poles of “very abstract” (1) to “very concrete” (7), as well as word knowledge where the ends of the rating scale were defined as “no knowledge about a word’s meaning” (1) to “very good knowledge of a word’s meaning” (7). There was no time limit for responses and the subsequent word appeared on screen directly after the rating for the previous word was given. In case participants wanted to change their rating post hoc they were allowed to write down the respective word, semantic scale and intended rating, so that ratings could be corrected manually in the E-prime output file after the end of a rating session. At the beginning of ratings on a new semantic scale, participants were given short printouts of written instructions on the semantic scale in question, including two example ratings for words that were not part of the words in the rating procedure stimuli. Given the large amount of ratings that were collected (overall up to 20397 per subject), the rating paradigm was split up into different rating sessions, each covering ratings of up to four semantic features with the order of features being randomized between participants. In addition, rating stimuli were split up into 2 sublists, to further decrease the duration of each rating session to approximately 1 hour each. In total 33 participants were recruited for the ratings study (average age 22.9 years, SD = 3 years, 21 women) and were reimbursed for their participation. Rating sessions were scheduled according to participant's preferences, with the limitation of a maximum of two sessions per day per participant, separated by a break of at least three hours. Due to the high number of rating sessions, with a maximum of 12 sessions per participant, not every participant was able to give ratings for every word on all scales. To this end each word was rated on each scale by 10 to 20 individual participants, with a mean of 15.7 raters across words.

Rating results and lexicon composition

For each participant those words were excluded from further analysis which achieved a word knowledge score of less than 6, to assure that participants had sufficient knowledge of a word's meaning to give valid ratings on semantic scales. Valid ratings were averaged over participants on each scale for every word and resulting mean semantic scores were summarized in a matrix holding 21 semantic scores per word. To increase the ease of usage for stimulus selection in the subsequent dissertation paradigms, all words were allocated to 11 preliminary semantic categories, according to the following criteria: For the categories of tool nouns and arm/hand action-related verbs, items had to present a hand/arm action-relatedness score larger than the neutral mid-point of 4, while their scores for relation to face/mouth and leg/foot actions had to be less than 4. Following the same rationale, food nouns and face action verbs showed an action-relatedness score greater than 4 exclusively for face/mouth action-relatedness and likewise leg action verbs exclusively for leg/foot action-relatedness, with the respective other effector specific action-relatedness scores being below the neutral midpoint. For the categories of animal nouns and nature state verbs (like e.g. 'raining', 'burning'), the maximum of all effector specific action-relatedness scales had to be smaller than 4, while their concreteness had to be rated higher than 4. For abstract emotion nouns and verbs, as well as for abstract mental/cognitive nouns and verbs the same restrictions regarding their action-relatedness applied, with the addition that also the maximum of all sensory scales (relatedness to tactile, auditory, visual, olfactory and gustatory sensation) had to be lower than 4. Furthermore, abstract emotion nouns and verbs had to present an emotion-relatedness greater than 4 each, whereas for abstract mental/cognitive nouns and verbs ratings needed to be smaller than the neutral midpoint on this scale but larger on their relatedness to mental processes. Resulting group sizes for each category in the final stimulus lexicon after applying those criteria are summarized in Table 2.1.

Table 2.1: Items included in stimulus lexicon for stimulus selection of the three dissertation Projects in Chapters 3-5.

Semantics	Nouns	Verbs
Abstract Emotion	132	69
Abstract Mental/Cognitive	104	72
Arm/Hand Action Related	92	88
Face/Mouth Action Related	95	83
Leg/Foot Action Related		75
Animals	103	
Nature State		84

3. Is the motor system necessary for processing action and abstract emotion words? Evidence from focal brain lesions[1]

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[1] This chapter is based on Dreyer, F. R., Frey, D., Arana, S., von Saldern, S., Picht, T., Vajkoczy, P., & Pulvermüller, F. (2015). Is the motor system necessary for processing action and abstract emotion words? Evidence from focal brain lesions. *Frontiers in psychology, 6*. Author contributions**:** study concept and design (FRD and FP), material matching and selection (FRD), data collection (FRD, SvS and SA), clinical evaluations of patients (TP, DF and PV), data analysis (FRD), manuscript drafting and artwork (FRD) and revisions (FRD, FP, TP, DF).

3.1 Abstract

Neuroimaging and neuropsychological experiments suggest that modality-preferential cortices, including motor- and somatosensory areas, contribute to the semantic processing of action-related concrete words. Still, a possible role of sensorimotor areas in processing abstract meaning remains under debate. Recent fMRI studies indicate an involvement of the left sensorimotor cortex in the processing of abstract emotion words (e.g. ‘love’) which resembles activation patterns seen for action words. But are the activated areas indeed necessary for processing action-related and abstract words? The current study now investigates word processing in two patients suffering from focal brain lesion in the left fronto-central motor system. A speeded lexical decision task on meticulously matched word groups showed that the recognition of nouns from different semantic categories – related to food, animals, tools and abstract emotion concepts – was differentially affected. Whereas patient HS, with a lesion in dorsolateral central sensorimotor systems next to the hand area, showed a category specific deficit in recognizing tool words, patient CA suffering from lesion centered in the left supplementary motor area was primarily impaired in abstract emotion word processing. These results point to a causal role of the motor cortex in the semantic processing of both action-related object concepts and abstract emotion concepts and therefore suggest that the motor areas previously found active in action-related and abstract word processing can serve a meaning-specific necessary role in word recognition. The category specific nature of the observed dissociations is difficult to reconcile with the idea that sensorimotor systems are somehow peripheral or “epiphenomenal” to meaning and concept processing. Rather, our results are consistent with the claim that cognition is grounded in action and perception and based on distributed action perception circuits reaching into modality-preferential cortex.

3.2 Introduction

A fundamental theoretical debate about the nature of meaning and concepts dominates the cognitive and brain sciences. Classic cognitive psychologists propose that semantic and conceptual processes are carried out in a dedicated symbolic semantic system functionally detached from sensory and motor modules and specialized for handling information about meaning and concepts related to signs (e.g. Ellis and Young, 1988). An alternative approach, sometimes referred to by the terms "embodiment" and "semantic grounding", states that meaning is intrinsically related to (or grounded in) action and perception information and processed in the brain by distributed action perception circuits that reach into motor and sensory brain areas (Barsalou, 1999, 2008; Pulvermüller, 2005; Glenberg and Gallese, 2012). Some recent attempts to amalgamate both positions into one integrative proposal either maintain that semantic processing is carried out in an amodal system, whereas modality-preferential cortices, such as the sensorimotor areas, play an optional, merely "colouring" role (Mahon and Caramazza, 2008; Caramazza *et al.*, 2014), or they postulate semantic integration in a "semantic hub" (typically placed in temporal cortex) and allow for additional modality-specific semantic centres across the cortex (Patterson *et al.*, 2007; for review, see Binder and Desai, 2011; Kiefer and Pulvermüller, 2012). However, similar to the symbolic systems position, these proposals attribute true semantic processing and related deficits primarily to semantic hub areas. To cite but one relevant statement here: "understanding the word 'run' ***occurs in*** modality-independent neural systems" (p.92, Bedny and Caramazza, 2011; our own emphasis). Therefore, it is not clear whether this type of "integrative" position allows for the explanation of category specific deficits arising from a focal lesion in one modality-preferential cortical system.

Much recent imaging work has accumulated evidence that the motor cortex (Martin *et al.*, 1996; Damasio *et al.*, 1996; Hauk *et al.*, 2004; Hauk and Pulvermüller, 2004; Pulvermüller *et al.*, 2006) and a range of sensory systems (Barrós-Loscertales, 2012; González *et al.*, 2006; Kiefer *et al.*, 2008) become active when words and concepts from different semantic categories are being processed. In particular, the motor system instantaneously activates in a somatotopic fashion when subjects hear or read words semantically related to different parts of the body (Pulvermüller *et al.*, 2005b; Shtyrov *et al.*, 2014), thus arguing against the view that the "grounded" sensorimotor activations may only emerge at a late stage of post hoc interpretation and supporting their genuine role in semantic information access. Category specific semantic activation across the motor system has originally been reported for action-related verbs, but has recently been replicated for nouns semantically related to the mouth and hand (food and tool nouns; Carota *et al.*, 2012). Concerns have been raised by some groups on the reproducibility of these effects (Postle *et al.*, 2008; Caramazza *et al.*, 2014), but recent systematic comparison of studies across labs demonstrated that these results could indeed be reproduced in the majority of approaches (Carota *et al.*, 2012; Kemmerer *et al.*, 2012). Semantically related activation in the motor system has even been reported for abstract words related to emotions (Moseley *et al.*, 2012).

However, although these brain activation studies are consistent with, and confirm predictions of, the grounded-semantic account postulating the relevance of modality-preferential areas for semantics, neuroimaging and neurophysiological studies can never prove the functional relevance and necessity of brain areas for cognitive function. To investigate this crucial issue, lesion studies in neurological patients and neurostimulation approaches are necessary.

Here, a range of results has so far been suggestive of a role of sensorimotor systems in semantic processing. For example, Pulvermüller and colleagues (2005a) applied single TMS pulses to primary hand and foot motor cortex while verbs semantically related to hand or foot actions had to be recognized in a lexical decision task. As the recognition latencies for hand- and leg-related action verbs was differentially affected by TMS stimulation site (an effect confirmed by a significant interaction of these factors), a causal role of the motor cortex on semantic word type processing was evident. The latter conclusion was also supported by further TMS work in healthy subjects (Willems *et al.*, 2011) and by behavioural experiments in which subjects engaged in motor activity while linguistic-semantic information had to be processed (Glenberg *et al.*, 2008a; Witt *et al.*, 2010; Shebani and Pulvermüller, 2013). However, as most of the causal effects of motor activity on semantic processing were manifest in reaction times but not accuracies, it may still be that the functional role of motor systems for category specific semantic processing is only relevant for optimizing word processing, but not necessary for it.

Stronger claims about the necessity of modality-preferential, including sensorimotor, cortex for semantics can potentially be derived from lesions studies. Important and well-known classic work reported lesion-related category specific semantic impairments for words related to manipulable objects (Warrington and McCarthy, 1983, 1987), animals and foods (Warrington and Shallice, 1984; for a recent review see also Gainotti, 2010), which were manifest in task accuracies. On closer inspection, the observed patterns of impairments confirm that lesions which include motor areas can lead to selective and pronounced deficits in the processing of action verbs (Damasio and Tranel, 1993; Bak *et al.*, 2001; Neininger and Pulvermüller, 2001, 2003; Arevalo *et al.*, 2012; Kemmerer *et al.*, 2012). Similar results, supportive for theories of embodied cognition, were found after lesions of auditory (Bonner and Grossman, 2012; Trumpp *et al.*, 2013), and visual systems (Pulvermüller *et al.*, 2010; Gainotti, 2010) for the processing of words with auditory or primarily visual semantics. Whereas lesions in modality-preferential sensorimotor cortex bring about deficits in processing action-related words, the granularity of the category specific deficit is under discussion (see Arevalo *et al.*, 2012; Reilly *et al.*, 2014). At present no evidence exists for a differential involvement of hand- or face-related action words, which can be found amongst verbs (‘write’ vs. ‘chew’) but also amongst the nouns (hand-related tool vs. mouth-related food words) (Arevalo *et al.*, 2012).

Unfortunately, several limitations apply to the majority of previous patient studies. First, the patient populations under investigation typically suffered from large lesions typically caused by stroke or degenerative brain disease. Most of these lesions included motor or sensory cortex but, in addition, other parts of the brain, as in strokes, or even were of diffuse nature, as in motor neuron disease and semantic dementia. Therefore, fine grained conclusions about the functional role of specific brain areas in word processing are difficult to derive and it is not entirely clear whether the sensorimotor lesion was indeed the primary cause of the patterns of deficits reported. Second, from a psycholinguistic perspective, the choice of stimulus materials allowed different interpretations of the results. For example, the popular comparison between action-related verbs and object-related nouns frequently led to evidence of a category specific deficit, but it is not always clear whether such a deficit is best explained by semantic factors (action- and object-relatedness) or in terms of the lexical (or grammatical) category difference instead (nouns vs. verbs). In addition, relevant psycholinguistic variables such as word length and word frequency were not always matched in previous studies, thus opening further options for alternative explanation of presumed “category differences”. However, a small number of recent studies looking at rather focal lesions suggest that auditory and action-recognition systems may also be necessary for processing the semantically related words (Neininger and Pulvermüller, 2001; Campanella *et al.*, 2010; Trumpp *et al.*, 2013).

Although some evidence for a causal and possibly even necessary role of modality-preferential cortex for category specific semantic processing exists, no similar data are available for abstract words whose semantic information is somewhat detached from specific sensory and motor modalities. A major claim held by most symbolic systems accounts, and equally the integrative proposals mentioned above, is that abstract semantic processing is removed from, and does not require, sensory and motor systems of the brain. In contrast, proponents of grounded cognition have argued that, in order to learn the meaning of an abstract word, it is necessary to know at least some concrete semantic instantiations and contexts in which it can be used (Barsalou and Wiemer-Hastings, 2005; Borghi and Cimatti, 2013; Pulvermüller, 2013a). At the neuromechanistic level, it has therefore been proposed that abstract meanings, similar to concrete ones, are organized as distributed neuronal circuits including neurons in multimodal and sensorimotor systems, although their links into modality-preferential areas may be weaker than those of concrete conceptual representations. This idea is supported by behavioural (Glenberg *et al.*, 2008a,b) and fMRI findings (Moseley *et al.*, 2012), both indicating an involvement of motor processing in comprehension of abstract words. A strong version of a semantic grounding position thus implies that modality-preferential sensorimotor cortex also takes a crucial role in abstract word processing (Glenberg *et al.*, 2008a,b; Havas *et al.,* 2010), but to our knowledge this has so far not been shown with neither neurostimulation, nor lesion approaches. If correct, this position predicts that lesions in modality-preferential cortex, and in motor areas specifically, can lead to category specific semantic deficits in processing abstract words. Positive evidence for this statement would certainly falsify symbolical semantic accounts and most integrative proposals still leaning towards abstract-symbolism, too (Mahon and Caramazza, 2008; Dove, 2009).

On the background of this pre-existing work, the current study addresses the putative necessary role of the modality-preferential sensorimotor cortex in the processing of both, action-related and abstract words by examining two patients with focal brain lesions. Although group studies were once claimed necessary for drawing strong conclusions on the brain basis of cognition and language, we would argue that single case reports are indeed suited perfectly well to provide existence proofs for the claimed causality, as they are relevant for the current debate. In addition, some researchers have highlighted the advantages of single case studies, especially if brain localizations of function can strongly differ between individuals – as it is known to be the case for sensorimotor functions (Elbert *et al.*, 2005; Buonomano and Merzenich, 1998) – and the grouping of patients with necessarily non-identical lesions is always debatable (Caramazza, 1986). However, we hasten to add that, whereas case studies can confirm claims about existence (“there is one case for which it applies that…”), they cannot found general (“all”) statements.

To overcome the mutual confounding of word semantics and grammatical class, as present in previous patient studies, the current study probed both nouns and verbs separately. This opens the possibility of finding category-semantic deficits that are, in addition, specific to lexical class. With the inclusion of abstract word categories, it becomes possible to investigate whether semantic grounding in modality-preferential cortex applies exclusively to concrete words, or extend also to the domain of abstract semantics. To allow conclusions about semantic processing rather than to other stimulus features, semantic categories were matched for a range of psycholinguistic features (see Methods). Word recognition was monitored using a speeded lexical decision task (LDT). Performance on this task has previously been shown to be sensitive to aspects of word semantics (Chumbley and Balota, 1984; see also Neininger and Pulvermüller, 2001, 2003). Furthermore, the LDT has important advantages over other tests frequently used in previous studies of semantic category specificity, including, for example, picture naming or categorical classification. These latter tasks require a similar semantic relationship between words and pictures (which, however, differs between concrete and abstract items) and similar perceptual-semantic similarity structure (which differs, for example, between animals and tools), the absence of which limits the scope of their use. In contrast, the LDT offers a straightforward possibility to test performance across word categories differing in their (e.g. abstract vs. concrete) semantics; it has therefore been applied frequently in previous research targeting effects of concreteness and semantic category specificity (e.g. James, 1975; Kroll and Merves, 1986; Jin, 1990; Neininger and Pulvermüller, 2001, 2003; Samson & Pillon, 2004). The rational underlying this research strategy is the following: If semantic processes elicited by one semantic type of words are specifically supported by a given area and if this area is lesioned, the recognition process of the respective word category can be impaired (delayed and/or less accurate). And if a deficit specific for a specific semantic category results from a focal lesion, the lesioned area is a likely key site for processing the affected semantic type. The theoretical background for this prediction is the theory of distributed semantic circuits, according to which neuronal networks with different cortical distributions underlie the processing of different semantic word types (see Pulvermüller, 2013). A focal lesion in an area belonging to the distributional pattern of one semantic word type, but no other word types, would lead to a reduction of the excitatory feedback in the respective category specific semantic circuits and therefore to delayed and more errorful word recognition. By testing two patients suffering from focal lesions in their fronto-central sensorimotor cortices, this study aims at fine grained conclusions on the functional involvement and necessity of the focal brain areas for the recognition of words from specific semantic categories. Adding abstract words to the stimulus material allows to test whether such a crucial role of these modal areas just applies to the processing of words related to concrete concepts or even extends to words with abstract semantics.

3.3 Methods

Patients and clinical examination

Patient HS

Patient HS was a 41 years old man, with a singular focal precentral lesion, situated directly inferior to the left hand motor cortex. HS was a native, monolingual German speaker and right handed (LQ = 80), with a total of 18 years of formal education and was serving in the military at the time of testing. Following biopsy, HS' lesion was diagnosed to be the single residual core of an Acute Disseminated Encephalomyelitis (ADEM) of 18 mm in diameter. Fiber tracking on Diffusion-Tensor-Imaging (DTI) data, using hotspots of a navigated TMS guided motor mapping procedure as seed regions (see Frey *et al.*, 2012 for details on this procedure) revealed his lesion to be situated in the precentral gyrus, half a centimeter away from the pyramidal tract of the hand motor cortex. A T1 weighted magnetic resonance imaging (MRI) scan of this lesion is shown in Fig. 3.1A. At the time of language testing, neurological examination revealed mild paresis of the right arm and leg (grade 4, i.e. movement against external resistance, but less than normal), but no other cognitive or language impairment.

Patient CA

Patient CA was a 52 years old woman with a single lung cancer metastasis (histology: adenocarcinoma as non-small-cell lung carcinoma) in the superior frontal gyrus, affecting the supplementary motor area (SMA) of the left hemisphere, as shown in Fig. 3.1B. The patient had been under chemotherapy for 3 cycles, underwent radiation therapy for 2 cycles and a first extirpation of the tumor had been performed six month prior to testing. All therapeutic measures did not result in control of the solitary cerebral metastasis. Due to growth of the tumor (with an extent of roughly 1.2 cm x .9 cm x 2 cm), indication for additional surgical removal was yielded at the time of testing. History revealed hypertension, chronic obstructive pulmonary disease and the regular administration of Pregabalin and Amitriptylin. CA was right handed (LQ = 80 at the time of testing) and a native, monolingual German speaker with 12 years of formal education and had been working as a chef pre-morbidly. CA did not report any sensory, motor, cognitive or language deficits and neurological examination did not reveal any impairments on those dimensions at the time of testing.

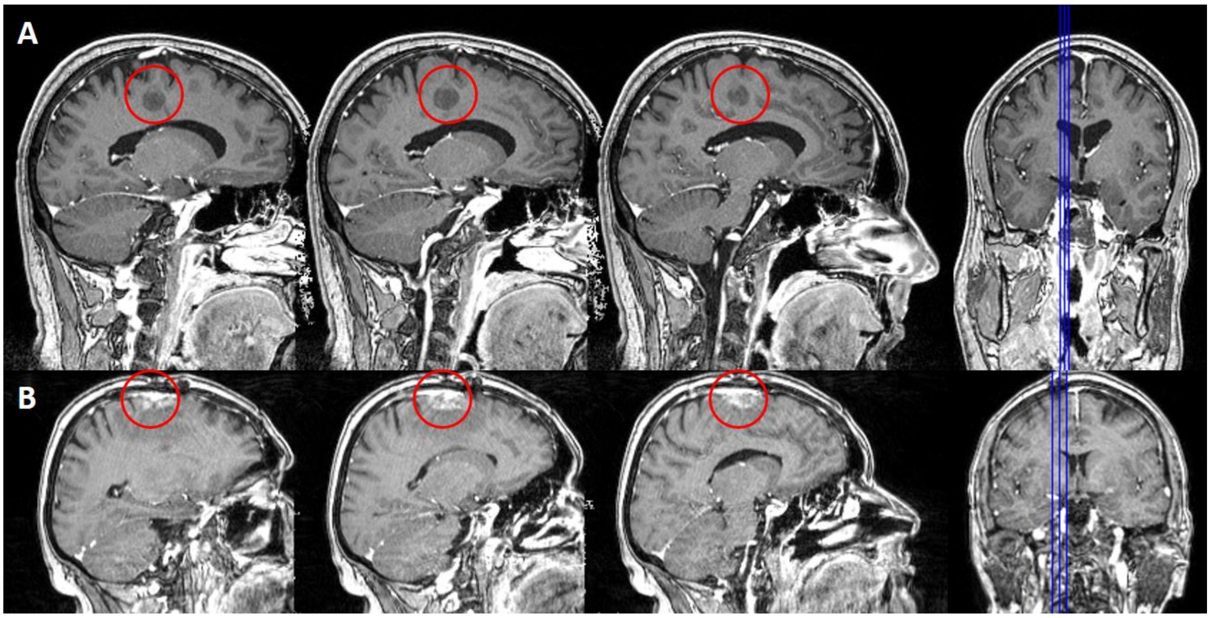

Figure 3.1: T1 weighted MRI MPRAGE Sequences of patients HS (A) and CA (B). Lesion sites are marked with a red circle.

Control Participants

A group of 21 participants (5 males) without neurological records served as control sample for the LDT paradigm. On average, controls were 40.7 years (*SD* = 18.7 years) old at the time of testing, with an age range from 18 to 79 years, covering that of the two neurological patients. Likewise, years of formal education were similar to CA and HS, spanning between 11 and 24 years, with an average of 16.5 years (SD = 3.5 years).

Both, patients and healthy control participants, provided written informed consent prior to participating in the study and procedures were approved by the ethics committee of the Charité University Hospital, Berlin, Germany.

Paradigm

As critical test, a speeded lexical decision task was carried out, as explained below. To assess clinical language proficiency the Token Test, and the repetition, naming and language comprehension subtests of the “Aachener Aphasie Test” (AAT), a standardized German aphasia test battery (Huber *et al.*, 1983), were applied. Handedness was tested using the Edinburgh Inventory (Oldfield, 1971).

LDT stimuli

160 nouns and 160 verbs were presented, along with 320 matched pseudo-words. Each of the lexical/grammatical categories included 40 stimuli from 4 semantic groups or categories. Among the nouns, there were words used to speak about tools, food items, animals and abstract-emotion entities. The semantic category groups of the verbs included words typically used to speak about actions performed with parts of the face (e.g. 'kauen', *to chew*), hand (e.g. 'greifen', *to grap*), or leg (e.g. 'rennen', *to run*) and about abstract concepts ('hassen', to *hate;* see Supplementary Material for a complete overview of word stimuli).

Within each lexical category or grammatical word class, all semantic category groups were matched for a range of lexical and sub-lexical psycholinguistic variables, as determined by the dlex corpus (Heister *et al.*, 2011). Matching was achieved for word length, number of syllables, phonological stress, normalized lemma frequency, character bigram frequency, character trigram frequency, initial character-, initial character bigram- and initial character trigram frequency as well as for number of orthographic neighbours in terms of Coltheart's and Levenshtein's N. F/t tests did not reveal differences between semantic category groups for any of these psycholinguistic variables (all $p > .05$, see Tables 3.1 and 3.2 for details).

In addition, an equal number of pronounceable pseudo-words was generated on the basis of the proper words using the "Wuggy" software (Keuleers and Brysbaert, 2010). These pseudo-words were chosen to be not homophonous to proper words and to match all proper word categories, both combined and individually, in their sub-lexical psycholinguistic properties of average word length, number of syllables, character bigram frequency, character trigram frequency, initial character frequency and initial bigram frequency (all $p > .05$, see Table 3.3 for details). To further mimic appearance of proper words, pseudo-nouns all started with a capital letter and pseudo-verbs all ended in the "-en" suffix, consistent with German noun and verb orthography and morphology.

To empirically evaluate the semantic properties of the word stimuli, semantic ratings were collected from 20 healthy participants (monolingual native speakers of German aged 18-28) before the main experiment. Similar to previous studies (Pulvermüller *et al.*, 2001; Hauk and Pulvermüller, 2004), semantic ratings were expressed on Likert scales ranging from 1 (no relation) to 7 (strong relation). Each word was rated for its semantic relatedness to hand/arm-, face/mouth-, leg/foot actions, to visual, gustatory, and haptic/tactile perceptions, as well as to emotions and mental processes. Ratings of concreteness and word familiarity were also obtained. The concreteness scale was designed with the poles of high abstractness (1) to high concreteness (7). For inclusion into an effector-specific action word category (action verbs and tool/ food nouns), words had to achieve an average rating above the neutral mid-point of 4 for the related question while being rated lower on all other action semantic scales. For animal nouns and abstract words, all action ratings were < 4, with abstract items also rating < 4 on concreteness and perceptual scales, but > 4 on the scale for relation to mental processes. In addition, all abstract emotion nouns, and also the majority of abstract verbs had strong emotional connotations with values > 4 on the respective semantic scale. Semantic ratings for all categories are shown in Fig. 3.2.

Table 3.1: Matching on psycholinguistic variables between semantic classes in nouns. P-values denote results from one-way ANOVAs on the effect of semantic category.

	Nouns								
	Abstract Emotion		Animals		Foods		Tools		
Variables	M	SD	M	SD	M	SD	M	SD	p
Lemma Frequency p. Mio.	8.41	5.56	7.26	5.47	5.95	7.74	6.86	5.97	.37
Length	5.7	1.4	5.5	1.66	5.78	1.37	5.93	1.47	.64
Number of Syllables	1.7	.46	1.7	.46	1.78	.42	1.88	.33	.21
Character Bigram Frequency p.Mio.	216786	101041	243304	123503	210825	120275	250937	145228	.39
Character Trigram Frequency p.Mio.	120397	67480	148481	68331	124296	78409	125515	88827	.35
Initial Character Frequency p.Mio.	12171	5742	13974	5816	14427	6163	14992	7248	.21
Initial Bigram Frequency p.Mio.	2346	1926	2349	1901	1956	2000	2599	2321	.57
Initial Trigram Frequency p.Mio.	414	926	748	1703	473	1262	913	1882	.4
Coltheart Neighbours Frequency p.Mio.	126	488	82	269	28	74	56	117	.47
Coltheart's N	6.08	6.07	7	6.65	6.01	5.77	7.16	5.7	.76
Levenshtein Neighbours Frequency p.Mio.	256.35	1272.33	165.29	547.99	147.26	594.08	61.24	118.91	.72
Levenshtein N	8.63	7.47	9.9	8.26	8.79	7.32	10.36	6.72	.67

Table 3.2: Matching on psycholinguistic variables between semantic classes in verbs. P-values denote results from one-way ANOVAs on the effect of semantic category

	Verbs								
	Abstract		Face		Leg		Arm		
Variables	M	SD	M	SD	M	SD	M	SD	p
Lemma Frequency p. Mio.	25.95	26.71	28.32	57.01	28.97	67.23	26.26	35.18	.99
Length	6.68	1.29	6.98	1.33	7.08	1.35	6.83	1.24	.54
Number of Syllables	2	0	2	0	2	0	2	0	1
Character Bigram Frequency p.Mio.	544785	123466	536853	104691	534851	151015	530002	123341	.96
Character Trigram Frequency p.Mio.	367231	73446	366884	58928	359082	65621	369878	55976	.89
Initial Character Frequency p.Mio.	30979	27868	25033	18439	28458	18747	28579	25280	.71
Initial Bigram Frequency p.Mio.	4375	8943	3245	3407	3098	3690	3149	2864	.67
Initial Trigram Frequency p.Mio.	1368	2173	1155	2200	1012	1880	1320	2280	.87
Coltheart Neighbours Frequency p.Mio.	145	227	61	135	104	347	87	262	.51
Coltheart's N	5.36	4.08	5.25	4.32	4.38	3.40	4.94	3.5	.66
Levenshtein Neighbours Frequency p.Mio.	164.41	233.91	103.64	189.97	114.06	363.51	92.55	262.01	.65
Levenshtein N	8.47	5.92	7.73	5.14	6.51	4.64	7.33	4.18	.37

Table 3.3: Matching on psycholinguistic variables between real and pseudo-words. P values denote results of t-test between both stimulus types.

	Real words		Pseudo-words		
	M	*SD*	*M*	*SD*	*p*
Character Bigram p.Mio. (Sum)	383542	197428	378278	189726	.73
Character Trigram p.Mio. (Sum)	247720	137424	245700	135682	.85
Initial Character p.Mio	21076	18206	22311	21276	.43
Initial Bigram p.Mio	2890	4051	2476	3274	.16
Mean Bigram p.Mio	51299	22628	51973	23000	.71
Mean Trigram p.Mio.	29493	15449	29945	15739	.71
Length	6.31	1.5	6.12	1.3	.08

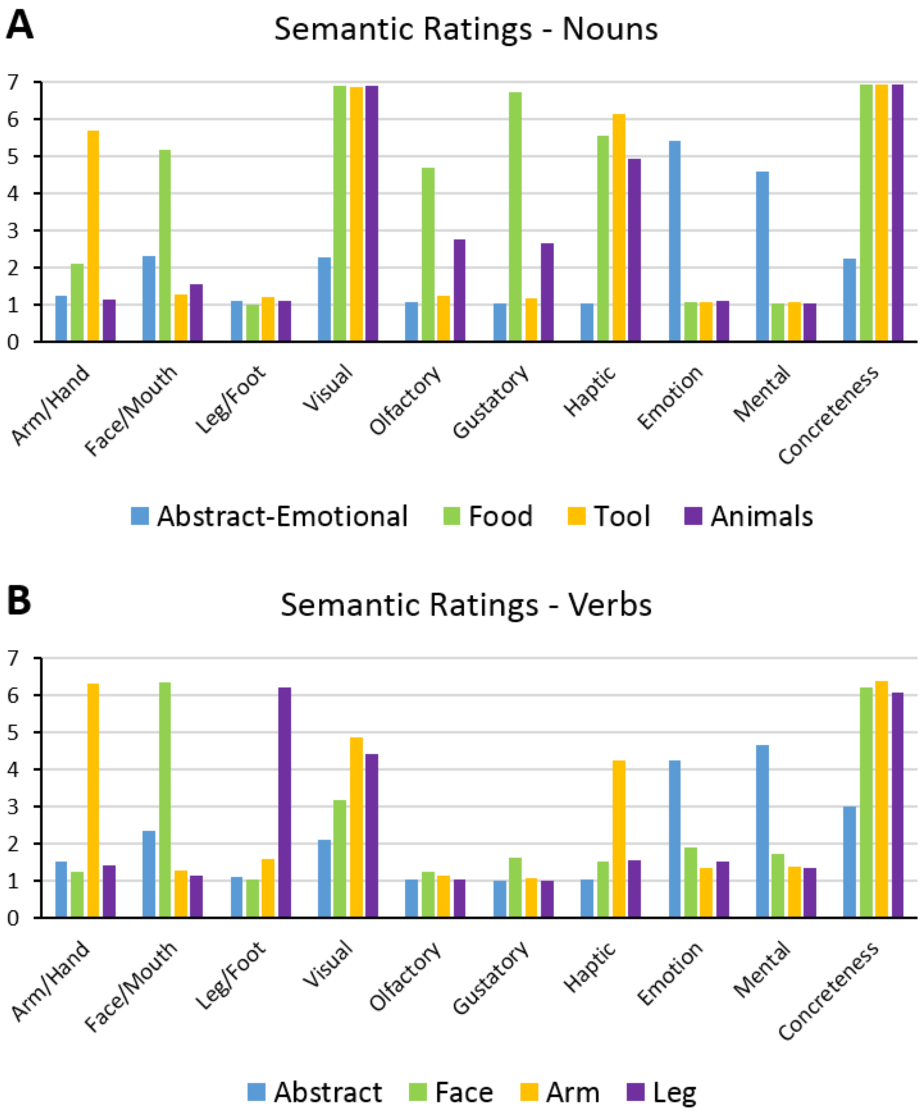

Figure 3.2: Average semantic ratings for noun (A) and verb (B) categories, given on a scale from 1 (no semantic relation) to 7 (very strong semantic relation).

LDT procedures

Participants were seated approximately 70 cm in front of a computer screen and were instructed to decide whether or not a word flashing on screen resembles a meaningful German word, or a pseudo-word instead. Responses were given via left hand mouse clicks, to assure that responses were not affected by possible motor impairments caused by left hemispheric lesions. Each trial started with a presentation of a central fixation cross. Its presentation time was pseudo-randomly varied between 2250 and 2750 ms (2500 ms on average) and it was followed by an acoustic beep signal of 200 ms length. 800 ms after the offset of this acoustic signal, the fixation cross disappeared and a word was presented tachistoscopically in the center of the screen for 130 ms. After word offset, the screen remained blank until a response was given, or for a maximum of 3000 ms after which the central fixation cross re-appeared. All stimuli were printed in black letters on a light grey background, using monospaced Courier New font with a font size of 13.5 and were spanning a maximum of 2° horizontal and .6° vertical visual degree.

Each test session started with 10 practice trials for the LDT, which applied stimuli that were not used in the actual experiment. Those trials were repeated until a task accuracy of 80% was achieved, to assure that participants were sufficiently familiarized with task procedures.

The LDT experiment was split up into 8 blocks, each including 80 letter strings, 5 words from each of the 8 lexico-semantic categories as well as 20 pseudo-nouns and 20 pseudo-verbs. In addition, 2 words were presented as filler items at the beginning of each block, which were excluded from analysis. Each block lasted between 6-8 minutes, depending on participants' response speed. Between experimental blocks, participants were offered breaks.

Following the LDT testing, patients conducted the AAT subtests in the following order: Token Test, Verbal Repetition, Naming and Comprehension. To save time, subjects who performed < 7 corrected error points on the Token Test (no aphasia diagnosis) were only given the most difficult part of the other subtests and if their performance was flawless, the rest of the subtest was omitted. On average, the whole aphasia test battery could be conducted within 20 minutes. Each test session was thereafter concluded by the Edinburgh Handedness Inventory and the basic demographics questionnaire.

3.4 Data Analysis

Healthy Control Participants

LDT analyses were conducted separately for noun and verb categories. Note again that all noun categories were matched with each other with regard to psycholinguistic variables, and the same applied for verb categories, but it was not possible to match across lexical (grammatical) categories. To allow response bias corrected comparisons with patients, task accuracies for individual lexico-semantic categories were converted into D-prime scores. To calculate D-prime values for each lexico-semantic group of nouns (verbs), each category's hit rate and the overall false positive rate of the entire lexical (i.e., either pseudo-noun or pseudo-verb) category was used (see also Pulvermüller *et al.*, 2010). Resultant D-prime scores were compared between semantic categories using by-subject repeated measures analyses of variance (ANOVAs), by-item ANOVAs, and t-tests with Bonferroni correction for post hoc comparisons. Further testing was done to compare the entire noun and verb groups against each other.

Reaction Times (RTs) for correct responses were corrected for individual outliers > 2 standard deviations away from the mean of individual participants, separately for noun and verb categories. After correction, average RTs for each lexico-semantic category and individual participant were calculated and performance between semantic categories was compared separately for nouns and verbs. By-subject and by-item repeated measures ANOVAs were then used for overall analyses and t-tests for planned comparison testing. An additional analysis step compared the performance between nouns and verbs with repeated measures ANOVAs on D-prime and RT results.

Patients

Raw AAT scores were calculated, converted into normalized scores and compared to control samples according to the tests' instructions.

LDT accuracies for individual lexico-semantic categories were converted into D-prime scores as described above, for each patient individually. We tested for general performance differences between semantic groups within each lexical/grammatical category. To this end, accuracy (here expressed as number of hits and misses) was compared using χ^2- and, in case of insufficient cell sizes ($n < 5$), Fisher's Exact Tests. In case those tests indicated significant differences, χ^2 tests with Bonferroni correction were conducted once for each semantic category versus the combined other categories within one grammatical word class (4 comparisons). In case of significantly different semantic noun categories, a second set of analyses compared each action or abstract category against the reference category of non-action animal nouns (3 comparisons). For completeness, all categories were finally pairwise compared against each other (6 comparisons). Note again that analyses were done separately for nouns and verbs.

In the analysis of RT of correct responses, individual outliers > 2 standard deviations away from the mean were first removed and the corrected single trial RTs were analyzed for effects of semantic word category using by-item ANOVAs and t-tests with Bonferroni correction.

To test whether differences across semantic categories in a specific patient can indeed be considered to be abnormal compared with performance differences between categories seen in the control sample, revised standardized difference tests (RSDT; Crawford and Garthwaite, 2005) were conducted as post hoc tests. The RSDT resembles a derivate of the t-test, specifically designed to relate performance differences of individual patients directly to results of a group of control participants. To account for the inflated Type II error rate of the RSDT, these additional post hoc tests were one-tailed (see Crawford & Garthwaite, 2006 for discussion).

Furthermore, to test for effects of grammatical class, performance in terms of accuracy was compared between all nouns and verbs using the χ^2 test and with ANOVAs on corrected RTs respectively in a separate analysis.

3.5 Results

AAT

No patient exhibited aphasic language impairments, as the AAT scores fell well within the range of healthy control population performance. Individual results for each patient and subtest are listed in Table 3.4.

Table 3.4: Performance of patients in AAT subtests given in T-Scores. Tests marked with an * were conducted in an abbreviated version,

	T-Scores	
	CA	HS
Token Test*	73	73
Verbal Repetition*	74	74
Picture Naming	80	80
Language Comprehension	78	73
Average	76	75

LDT

Healthy control subjects

A repeated measures ANOVA on D-prime scores did not reveal any significant differences between semantic noun categories [$F(3,60) = 1.59$, p > .1, $\eta^2 = .08$, n.s.] or across verbs subtypes [$F(3,60) = 1.56$, $p = .1$, $\eta^2 = .08$, n.s.]. However, RTs differed significantly across both semantic categories of nouns [$F(3,60) = 21.4$, $p < .001$, $\eta^2 = .52$] and verbs [$F(3,60) = 8.3$, $p < .001$, $\eta^2 = .29$]. This pattern of results was confirmed with additional item-wise ANOVAs on D-primes [Nouns: $F(3,159) = .32$, $p = .81$, $\eta^2 = .01$; Verbs: $F(3,159) = .76$, $p = .52$, $\eta^2 = .01$] and RT [Nouns $F(3,159) = 7.95$, $p < .001$, $\eta^2 = .13$; $F(3,159) = 3.76$, $p = .01$, $\eta^2 = .07$]. For nouns, Bonferroni corrected post hoc t-tests revealed that RTs for abstract emotion (*M* = 693 ms, *S.E.* = 15 ms) and tool words (*M* = 689 ms, *S.E.* = 15 ms) were significantly longer than for food (*M* = 653 ms, *S.E.* = 14 ms) and animal words (*M* = 662 ms, *S.E.* = 16 ms, all $t(20) >= 5$, p < .001, Cohen's $d > 1$). Post hoc tests conducted on verbs showed RTs for hand verbs (*M* = 683 ms, *S.E.* = 19 ms) to be significantly shorter than for abstract [*M* = 710 ms, *S.E.* = 17 ms, $t(20) = 3.5$, $p = .01$, Cohen's $d = .77$] and face- [*M* = 704 ms, *S.E.* = 18 ms, $t(20) = 3.3$, $p = .02$, Cohen's $d = .72$] as well as leg-related action verbs [*M* = 720 ms, *S.E.* = 18 ms, $t(20) = 3.9$, $p < .01$, Cohen's $d = .86$]. Overall, accuracies in terms of D-prime values for nouns and verbs were both high, with a significant advantage of nouns (*M* = 3.9, *S.E.* = .09) over verbs [*M* = 3.6 *S.E.* = .13, $t(20) = 3$, $p < .01$, Cohen's $d = .65$]. RTs results showed a similar pattern, with RTs for nouns (*M* = 674 ms, *S.E.* = 14 ms) being significantly shorter than for verbs [*M* = 704 ms, *S.E.* = 18 ms, $t(20) = 6.4$, $p < .001$, Cohen's $d = 1.17$].

Patient HS

Analysis of accuracy revealed a significant difference in task performance between the noun categories (χ^2 = 10.45, *df* = 3, *p* = .01, Cramer's *V* = .26) with performance on tool nouns (accuracy = .83) being more impaired than that the other 3 categories combined (accuracy = .97 on average, χ^2 = 9.4, *df* = 1, *p* = .02, Cramer's *V* = .24). When comparing tool nouns against the reference category of non-action-related animal nouns, a significant difference emerged [χ^2 = 7.67, *df* = 1, *p* = .036 , Cramer's *V* = .31]. For verbs no significant differences in accuracy between semantic categories was observed (χ^2 = 2.11, *df* = 3, *p* = .64, Cramer's *V* = .14). The ANOVA on RTs did not show significant differences between categories for either nouns [*F*(3,136) = .62, *p* > .1, η^2 = .01, n.s.] or verbs [*F*(3,137) = .62, *p* > .1, η^2 = .01, n.s.] . As the RT distribution for verbs hinted a positive skew (Skewness = .84, *S.E.* = .2), the corresponding ANOVA was repeated on log-transformed data, but again did not hint significant differences between verbs categories [*F*(3,137) = .59, *p* = .62, η^2 = .01].This pattern of results was replicated when comparing HS' performance with that of healthy controls. HS performance fell within the healthy range (mean ± 2 SDs) in terms of accuracy and his RTs on verbs even tended to be faster than those of healthy control subjects. In contrast, for tool words, HS' RT was more than 2 SDs away from the mean of the control group, thus indicating significant slowing and therefore further confirming a selective impairment for tool nouns. Post hoc RSDT results confirmed this observation, as the difference in accuracy between animal and tool nouns was significantly more severe in patient HS than in the control sample [*t*(20) = -2.72 , *p* = .008, *z-DCC* = -2.77].

In direct comparison of noun and verb performance, HS exhibited no processing advantage for either word class in terms of accuracy [Noun accuracy = .93, Verb accuracy = .95, χ^2 = .5, *df* = 1, p = .48, Cramer's *V* = .04] or RT [RT Nouns: M = 556 ms, S.E. = 6 ms; RT Verbs: M = 543 ms, S.E. = 8 ms, t(267.8) = 1.19, p = .23, Cohen's *d* = .15]. A summary of HS' LDT performance in comparison to results of healthy control participants can be found in Fig. 3.3.

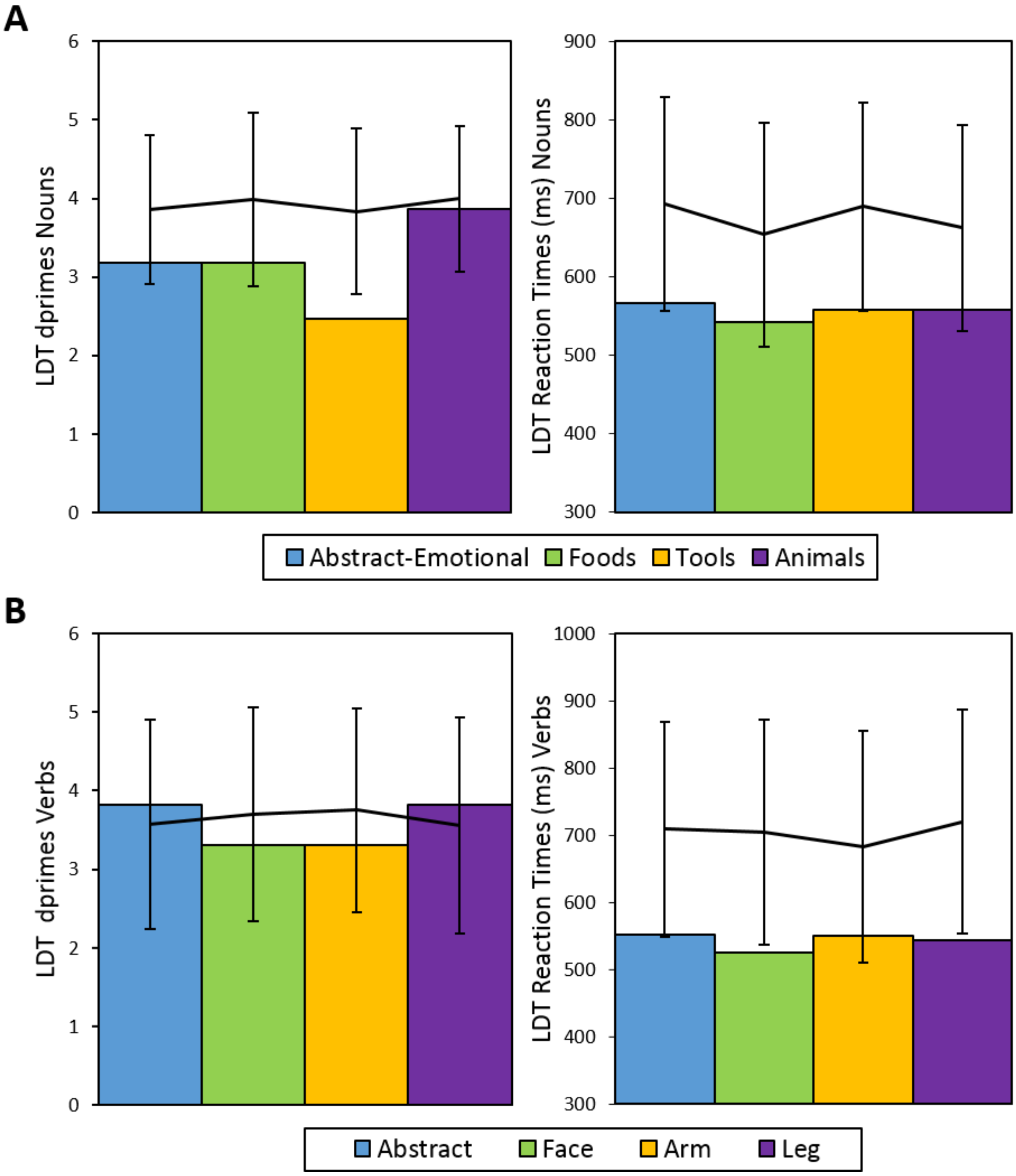

Figure 3.3: D-prime and Reaction Time results of patient HS for nouns (A) and verbs (B) given in bar charts. The line diagrams represent average performance of the control sample with error bars representing ± 2 SDs.

Patient CA

CA exhibited a strong impairment for the domain of abstract emotion nouns, with an accuracy of .43 while the other noun categories showed to be relatively intact in comparison (accuracy = .78 on average). These differences were revealed to be statistically significant, both generally, between noun categories ($\chi^2 = 19.15$, $df = 3$, $p < .001$, Cramer's $V = .37$) and for the comparison of the abstract emotion nouns versus the other categories combined ($\chi^2 = 18.13$, $df = 1$, $p < .001$, Cramer's $V = .34$), whereas post hoc comparisons for the other semantic noun categories yielded no significant differences (all $p > .2$, n.s.). Furthermore, performance on abstract nouns was also more error-prone than that on the non-action reference category of animal nouns ($\chi^2 = 13.65$, $df = 1$, $p < .001$, Cramer's $V = .41$). Post hoc RSDT results confirmed this observation, as the difference in accuracy between animal and abstract nouns was significantly more severe in patient CA than in the control sample [$t(20) = -2.05$, $p = .027$, *z-DCC* = -2.19] and likewise the comparison of abstract nouns vs. all other noun categories combined [$t(20) = 3.15$, $p = .002$, *z-DCC* = -3.39]. Finally, even the pairwise χ^2 noun category comparisons showed abstract word accuracies to be lower compared with each of the other noun categories (all $p < .05$, Bonferroni corrected), whereas the other noun groups did not significantly differ between each other.

For verbs, overall accuracy was poor across categories (.46 on average) and differences between categories were not significant ($\chi^2 = 6.13$, $df = 3$, $p = .11$, Cramer's $V = .2$). Analysis of RTs did not show significant effects of semantic word category in either nouns [$F(3,103) = .78$, $p > .2$, $\eta^2 = .02$, n.s.] or verbs [$F(3,67) = .71$, $p = .2$, $\eta^2 = .03$, n.s.]. Across semantic categories, performance was worse for verbs, than for nouns, as measured by accuracy (Noun accuracy = .69, Verb accuracy =.46, $\chi^2 = 17.5$, $df = 1$, $p < .001$, Cramer's $V = .23$) and RT [RTs Nouns $M = 853$ ms, *S.E.* =14 ms, Verbs $M = 913$ ms, *S.E.* = 20 ms, $t(176) = 2.5$, $p = .01$, Cohen's $d = .38$]. Taking the healthy participant sample as a benchmark, RTs and accuracies were considerably impaired across all noun and verb categories in patient CA, with all measures being outside of the range of ± 2 SDs from the mean of the control sample. Fig. 3.4 provides an overview of CA's LDT results in comparison to performance of healthy control participants.

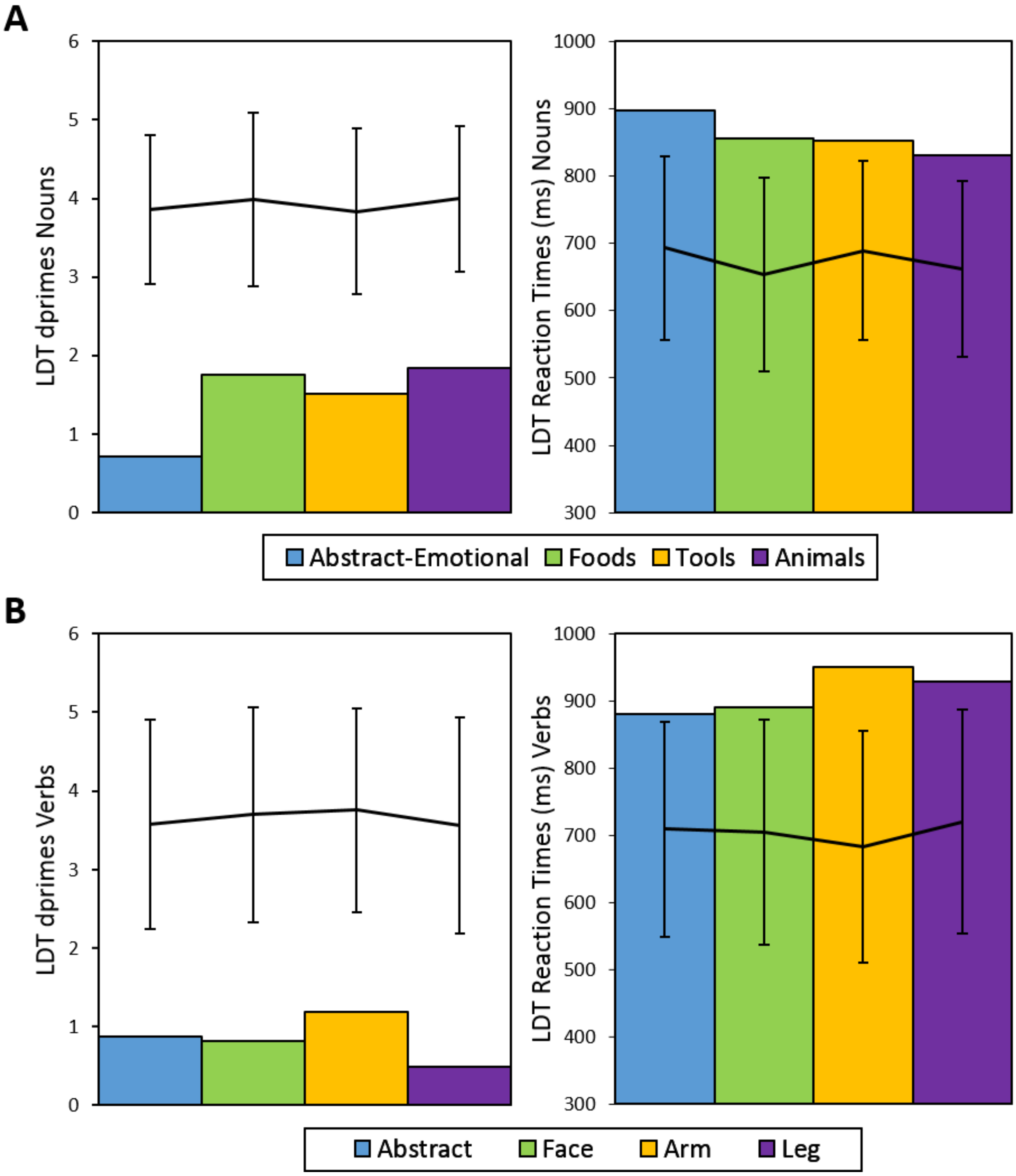

Figure 3.4: D-prime and Reaction Time results of patient CA for nouns (A) and verbs (B) given in bar charts. The line diagrams represent average performance of the control sample with error bars representing ± 2 SDs.

Post hoc Matching of semantic categories for RTs

Despite the careful matching of word stimuli for psycholinguistic features, RTs in healthy control subjects happened to differ significantly between semantic categories within nouns and verbs classes. To investigate whether this RT difference may affect the patterns of category specificity seen on accuracy data in our patients, an additional post hoc stimulus matching was performed, now using average RTs in the healthy control cohort as an additional matching criterion.This was done by removing 20% (i.e. 8) of the items of each semantic noun category, those with the shortest average RT for foods and tools and the 20% slowest items for abstract and animal nouns. The resulting item set did no longer show significant RT differences in the healthy controls [By-subjects: $F(3,60) = 1.19$, $p > .2$, $\eta^2 = .06$; by-items: $F(3,124) = 1.02$, $p > .2$, $\eta^2 = .02$, n.s.] while, the previously reported category specific patterns in the patients' accuracy data could be confirmed for the same item selection on χ^2 and RSDT measures, with patient CA showing the selective deficit for abstract emotion nouns compared to the other categories [$\chi^2 = 5.4$, $df = 1$, $p = .02$, Cramer's $V = .21$; RSDT: $t(20) = 1.95$, $p = .03$, *z-DCC* = -2.1] and patient HS exhibiting a selective impairment for tools compared to the other semantic noun categories [$\chi^2 = 6.4$, $df = 1$, $p = .02$, Cramer's $V = .22$; RSDT: $t(20) = 2.75$, $p = .01$, *z-DCC* = -2.96].

3.6 Discussion

Two patients with focal lesions in their dorsal fronto-central primary, premotor and supplementary motor areas participated in standard aphasia tests as well as a speeded lexical decision paradigm. Albeit general aphasia measures and especially tests for text comprehension did not indicate neurological language disorders, LDT results of both patients revealed differential impairments of semantic categories of nouns. In patient CA, who suffered from a focal lesion of the left SMA, this impairment was most pronounced for abstract emotion nouns, whereas patient HS, who suffered from a mild paresis of the right extremities and focal lesion just inferior to the typical hand representation in the primary motor cortex, showed a category specific deficit in recognizing tool-related nouns. Both observations demonstrate that the motor system can be necessary for recognizing and processing of words from specific semantic categories. HS' data confirm a necessary role of motor cortex for action-related tool word processing and CA's results show that motor systems, especially the SMA, can be of relevance for abstract emotion symbols. These results refute the hypothesis that motor brain areas play merely an epiphenomenal role in processing words with action-related and abstract meaning. It is clear that our present results emerging from the performance patterns of two patients cannot motivate general conclusions on all patients with similar lesions. Single case studies as the ones presented provide the existence proof that category specific action-semantic deficits can arise from motor system lesions and this observation can be computed against the predictions of established semantic brain theories, as discussed below.

Category specificity, general cognitive deficits and lesion localization

Our proposed conclusions on category specific semantic deficits imply that the observed performance pattern cannot be a result of general cognitive or linguistic impairments in the patients. Clinical language performance revealed by AAT results showed almost errorless performance and therefore demonstrates absence of aphasia. In particular, the excellent results obtained by both patients on the subtest on Word Comprehension show good general reading skills, which are important for written word and pseudo-word processing required in the LDT. Despite the absence of aphasia, both patients exhibited impairments in the LDT, arguably due to its higher processing load, especially the strict time constraints and emphasis on accuracy, compared with clinical testing with the AAT battery, where speed is not an issue. One might still argue that, possibly, additional general cognitive deficits, e.g. in praxis, attention, memory or planning might have been present in the patients, but remained undetected and may have affected the results. However, general cognitive deficits can be expected to lead to reduced performance across semantic word categories. In contrast, the processing deficits observed in both patients, which were significantly most pronounced for one semantic word category, argues against an explanation in terms of general cognitive defects and in favor of one emphasizing specific and semantic origins. It is possible that the overall very poor LDT performance across all semantic categories seen in CA was due to the functional role of the affected SMA and adjacent pre-SMA in decision and motor response selection (Hernandez *et al.*, 2002; Forstmann *et al.*, 2008; Nachev *et al.*, 2008); however, again, the fact that this deficit was most pronounced for abstract emotion nouns cannot be explained by such a general cognitive processing impairment.

Given the etiology of the lesions in CA and HS, it may seem that the lesions might not entail the focality needed to draw conclusions about the functional roles of specific brain areas, as proposed in the introduction. As discussed by Karnath and Steinbach (2011), it might be problematic to precisely tell apart functional and non-functional tissue in brain tumor patients. Furthermore, Karnath and Steinbach also highlight the possibility that gradual functional reorganization may continuously occur during the extended period of tumor growth, thus compensating for the impaired functionality. Both objections would resemble a blurring of the inferences that can be drawn on the functional role of lesioned brain areas. With regard to the former objection, it has to be noted that HS showed a rather circumscribed lesion and patient CA's metastasis (in contrast to other tumors like for example high grade gliomas) did allow for fine grained differentiation between lesioned and non-lesioned tissue. In addition, the disadvantage of a possibly poor spatial resolution of causal inferences on the functional role of brain areas is not unique to tumor patients, but indeed resembles a general problem for all kinds of lesion studies (Shallice and Skrap, 2011). This has been investigated in detail, for example in the context of reperfusion of the "penumbra" of stroke-related lesions (Hillis *et al.*, 2006). Similarly, the argument of better functional restitution in tumor patients does not apply to the current cases, as a category specific deficits were in fact manifest and detectable using psycholinguistic methods in both patients, whereas functional reorganization would have predicted absence of such specificity. Even if functional reorganization occurred in any of the patients, it can be assumed to be insufficient to recover normal function so that a functional role of the lesioned brain areas can still be soundly derived (Duffau, 2011). However, we should remark that for many other patients, the argument is still valid and significant category specific deficits may not arise from motor systems lesions. Functional reorganization provides one important reason why category differences may be frequently absent after focal lesions.

With regard to the lesion in patient HS, it has to be noted that although ADEMs are most often diagnosed with multiple lesion foci (Karussis, 2014; Koudriavtseva, 2015), cases with monofocal lesions have been reported on multiple occasions (Kesselring *et al.*, 1990; Miller *et al.*, 1993; Murthy *et al.*, 1999), allowing to assume a focal etiology. In patient CA, who suffered from a circumscribed metastasis, areas adjacent to the lesioned SMA, including pre-SMA and primary and pre-motor cortex, may have been affected in their function. We should however draw attention to the fact that the patient's tumor had been subject to intensive therapy previous to testing, including partial extirpation, so that it appears unlikely that pressure was exerted on adjacent areas. Still, the possibility that partial lesion of pre-SMA played some role in causing the deficit in abstract noun processing cannot be ruled out with certainty based on our present data.

Clinical observations are consistent with the claim that patient CA, but not HS, was suffering from depressive symptoms at the time of testing, although this could not be objectified using psychological tests. Intuitively, this depressive mood could be seen as a (non-neurological) reason for the processing deficit for abstract emotion words. However, previous studies either indicated that LDT performance was not affected by depression (Challis and Krane, 1988; Clark *et al.*, 1983) or even led to a facilitation of LDT performance on emotionally congruent word stimuli (Olafson and Ferraro, 2001). Note that most of the abstract emotion words used in the present study were negative in valence and therefore congruent with the negative emotional state of depression. The observed performance reduction for abstract emotion words seen in patient CA contrasts with these earlier observations, rendering it unlikely that the observed category specific semantic word processing deficit was based on emotional state of the patient at the time of language testing.

Apart from the neurological and clinical factors mentioned above, one could try to argue that the specific impairments found in the two patients might in fact not be due to compromised processing of word semantics, but rather to impairments of basic visual or linguistic processing. It is well-known that, in order to perform successfully in the LDT, it is not necessary to engage semantic processing, because words, but not pseudo-words, are familiar entities stored as whole lexical entries in the brain-internal "mental lexicon". Nevertheless, the LDT paradigm has previously been shown to be sensitive to manipulation of semantic content (James, 1975; Chumbley and Balota, 1984; Kroll and Merves, 1986; Jin, 1990; Samson & Pillon, 2004) and a range of pre-existing neuropsychological studies demonstrated category specificity in processing semantic word categories after focal brain lesions (Gainotti, 2010). In the present study, the examined semantic word categories, within each greater lexical category, were meticulously matched for a range of psycholinguistic features, including word length, lemma frequency, character, bi- and trigram frequencies and their word-initial counterparts, as well as number and word frequency of orthographic neighbors. Therefore, the observed category-effects can soundly be attributed to differences in word semantics and not to sub-lexical, morphological or other psycholinguistic properties, some of which have previously been shown to modulate the activity of motor areas during language processing, independent of semantics (Pulvermüller *et al.*, 2006; de Zubicaray *et al.*, 2013). In addition, the close matching of words and pseudo-words with regard to character, bi- and trigram frequencies as well as word initial character and bigram frequencies, argues against the possibility that sublexical strategies played a role in the present LDT, instead of actual semantic processing of target stimuli.

Category-effects across participants, measures and lexical classes

In contrast to the category specific patterns shown by both patients with focal lesions in the motor system, D-prime and accuracy data showed that the healthy control population performed similarly on all semantic noun categories and the same applied for the matched verb categories too. However, semantic category differences may be suggested by the control subjects' response time data, which yielded significant differences due to slightly slower responses to abstract and hand action-related nouns. These were the two categories respectively affected in our patients. To examine the theoretical possibility that the processing difference suggested by controls' RT data may explain the category specific patterns in our patients, analyses were repeated with a subset of the word stimuli matched for response times in healthy controls. The RT-matched semantic word category sets did not yield any significant performance difference in our healthy subjects, neither in accuracies nor in RTs, but the category-differences for semantic noun categories in both patients' accuracy values were reconfirmed. These results rule out the possibility that, whatever might have caused the RT differences in our control population could explain the category differences seen in the patients.

In both patients, the category specific impairments were only found for nouns, but not for verbs. This observation might appear surprising, as the majority of previous studies on motor semantics highlighted the role of the sensory-motor systems for the processing of action verbs. Considering the stimuli selected for the present LDT though, one cannot conclude from this result that the functional role of motor areas applies exclusively to the processing of nouns. The experimental setup was designed to compare processing of semantic categories separately within semantic subtypes of nouns and, again, for subtypes of verbs. Because psycholinguistic matching was not performed across noun and verb categories, a direct comparison between the lexical classes is not straightforward. For example, verbs had higher lemma frequencies than nouns and therefore were more familiar. This implies that the LDT was generally easier for verbs compared with nouns. At the same time, pseudo-verbs consistently differed in only one syllable from proper verbs (because of the shared suffix '-en'), whereas nouns differed between each other in both of their syllables, thus making it necessary to process more information for making lexical decisions on nouns than on verbs. In addition, it is well known that verbs carry more syntactic information and are generally more strongly action-related semantically but are, on the other hand, less imageable than nouns (Pulvermüller *et al.*, 1999; Bird *et al.*, 2000). Some of these differences between the lexical categories (e.g. the greater imageability of nouns) may underlie the observed processing advantage of nouns over verbs, as found in the healthy controls' D-prime and RT results and in CA's reduced performance on all verb categories. These general psycholinguistic differences between nouns and verbs may also in part account for the fact that category differences could only be documented for one of the lexical categories, because a difference on one of the psycholinguistic dimensions may have moved one of the categories away from a ceiling or floor so that performance differences could become selectively manifest.

While patient HS' overall performance for verbs on the LDT was comparable to that of healthy controls, results for CA revealed a strong impairment across all verb categories, which was only paralleled by the severely affected abstract word category of nouns. Being aware of the mentioned psycholinguistic confounds of our lexical class stimuli, we should still mention the possibility that the latter observation could, in theory, originate from the relatively higher relevance of action knowledge for the semantics of verbs. From an embodied cognition perspective, the observed impairment for all verb categories with action dominant semantics seem to fit to CA's lesion site in the left SMA, an area known to be involved in motor planning independent of motor effector and body part (Roland *et al.*, 1980; Fried *et al.*,1991). Nevertheless, given that potential differences in task difficulty cannot be ruled out when comparing nouns and verbs, this interpretation has to be treated with caution before less ambiguous experimental evidence is available. In the case of patient HS, the fact that no semantic category effects were seen for verbs could be seen as a side effect of the high performance close to ceiling for verbs, whereas average performance on nouns was relatively reduced. Our data did not show significant differences in processing different semantic sub-categories of verbs, thus confirming the corresponding observation by Arevalo and colleagues (2012). To disentangle the possible factors influencing verb and noun performance, future studies should aim to match semantic categories between those grammatical word classes in terms of semantic features, psycholinguistic characteristics as well as general task difficulty. However, we once again remind the reader that such matching is not trivial and might be not possible on all dimensions (for discussion, see Neininger and Pulvermüller, 2003; Bird *et al.*, 2000).

Relationship of the present results to known neuropsychological dissociations

The reported selective impairment for tool nouns in patient HS adds to previous findings on impairments in neurological patients, specifically for words with action-related semantics (Bak *et al.*, 2001, 2006; Neininger and Pulvermüller 2001, 2003; Pulvermüller *et al.*, 2010; Arevalo *et al.*, 2012; Kemmerer *et al.*, 2012). In contrast to these earlier works, the current study shows that those selective impairments can be induced by rather small focal lesions (of 18 mm diameter in the case of HS) in the motor areas and confirms that the corresponding category specific semantic deficits are not restricted to action-related verbs but can also arise for nouns used to speak about objects that afford actions, as for example tool words. HS' results on tool nouns also fit well with the results of earlier neuro-stimulation experiments, which pointed out the functional relevance of motor areas for action verb processing, using facilitatory (Pulvermüller *et al.*, 2005) or virtual lesion approaches (Willems *et al.*, 2011), although in those studies effects were found solely on reaction times. As substantial numbers of errors were here documented to arise from motor system lesion for nouns with action-affording referents, the present results show a necessary role of motor and premotor cortex in one single neurological case. Over and above previous research, we show a rather narrow level of category specificity, in so far as it applied only to nouns used to speak about objects affording actions typically performed with the hand. This specificity is consistent with semantic somatotopy in the motor system (Pulvermüller, 2005; Pulvermüller and Fadiga, 2010).

Observations on the performance of patient CA on the other hand revealed a functional involvement of supplementary motor systems also for the processing of abstract emotion nouns, which lack the transparent sensory-motor components of their concrete counterparts. This can be seen as first evidence that activity in motor areas during the processing of abstract emotion nouns, as revealed by earlier fMRI results (Moseley *et al.*, 2012), does in fact not resemble an epiphenomenon, but an integral part of word comprehension instead, which is necessary for optimal word processing. This result appears consistent with semantic grounding theories postulating involvement of motor circuits in abstract semantic processing, thus suggesting that the "embodiment" does not necessarily need to limit its scope to the processing of words referring to concrete entities. At the theoretical level, there is indeed motivation to see an intrinsic connection between abstract emotion meaning and the bodily actions with which such meanings are expressed (for discussion, see Barsalou and Wiemer-Hastings, 2005; Moseley *et al.*, 2012; Pulvermüller, 2013a). Whether this holds exclusively for abstract emotion words, or renders an effect that is valid also for non-emotional abstract symbols and concepts, has to be determined by future studies, for example by investigating stimuli across different subcategories of abstract words.

Distributed semantic circuit account of the current results

In order to explain the category-preferential semantic deficit in processing hand action-affording and abstract emotion nouns, one may claim that our results are consistent with theories that view the motor system as the main carrier of meaning processing for these specific semantic types. Although such strong statements – that motor cortices but no other areas integrate concepts and word meanings – have hardly been made, some arguments against semantic grounding (e.g. in Mahon and Caramazza, 2008) seem to focus on this hypothetical position. Indeed, some authors have stated "that the modalities of action and perception are integrated at the level of the sensorimotor system itself and not via higher association areas" (p. 459, Gallese and Lakoff, 2005), and such statements may have laid the ground for the idea that motor systems, but not association or convergence zones such as the prefrontal or anterior-temporal cortex, might carry meaning. Although even such a strong postulate about semantic integration in motor but no other multimodal brain systems could indeed be strengthened by the present data, it is not the only position that explains the present results. Considering a wider spectrum of data, which also show semantic activation of and semantic deficits after lesion in multimodal areas (e.g. Binder *et al.*, 2009; Patterson *et al.*, 2009; Vigliocco *et al.,* 2014), the more appropriate explanation of the present data needs to be phrased in terms of distributed semantic circuits in which neurons in motor areas play a functional, causal and necessary role.

In this perspective, the sensorimotor parts of the distributed semantic circuits would carry aspects of word meaning and contribute to a process of immediate "simulation" of semantic information (in the sense of Jeannerod, 2006) when symbols are perceived, even if subjects do not actively attend to them (Pulvermüller *et al.*, 2005b; Shtyrov *et al.*, 2014). Therefore, the observations made in both patients on nouns seem to fit especially well into theoretical frameworks that assume distributed cell assemblies with different cortical distributions to be the basis of semantic processing of words (Pulvermüller, 1999, 2005, 2017). Those cell assemblies are assumed to be the result of correlational learning mechanisms driven by Hebbian learning principles (Hebb, 1949). If a word often co-occurs with specific sensory and or motor experiences, or likewise with specific sensory or motor imagery, that word's semantic circuit would gradually be represented by a distributed cell assembly reaching into the sensory or motor areas where relevant activations had been present. A word like 'hammer' co-occurring with performance, perception or imagery of specific motor movements afforded by the tool, would co-activate the perception action circuit for the word form and the action-related neuronal circuit, thus yielding a higher-order distributed semantic circuit in which neurons in motor areas take a causal and necessary functional role. This proposal does not postulate a unique role of the motor system (or modality specific cortices) as a seat of semantics, but a semantic role of cortical circuits distributed over perisylvian, sensorimotor and multimodal convergence areas, across all of which semantic circuits are distributed. Specificity in cortical function arises from the fact that, for different meaning types, these semantic circuits have different cortical distributions – with some (action-related) semantic circuits, but not others (non-action-related ones), reaching into the motor system. Importantly, in this view, the word 'hammer' is not exhaustively semantically processed in multimodal areas, as postulated by disembodiment (or weak "integrative") approaches to semantics, and there is no preferential status of the motor system for semantics either. Semantic circuits for abstract emotion words would include neurons in the limbic system – because emotional-affective "inner states" are essential for at least some abstract words (Meteyard *et al*., 2012) – and in the motor system – because the learning of at least some abstract emotion words requires the grounding of word forms in emotions expressed in overt body movements (Moseley et. al., 2012). This integrative action perception model appears to us to be consistent with known lesion results on brain-lesion-elicited semantic impairments (Kiefer and Pulvermüller, 2012; Pulvermüller, 2013a) and to do best justice to the present data.

3.7 Conclusion

Category specific semantic deficits in a lexical decision task seen in two patients with focal lesions in their left hemispheres reveal the functional necessity of primary/pre- and supplementary motor areas for the processing of concrete hand action affording as well as for abstract emotion nouns. Processing of concrete tool nouns was selectively impaired after lesions of hand motor cortex, while a lesion in the left SMA resulted in impaired processing of abstract emotion nouns.

4. The functional relevance of modality specific motor systems for processing abstract and concrete semantics – evidence from patient samples with focal lesions

4.1 Abstract

In this study we asked whether cortical lesions in different parts of the cortex (dorsal fronto-parietal cortex, dorsal and ventral frontal cortex, anterior perisylvian cortex, temporal lobe) have different effects on the processing of words typically used to refer to objects with and without action affordances (e.g. tool vs. animal nouns) and to abstract emotion-related words. A cohort of neurological patients with focal lesions participated in a lexical decision paradigm where nouns semantically related to tools, foods, and abstract emotions and animals were presented along with matched pseudowords. Differences in semantic features between the categories where confirmed using extensive semantic ratings. Semantic word categories were matched for a range of psycholinguistic variables. Semantic category specific performance deficits were observed for tool nouns in patients with dorsal motor or parietal lesions and for abstract emotion nouns in patients with dorsal and/or ventral motor lesions, when compared to animal nouns. In contrast, patients with lesions primarily affecting perisylvian inferior-frontal and superior temporal and/or inferior temporal regions presented deficits across all semantic word categories tested and likewise a group of age and education matched healthy control participants did not present any category specific differences. These findings falsify brain language models denying the fronto-parietal cortex’ role in word recognition and semantic understanding. They are best accounted for by frameworks that acknowledge a role of prefrontal, dorsoparietal and sensorimotor cortex in the semantic binding of action-related affordances and abstract concepts.

4.2 Introduction

Evidence from the domain of neuroimaging approaches, gathered in the past few decades, points to an involvement of modality specific sensory and motor areas in the processing of linguistic semantics. As presented in Chapter 1, this involvement was observed to not occur arbitrarily but in a systematic fashion, following the predictions of theories towards semantics which assume a word's meaning to be grounded in sensory and motor experience related to its usage and meaning (Barsalou, 1999, 2008; Pulvermüller, 1999, 2005; Pulvermüller and Fadiga, 2010; Glenberg and Gallese, 2012). Words related to face, hand and leg movements were shown to recruit motor regions normally involved in actual effector-specific action execution (Hauk *et al.*, 2004; Hauk and Pulvermüller, 2004; Martin *et al.*, 1996; Pulvermüller *et al.*, 2005; Carota *et al.*, 2012; Shtyrov *et al.*, 2014) and words with high semantic relation to smells (González *et al.*, 2006), tastes (Barrós-Loscertales, 2012) or sounds (Kiefer *et al.*, 2008) were related to activation patterns specifically reaching into brain areas involved in corresponding perception processes. Furthermore, an involvement of motor systems in semantic processing could even be demonstrated for the domain of abstract words, as passive reading of abstract emotion words like "fear" activated not only limbic areas, involved in processing affective information, but also hand- and face-related motor areas (Moseley *et al.*, 2012). Despite this ample evidence on concrete and (in parts) also on abstract semantics in favor of grounded approaches towards semantic representation, proponents of semantic representations in an entirely amodal format, functionally detached from basal sensory and motor processing, point out that all these neuroimaging results could be of purely correlational nature, epiphenomenal to the actual processes of semantic processing. In a framework of abstract symbol systems, where information is assumed to be stored in an amodal format (e.g. Anderson, 1983; Ellis and Young, 1988), these observed activations could occur as conscious or unconscious imagination processes post hoc, in the aftermath of the actual comprehension process. Although this interpretation seems unlikely, given that some of the aforementioned approaches were able to show somatotopic dissociations in the motor system already very early in processing, just before 200 ms or even 80 ms after critical phonological information was perceived (Pulvermüller *et al.*, 2005b; Shtyrov *et al.*, 2014), it has been argued that evidence on the time domain is not useful with regards to the question of causality, as there is no definition what time range of category specific effects exactly would allow to assume or exclude the existence of potential earlier comprehension processes (Mahon and Caramazza, 2008). Hence, to solve this issue, one has to resort to the domain of neurostimulation evidence and/or consider investigation of clinical populations as these methods allow to draw direct inferences on the functional relevance of stimulated or lesioned areas for cognitive function.

As presented in Chapter 1, TMS work from Pulvermüller and colleagues (2005b), as well as Willems and coworkers (2011) revealed effects of motor area stimulation on response times in a lexical decision paradigm for hand action-related verbs, while matched control verbs which had no such relation to manual action remained unaffected. These observations are in line with an indeed causal role of these motor areas in the processing of action-related semantics. However, even this kind of evidence is questioned by some authors (Mahon and Caramazza, 2008) and interpreted in terms of possible spreading of neurostimulation induced activity from modality specific motor systems to the neural substrate of a potentially underlying amodal concept.

This attempt to integrate aforementioned neurostimulation findings into an entirely amodal symbolic framework however cannot be applied one-to-one to evidence for a causal role of sensorimotor areas in language processing when it is based on observations of clinical populations, with well-defined neural dysfunctions and lesions. In case a lesion in a motoric area, characterized by the absence of neural function, were to result in specific processing deficits of motoric semantics, this could not be attributed to missing activation spreading from motor areas to an alleged amodal meaning representation, unless this activation spreading were of functional relevance and constitutive for said amodal meaning representation.

Furthermore, this scenario would resemble a single dissociation, a standard inference scheme in neuropsychology (Crawford *et al.*, 2003): when the lesion in one brain area impairs certain functions more than others, then this region is crucial, causal, or even necessary role specifically for these impaired functions. We here explore whether a group of brain lesioned patients with lesions in dorsal fronto-parietal cortex are characterized by processing deficits for words whose concepts afford hand-related actions. We also test whether a lesion in fronto-central cortex leads to deficits in processing abstract emotion words.

As summarized in Chapter 1, previous research has shown that lesions reaching into motor areas were reported to be related to specific deficits in processing of action-related semantics in a stroke patients with inferior-frontal or fronto-parietal lesions (Damasio and Tranel, 1993; Neininger and Pulvermüller, 2001, 2003) or patients suffering from motor neurone disease (Bak *et al.*, 2001; Bak and Hodges, 2004). These reports however, suffer from a methodological noun-verb confound, meaning that performance of action-related verbs was compared to that of nouns. This procedure renders it difficult to disentangle effects of grammatical and semantic word type, when interpreting results, i.e. the possibility remains that motor areas are functionally involved for the processing of all kinds of verbs, irrespective of semantics. Kemmerer *et al.* (2012) reported a more systematic approach, using voxel-based lesion symptom mapping (VLSM) to investigate neural processing on a large cohorts of neurological patients with different etiologies. Here, a functional role for precentral motor areas for the processing of action verbs on a wide range of tasks (e.g. word-picture matching, as well as comparison and direct evaluation of word semantic) was shown, among inferior-frontal and temporal regions. This approach however, was lacking a proper (matched) control condition, again rendering it difficult to ascribe a functional role of the observed areas specifically to processing of action-related semantics. To avoid this issue, Arevalo and coworkers (2012) analyzed word-picture matching performance of nouns and verbs of both, action-related and action unrelated semantics, using VLSM in a cohort of stroke patients. Significant voxels were found not only in posterior and superior temporal and inferior frontal cortex, but also in premotor areas. An effector specific semantic somatotopy in motor areas contribution however, could not be observed (as it was also the not the case for results of Kemmerer *et al.*, 2012). The reason for this finding might be seen in typically large lesions of patients included in analyses that may have led to confounds in lesion profiles between effector specific motor areas. As a consequence, the differential contributions to action semantic processing of effector specific sub-parts of the motor system could not be disentangled. Although the authors do not investigate this issue further, this interpretation seems likely, as they investigated stroke patients, which often do not show focal lesion profiles (though see Neininger and Pulvermüller, 2001, 2003 for notable exceptions).

Considering the aforementioned issues, Dreyer *et al.* (2015, see Chapter 3) compared lexical decision performance of action and non-action-related categories within a grammatical word class in a pair of two patients showing lesions of high focality in their motor systems. To this end, hand action-related tool nouns, face action-related food nouns, abstract emotion nouns and animal nouns, as a non-action baseline, were applied in a LDT paradigms. A lesion in the left supplementary motor area was associated with a selective deficit of abstract emotion nouns compared to animal nouns, whereas a focal lesion in white matter directly adjacent to hand motor areas was revealed to be related to a specific processing deficit for tool words. These results directly demonstrate the functional necessity of motor areas for processing of action-related and abstract emotion semantics, independent of confounds of grammatical class and with high spatial specificity. In the context of the debate on the role of sensorimotor systems in semantic processing, one can use these results to argue that in at least one case, a focal lesion impacting on the connections of dorsolateral motor areas led to a processing deficit for words with hand action affording object related meaning. One may of course question these results because a single case could always be exceptional and not representative of language processing in the brain as it is present in the majority of the population. Therefore, we set out to validate our observation from Chapter 3 by selecting from a large group of patients only those with lesion in specific parts of the cortex. We asked whether the selected populations showed an impairment in processing nouns from specific semantic categories, relative to matched nouns from other semantic types. We focused on tool names, which relate to objects affording hand actions, and on abstract emotion words, which semantically related to internal emotional states.

Based on models that propose words to be represented in distributed cell assemblies, covering perisylvian inferior frontal and temporal areas (Pulvermüller, 1999, 2005; Fadiga and Pulvermüller, 2010), while at the same time reaching into extrasylvian sensorimotor areas, according to exact word semantics, we predict the following performance patterns:

Tool nouns which relate to objects affording hand actions should be specifically impaired in comparison with the non-action animal baseline, after focal lesions in the dorsal fronto-parietal cortex. Relevant areas include those necessary for moving the hands, i.e. dorsal hand motor areas in Brodmann Areas (BAs) 4 and 6, as well as anterior parietal areas (BA 40 and 7), previously reported to be relevant for the manipulation of tools (Moll *et al.*, 2000; Choi *et al.*, 2001; Johnson-Frey, 2004; Ohgami *et al.*, 2004). Likewise, processing of food nouns should specifically be impaired compared to animal nouns following lesions focally affecting ventral motor lesions, in addition to lesions in orbito-frontal regions related to processing food-related gustatory, olfactory and affective semantics (González *et al.*, 2006; Lewis *et al.*, 2006; Barrós-Loscertales *et al.*,2011; Carota *et al.*, 2012). Furthermore, if fMRI findings of Moseley *et al.* (2012) were to be interpreted to reflect direct semantic processing and not mere related epiphenomena, the processing of abstract emotion words should be affected by lesions in either hand- or face-related motor areas, as well as by lesions in the insula orbitofrontal or (anterior/middle) cingulate cortex. In contrast, patients with lesions affecting predominantly perisylvian inferior-frontal and temporal, but not extrasylvian sensorimotor or affective systems should not present any processing advantage of animals over nouns of abstract emotion or action-related semantics. Likewise, also healthy controls should not exhibit any similar patterns of category specific performance impairments. These results would allow to rule out any interpretation of those areas being only involved in an epiphenomenal fashion during semantic processing. The current approach aims to validate findings presented in Chapter 3 in a larger patient sample. For the current analysis the focus is set specifically on noun performance, as they provide the concrete, non-action category of animal nouns as a baseline category, which is not as easily available for verbs, since many non-abstract verbs show at least some degree of action-relatedness.

4.3 Methods

Participants

Patient profiles and grouping

In total, forty-one patients participated in the LDT paradigm and, if time allowed, also in a subsequent shortened version of the AAT. Tumor patients were selected for this analysis due to their lesions being of smaller extend and not restricted by vascular properties of the brain, as it is the case for stroke patients investigated in earlier approaches, thus allowing for more fine grained examinations of the neural substrates of semantic processing. Three of those patients had to abort the LDT, before it was completed, due to medical examinations scheduled on short notice and were hence excluded from the current analysis while another patient was excluded due to pronounced left handedness (Oldfield laterality quotient of -69). Furthermore, 7 patients were excluded due to diagnoses of high grade tumors (Glioblastoma and Glioma of World Health Organization (WHO) Grade IV), as these tumors tend to infiltrate surrounding tissue in a diffuse fashion, rendering it difficult to effectively map and interpret lesions in terms of lesion site specific functional involvement in cognitive processes. Another two patients were excluded from analysis due to tumors growing on the dorsal meninges, rather than infiltrating brain tissue itself (anaplastic menigeomas). Lesion maps of the remaining 28 patients were screened for exact lesion site. Eight patients showed lesions in dorsal central areas, previously shown to be involved in processing of arm and hand movements and/or dorsal parietal areas of the parietal tool network, previously indicated to be relevant for the processing of tool usage (Moll *et al.*, 2000; Choi *et al.*, 2001; Johnson-Frey, 2004; Ohgami *et al.*, 2004) while at the same time perisylvian, or ventral precentral motor areas remained unaffected by their lesions. Another set of 7 patients, though largely overlapping with the one described above, presented lesions in either dorsal or ventral fronto-parietal areas, including arm/hand and face/mouth motor areas, but temporal or general perisylvian areas were not affected. A third group of 7 patients was identified to show lesions predominantly in perisylvian and inferior temporal regions, while motor areas remained largely unimpaired. Unfortunately, there was only one patient with a focal lesion in ventral motor regions, corresponding to processing face movements, without involvement of inferior frontal or temporal regions, thus no group of patients with this lesion profile could be formed for analysis. Grouping details and clinical characteristics of these patients are summarized in Tables 4.1-4.3 and lesion overlay maps for each patient sample are depicted in Figures 4.1-4.3.

Table 4.1: Sociodemographic and clinical characteristics of patients in sample selections. N.a. represents data that was not available for a patient as it could not be tested due to time constrains.

Patient ID	Age	LQ	Education (years)	Sex	Tumor Type	Lesion Size (cm3)
2	62	100	14	f	Oligodendroglioma, WHO Grade III	187
4	64	100	12	f	Astrocytoma, WHO Grade III	74.1
7	35	50	n.a.	m	Astrocytoma, WHO Grade II	7.8
13	41	100	23	f	anaplastic Oligodendroglioma, WHO Grade III	48.6
15	40	100	24	m	Astrocytoma, WHO Grade III	18.6
17	52	80	12	f	Metastatis	66
20	44	80	16	m	Astrocytoma, WHO Grade II	31.2
22	48	100	10	m	Cavernoma	4
24	66	100	13	f	Meningeoma, WHO Grade II	180.5
25	41	100	n.a.	m	Astrocytoma, WHO Grade III	24
28	41	80	18	m	ADEM (focal)	1.9
29	59	90	13	f	Non-Hodgin Lymphoma	27.9
31	69	100	18	m	Glioma, WHO Grade I-II	10.7
32	27	90	18	f	Astrocytoma	29
35	58	100	16	m	Astrocytoma	76.9
39	56	100	17	f	Glioma	34.3

Table 4.2: Allocation of Patients into Patient samples.

Patient ID	Inclusion in Patient groups Dorsal/Ventral Motor Lesions	Dorsal Motor/Parietal Lesions	Temporal Lesions
2			+
4			+
7			+
13	+	+	
15	+	+	
17	+	+	
20	+	+	
22			+
24			+
25		+	
28	+	+	
29	+	+	
31			+
32		+	
35			+
39	+		

Table 4.3: Patient characteristics per Patient sample.

	Perisylvian Lesion Patients		Dorsal Motor/Parietal Lesion Patients		Dorsal/Ventral Motor Lesion Patients	
	M	*S.E.*	*M*	*S.E.*	*M*	*S.E.*
Lesion Size (cm3)	77.3	29.8	30.9	6.8	32.6	7.8
Age	57.4	4.5	43.1	3.3	47.6	3
Handedness (Oldfielf LQ)	92.9	7.1	90	3.3	90	3.8
Education (years)	13.8	1.2	17.7	1.7	17.6	1.7
AAT Errors Token Test T Score	70.7	0.3	69.4	1.6	70.7	0.3
AAT Repitition T Score	73.3	0.7	70.3	2	71.7	1.7
AAT Object Naming T Score	76.3	1.7	59.3	5.4	63.4	5.5
AAT Auditory Comprehension T Score	65.3	3.2	68.4	5.3	72.6	3.5
AAT Reading Comprehension T Score	65.7	2.6	71.7	3.7	73.1	3
AAT Language Comprehension T Score	69.1	3.5	71	3.9	74.3	3

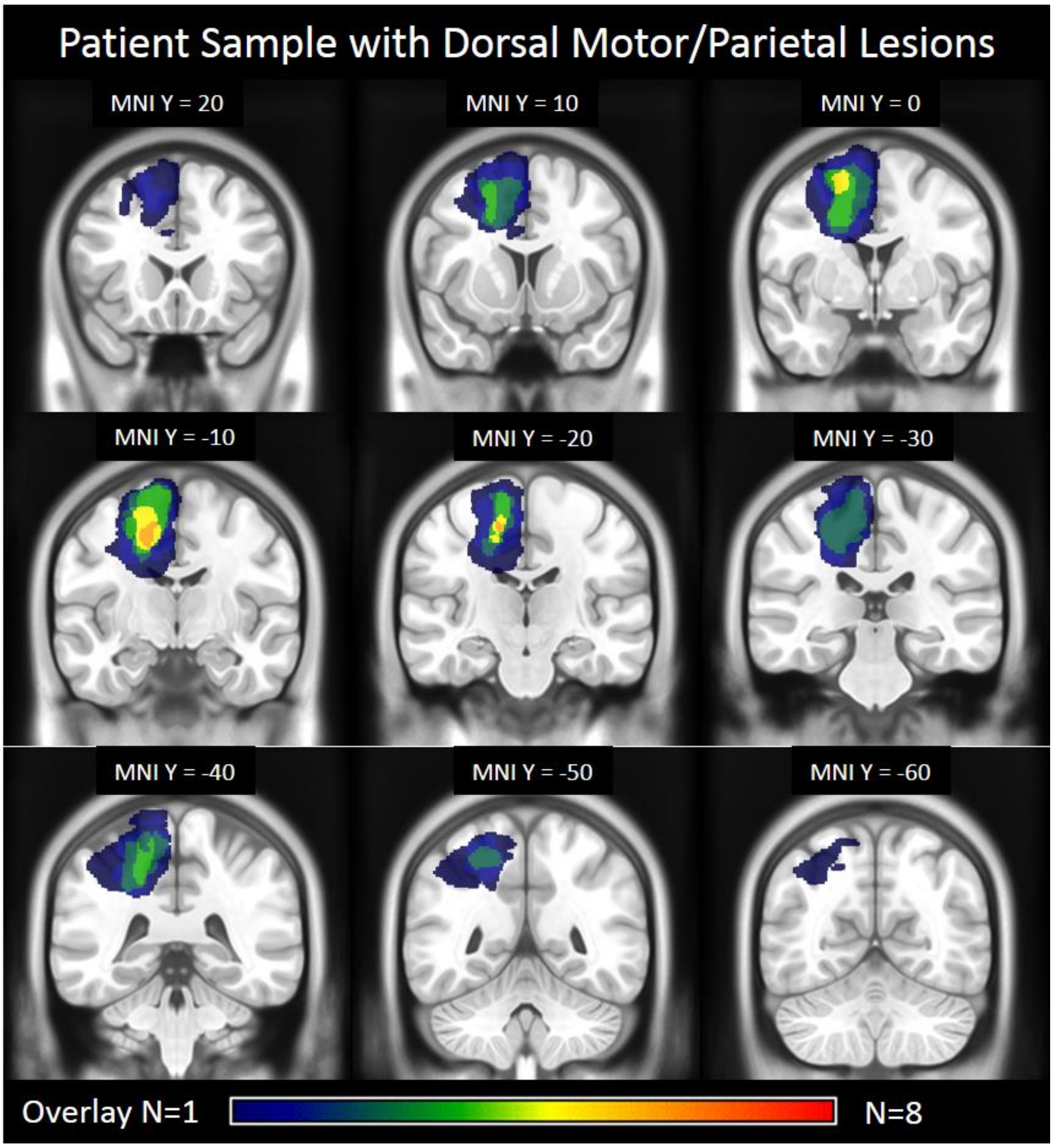

Figure 4.1: Lesion overlay map of patients with lesions in dorsal motor and/or parietal lesions. Color indicates number of overlapping lesions per voxel, ranging from dark blue (*N* = 1) to red for maximum overlap possible in the sample. Each coronal slide is presented with the respective Y coordinate in MNI space.

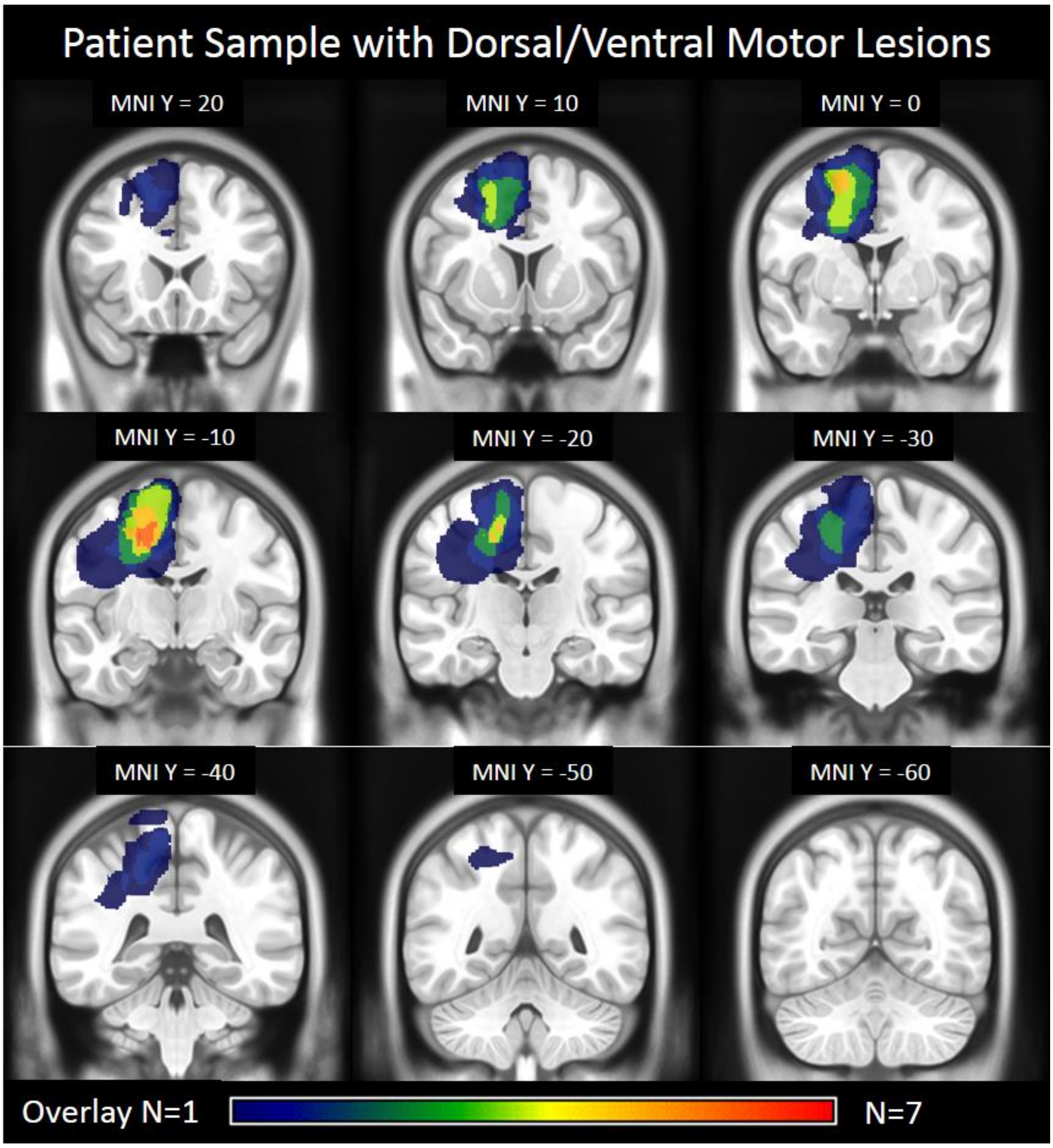

Figure 4.2: Lesion overlay map of patients with lesions in dorsal and/or ventral motor systems. Color indicates number of overlapping lesions per voxel, ranging from dark blue (*N* = 1) to red for maximum overlap possible in the sample. Each coronal slide is presented with the respective Y coordinate in MNI space

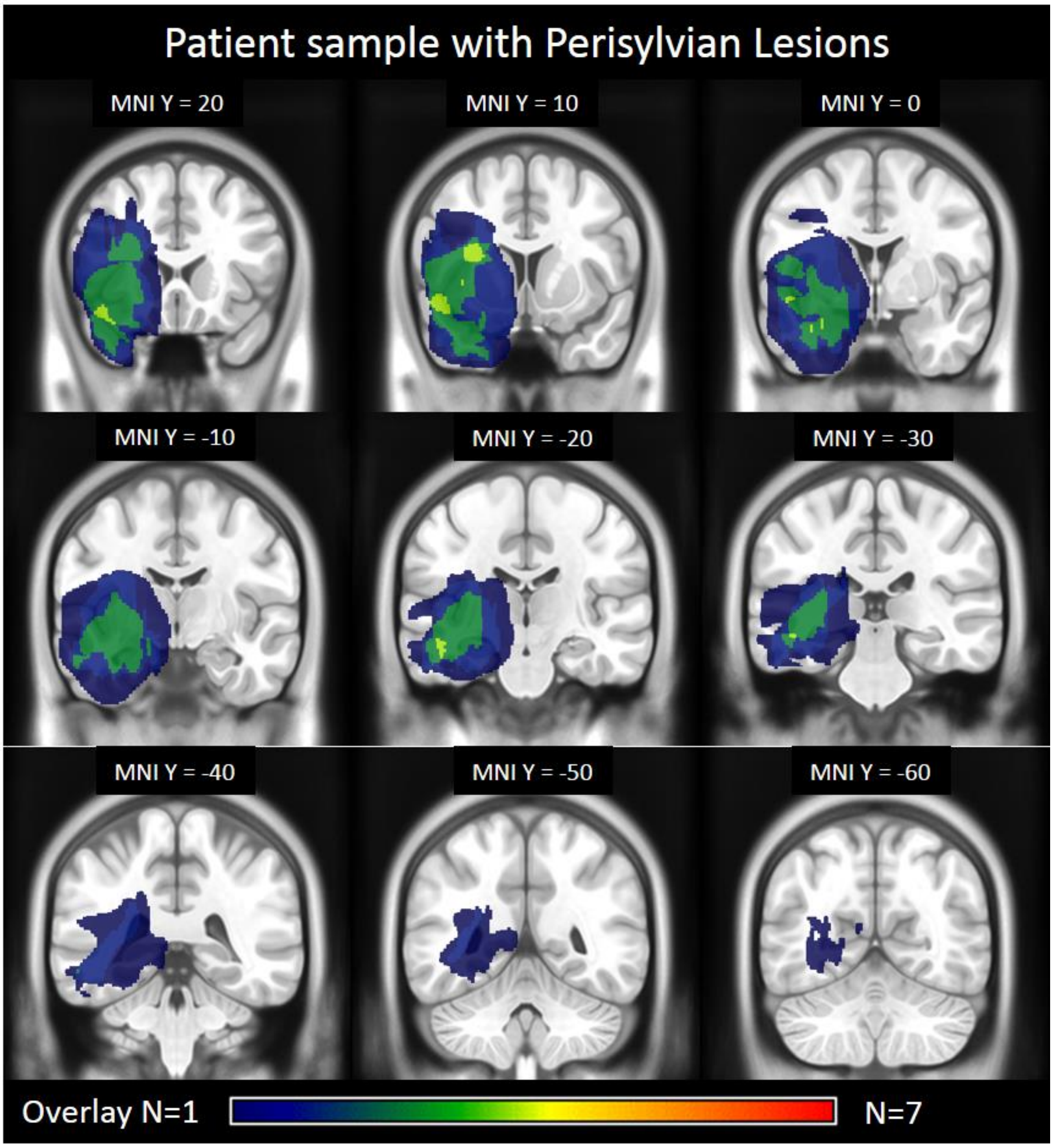

Figure 4.3: Lesion overlay map of patients with lesions predominantly in perisylvian inferior frontal and temporal areas. Color indicates number of overlapping lesions per voxel, ranging from dark blue (*N* = 1) to red for maximum overlap possible in the sample. Each coronal slide is presented with the respective Y coordinate in MNI space

Healthy controls

A group of 16 healthy participants (3 males) without neurological records served as control sample for the LDT paradigm. On average, controls were 50.1 years (*S.E.* = 3.2 years) old at the time of testing and received 17.1 years (*S.E.* = .9 years) on average of formal education.

Paradigm

The experimental paradigm was identical to the one applied in a previous dual-case study (Dreyer *et al.*, 2015). In essence, all participants were asked to first participate in a speeded lexical decision task, as described below. If time allowed, which was unfortunately not the case for all patients, subtests from the Aachen Aphasia Test battery were conducted and further socio-demographic data was collected using questionnaires.

LDT stimuli

One hundred sixty target nouns were presented, along with 160 verbs, which were of not of interest for the current analyses, and 160 matched pseudo-nouns, as well as 160 matched pseudo-verbs. Target nouns included 40 stimuli each from semantic categories of animals, foods, tools and abstract emotion nouns, which matched for a range of lexical and sub-lexical psycholinguistic variables, as determined by the dlex corpus (Heister *et al.*, 2011). Matching was achieved for word length, number of syllables, phonological stress, normalized lemma frequency, character bigram frequency, character trigram frequency, initial character-, initial character bigram- and initial character trigram frequency as well as for number of orthographic neighbours in terms of Coltheart's and Levenshtein's N. F/t tests did not reveal differences between semantic category groups for any of these psycholinguistic variables (all p > .05, see Table 3.1 for details).

Pseudo-words were generated based on proper word stimuli using the "Wuggy" software (Keuleers and Brysbaert, 2010). To best mimic appearance of proper words, pseudo-nouns all started with a capital letter and were pronounceable, though not homophonous to proper words. In addition, pseudo-words were matched to proper word stimuli in their sub-lexical psycholinguistic properties of average word length, number of syllables, character bigram frequency, character trigram frequency, initial character frequency and initial bigram frequency, as determined by the dlex corpus (all p > .05, see Table 4.4. for details).

Table 4.4: Matching on psycholinguistic variables between semantic noun classes and pseudo-words. P-values denote results of independent sample t-tests between both stimulus types.

	Proper Nouns		Pseudo Nouns		
	M	*SD*	*M*	*SD*	*p*
Character-bigram frequency p.Mio.	230463	123523	227015	118524	.79
Character-trigram frequency p.Mio.	129672	76340	129941	77891	.98
Initial Charcter Frequency p. Mio.	13891	6301	14596	6193	.31
Initial Charcter-Bigram Frequency p. Mio.	2312	2038	2296	2280	.94
Length	5.73	1.47	5.63	1.27	.49

Semantic properties of word stimuli were empirically controlled by semantic ratings, as collected from 20 healthy participants (monolingual native speakers of German aged 18-28) before the main experiment. Similar to previous studies (Pulvermüller *et al.*, 2001; Hauk and Pulvermüller, 2004; Dreyer *et al.*, 2015), semantic ratings were expressed on a Likert scales ranging from 1 (no relation) to 7 (strong relation). Each word was rated for its semantic relatedness to hand/arm-, face/mouth-, leg/foot actions, to visual, olfactory, gustatory, and haptic/tactile perceptions, as well as to emotions and mental processes. Ratings of concreteness and word familiarity were also obtained. The concreteness scale was designed with the extremes of high abstractness (1) to high concreteness (7). For inclusion into an effector-specific action word category (tool/food nouns), words had to achieve an average rating above the neutral mid-point of 4 for the related question while being rated lower on all other action semantic scales. For animal and abstract emotion nouns, all action ratings were < 4, with abstract items also rating < 4 on concreteness and perceptual scales, but > 4 on the scale for relation to mental processes. In addition, all abstract emotion nouns had strong emotional connotations with values > 4 on the respective semantic scale. Semantic ratings for all noun categories are shown in Fig. 4.4.

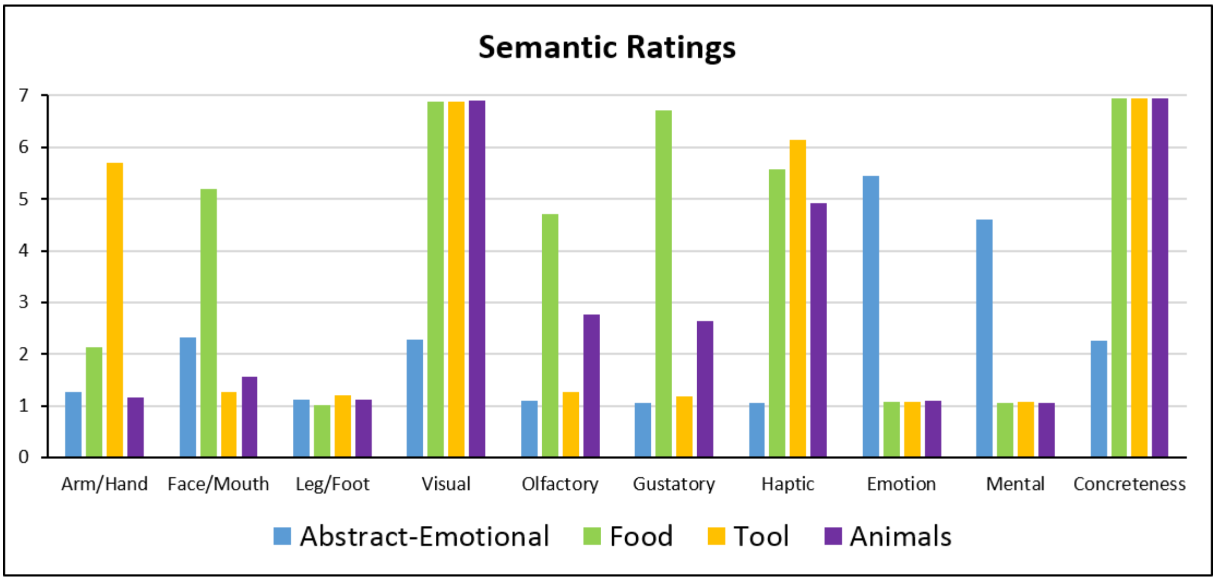

Figure 4.4: Average semantic ratings for noun categories, given on a scale from 1 (no semantic relation) to 7 (very strong semantic relation). Blue graphs represent results for abstract emotion nouns, green bars for food nouns, yellow bars for tool and purple bars animal nouns.

LDT procedures

Patients and healthy controls were positioned 70 cm in front of a computer screen and were instructed to decide whether or not a word flashing on screen resembles a meaningful German word, or a pseudo-word instead. Responses were given via left hand mouse clicks, to assure that responses were not affected by possible motor impairments caused by left hemispheric lesions. Each trial started with a presentation of a central fixation cross. Its presentation time was pseudo-randomly varied between 2250 and 2750 ms (2500 ms on average) and it was followed by an acoustic beep signal of 200 ms length. 800 ms after the offset of this acoustic signal, the fixation cross disappeared and a word was presented tachistoscopically in the center of the screen for 130 ms. After word offset, the screen remained blank until a response was given, or for a maximum of 3000 ms after which the central fixation cross re-appeared. All stimuli were printed in black letters on a light grey background, using monospaced Courier New font with a font size of 13.5 and were spanning a maximum of 2° horizontal and .6° vertical visual degree. Each test session began with a practice session, consisting of a series of 10 practice trials for the LDT, which applied stimuli that were not used in the actual experiment. Those trials were repeated until a task accuracy of 80% was achieved and until participants felt comfortable with the task, to assure that participants were sufficiently familiarized with task procedures.

The LDT was split up into 8 blocks, each consisting of 80 trials presenting 5 words from each of the 4 semantic noun categories as well as, 20 verbs and 40 pseudowords. In addition, 2 words were presented as additional filler items at the beginning of each block, which were excluded entirely from analysis. Each block lasted between 6-8 minutes, depending on participants' response speed. Between experimental blocks, participants were offered breaks of length at their own choosing.

Aphasia testing and further questionnaires

Following the LDT testing, patients conducted the AAT subtests in the following order: Token Test, Verbal Repetition, Naming and Comprehension. For the sake of shorter testing, subjects who performed < 7 age-corrected error points on the Token Test (no aphasia diagnosis) were only given the most difficult part of the other subtests and if their performance was flawless, the rest of the subtest was omitted. On average, this shortened version of the aphasia test battery could be conducted within 20 minutes. Each test session was concluded by the Edinburgh Handedness Inventory (Oldfield, 1971) and the basic demographics questionnaire.

4.4 Analysis

Lesion mapping procedures

Lesion templates were created manually for each individual patient on either T1 or T2 weighted structural MRI images in MRIcron (www.mricro.com/mricron), depending on availability and quality of images. Lesion maps included both, actual tumor tissue, if visible, and surrounding hemorrhages or edemas. Resulting lesion maps were used for lesion cost function masking (Brett *et al.*, 2001), to normalize patients' structural images and corresponding lesion templates to a Montreal Neurological Institute (MNI) standard space using the Clinical toolbox (Rorden *et al.*, 2012) of the Statistical Parametric Mapping software (SPM8, Wellcome Department of Cognitive Neurology).

LDT Analysis

To allow response bias corrected comparisons between patients, task accuracies for individual semantic noun categories were converted into D-prime scores. D-prime values for each category were derived by considering the category specific hit rate and the overall false positive rate of pseudo-nouns category (see also Pulvermüller *et al.*, 2010). In a first step of analysis, D-primes of tool, food and abstract emotion nouns were compared to animal nouns as a non-action-related control category. As the sample sizes of the three patient groups were considerably small ($N = 7$-8), normality of differences between pairs could not be assumed and non-parametric paired-sample Wilcoxon tests were performed. Given the results of Dreyer *et al.* (2015), we were interested whether abstract and action-related categories show stronger impairments than animal nouns and hence opted for one-tailed testing. Category specific performances of patients with dorsal motor/parietal lesion and dorsal/ventral motor profiles were compared to those of patients with predominantly perisylvian lesions using non-parametric Mann-Whitney-U-Tests. Likewise, category specific performances of all patient samples were contrasted to those of healthy control participants.

AAT Analysis

Raw AAT performance scores for each subtest were determined, converted into age normalized standard T-scores and compared to control samples, according to the tests' instructions. In case a participant did not conduct all items in a subtest, performance was interpolated on the bases of present data for analysis. AAT subtest-specific results for all patients are presented in Table 4.5.

4.5 Results

Patient Matching

Patient groups of with dorsal motor/parietal or dorsal/ventral motor lesion profiles did not differ significantly from the patient group of predominantly perisylvian lesions in terms of lesion size, years of education and handedness (all $z < 1.63$, ps $> .05$). Thus any difference in result patterns between groups could not be attributed to between group differences on these sociodemographic dimensions. In addition, the patient sample of dorsal/ventral motor lesions was matched age-wise to the perisylvian lesion sample ($z = 1.7$, $df = 22$, $p = .1$), whereas patients in the dorsal motor/parietal lesion sample were significantly younger ($M = 43.2$ years, *S.E.* = 3.3 years) than patients in the perisylvian lesion sample ($M = 57.4$ years, *S.E.* = 4.5 years; $z = 2.1$, $df = 23$, $p = .04$). These differences could potentially bias direct comparisons between these two patient samples, however one would assume such a bias to result in improved performance for dorsal motor/parietal lesion when contrasted to the sample of predominantly perisylvian lesions. Hence, any potential deficit observed in dorsal motor/parietal patients exclusively can still be soundly interpreted. When compared to the group of healthy controls, all patients as a whole, as well as individual patient samples were matched for age and education levels (all $z < 1.9$, $p > .05$). Hence neither age, nor education could explain any differences in LDT performance profiles between patients and healthy controls.

AAT results

Aphasia testing revealed mild to moderate aphasic symptoms in six of the 16 patients investigated in the different patient groups. Four of those were found in the sample of primarily perisylvian lesions (Patients 4, 24, 31 and 35) and two (Patients 25 and 32) in the patient sample of dorsal motor/parietal lesions, whereas the other patients were revealed to be a-symptomatic. While these results point to possible performance biases in the LDT for comparisons between patient samples and groups, it is important to note that comparisons of category specific performance (i.e. tool, food and abstract emotion vs. animal nouns) within one sample can still be soundly derived, as the presence of mild to moderate general aphasic symptoms would not predict differences in performance between categories.

Table 4.5: Aphasia testing results of patients in sample selections. Patient performances are given in age-corrected T-scores, n.a. represents data that could not be tested (due to time constrains) and was therefore not available for a patient.

Patient ID	Errors Token Test T Score	Repetition T Score	Object Naming T Score	Auditory Comprehension T Score	Reading Comprehension T Score	Language Comprehension T Score
2	71	74	71	60	60	60
4	71	n.a.	69	53	53	53
7	69	70	77	69	69	73
13	71	74	77	74	67	78
15	71	74	80	71	72	78
17	71	74	80	65	72	71
20	71	74	80	n.a.	67	n.a.
22	71	74	80	80	78	78
24	71	70	49	56	58	57
25	71	74	53	80	78	78
28	71	74	80	64	78	73
29	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
31	71	62	53	80	78	78
32	71	74	52	74	75	78
35	60	64	48	45	57	55
39	69	74	77	74	67	78

LDT results

For the first group of patients, presenting lesions exclusively in dorsal motor and/or anterior parietal regions, paired-sample Wilcoxon tests revealed LDT accuracy for tool nouns to be significantly worse than for animal nouns (D-prime tools: M = 3.08, *S.E.* = .35; D-prime animals: M = 3.51, *S.E.* = .31; z = 1.89, df = 7, p = .03), whereas such a difference was not observed for foods (D-prime M = 3.32, *S.E.* = .34; z = 1.36, df = 7, p = .09) and just showed a trend towards significance abstract emotion nouns (D-prime M = 3.13, *S.E.* = .46; z = 1.52, df = 7, p = .06). The second group of patients, with lesions in either dorsal or ventral motor, but not in perisylvian regions, exhibited deficits in the processing of abstract emotional nouns in comparison to the non-action control group of animal nouns (D-prime abstract emotion: M = 2.71, *S.E.* = .4; D-prime animals: M = 3.25, *S.E.* = .26; z = 1.86, df = 6, p = .03), while there was no significant difference to either tools (D-prime M = 2.91, *S.E.* = .33; z = 1.35, df = 6, p = .09), or foods (D-prime M = 3.04, *S.E.* = .29; z = 1.35, df = 6, p = .09). In contrast, the group of patients with lesions being predominantly situated in temporal and inferior frontal regions, did not exhibit any superiority of animal (D-prime *M* = 2.83, *S.E.* = .47) compared to food (D-prime *M* = 2.82, *S.E.* = .44; *z* = 0, *df* = 6, *p* = .5), tool (D-prime *M* = 2.64, *S.E.* = .42; *z* = 1.35, *df* = 6, *p* = .9), or abstract emotion noun performance (D-prime *M* = 2.6, *S.E.* = .56; *z* = .52, *df* = 6, *p* = .3). Likewise, the group of age-matched healthy controls did not show any significant differences in LDT accuracy between the abstract (abstract emotion D-prime *M* = 3.86, *S.E.* = .17, *p* = .2) or action-related categories of tool (D-prime *M* = 3.83, *S.E.* = .19, *p* = .15) and food (D-prime *M* = 3.84, *S.E.* = .15, *p* = .06) to animal nouns (D-prime *M* = 3.96, *S.E.* = .15). Category specific D-prime scores for all patient samples are summarized in Fig. 4.5.

Direct comparison patients with dorsal motor/parietal and healthy controls revealed no significant difference between dorsal motor/parietal tumor patients and healthy controls for performance on food, abstract emotion and animal nouns (all *z* < 1.54, *p*s > .05), whereas comparisons for tool nouns were significant (*z* = 1.74, *df* = 6, *p* = .046). For the patient group of dorsal and ventral motor lesions or perisylvian lesions exclusively, comparisons to healthy controls revealed significant differences for all semantic categories (tools, foods, animals and abstract emotion nouns; all *z* > 1.9, *p*s < .05). Comparisons to patients with predominantly perisylvian and temporal lesions revealed no significant differences on either semantic category for both patient groups (all *p*s > .05).

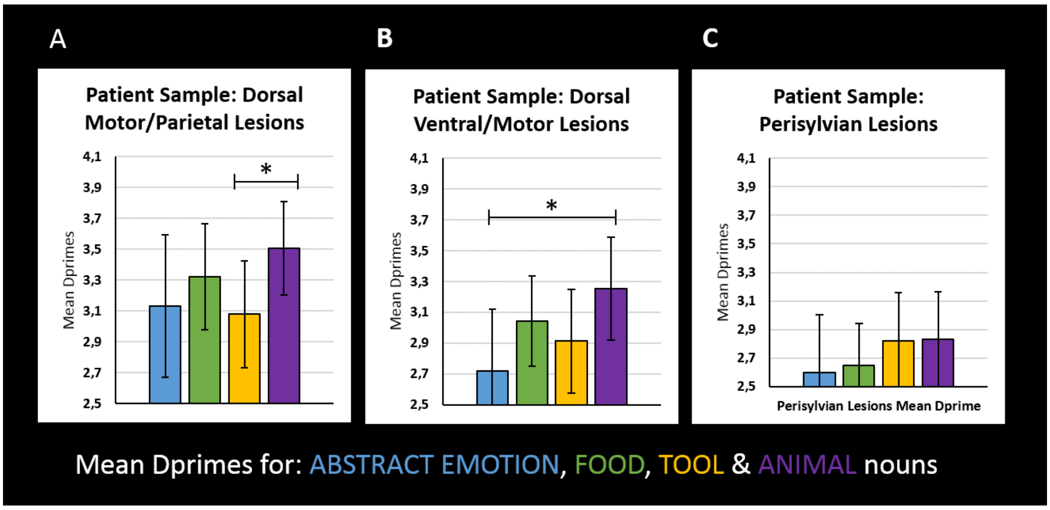

Figure 4.5: Lexical decision results. Bar graphs depict mean D-primes for abstract emotion (blue), food (green), tool (yellow) and animal nouns (purple) in the patient sample of dorsal motor/parietal lesions (A), dorsal/ventral motor lesions (B), predominantly perisylvian lesions (C). Error bars depict the standard error of the mean and * indicates significant between category differences.

4.6 Discussion

A lexical decision task, applying a set of different semantic noun categories, tightly matched on non-semantic psycholinguistic measures, was conducted on a cohort of brain tumor patients. Patients with focal lesions in dorsal motor and dorsal anterior parietal areas showed deficits for the recognition of tool nouns to be selectively pronounced in comparison to performance on animal nouns, as a non-action-related control. Likewise, another grouping of patients with fronto-parietal lesions in dorsal and/or ventral motor areas, but with perisylvian regions largely unaffected, resulted in selectively pronounced performance deficits for abstract emotion concepts, when contrasted to the animal noun category. In contrast, patients with tumors situated predominantly in temporal and perisylvian inferior frontal regions did not show such a pattern of semantic category specific performance differences. In comparison to a group of healthy control participants, dorsal motor and parietal lesions were associated with deficits in tool performance, whereas healthy controls outperformed patients with dorsal or ventral motor lesions and patients with purely perisylvian lesion sites in all semantic categories applied.

These results support the notion of an indeed functionally relevant, rather than just merely epiphenomenal involvement of fronto-parietal networks, including modality specific, sensorimotor areas for the processing of concrete, as well as abstract words. Results on tool nouns are in line with earlier observations on a functional involvement of motor areas in processing words of action-related semantics (Hauk *et al.*, 2004; Hauk and Pulvermüller, 2004;

Martin *et al.*, 1996; Pulvermüller *et al.*, 2005a; Carota *et al.*, 2012; Shtyrov *et al.*, 2014). In addition, the current results also relate to previous reports on action verbs deficits in patients with lesions involving the motor system (Damasio and Tranel, 1993; Bak *et al.*, 2001; Neininger and Pulvermüller, 2001, 2003; Bak and Hodges, 2004; Kemmerer *et al.*, 2012). In contrast to these earlier patient reports the current findings demonstrate deficits to occur also for nouns, independent of grammatical class confounds and thus relate directly to previous somatotopic deficits in processing of hand action-related semantics after lesions in dorsal motor areas (Dreyer *et al.*, 2015, see Chapter 3). The current results are therefore in line with distributed neural cell assembly models of semantics, which postulate sensorimotor contribution to semantics of action-related verbs and likewise also for hand action affording tool words.

The reported relation of dorsal and ventral motor areas to performance deficits for abstract emotion nouns directly reflect the notion of a grounding of words with abstract emotional semantics in the motor systems of those effectors that are related to expressing emotion and to perceiving emotional states is others, i.e. face and arms. Support for this notion can be seen already in fMRI findings on an involvement of face and hand motor areas in processing abstract emotion words (Moseley *et al.*, 2012). The crucial conclusion based on the current results would be that those contributions are not only of correlational but indeed of functional nature for processing this subclass of abstract words, as demonstrated by the reported single dissociation between abstract emotion and animal nouns, thus confirming earlier observations in a dual-case study (Dreyer *et al.*, 2015) on larger patient samples.

Importantly, these observations do not allow the conclusion that those areas exclusively, and not classical perisylvian language areas, hold a functional role for processing of specific semantic content. Such an interpretation would also contrast with grounded theories towards language processing proposing semantic representations to be realized in distributed cell assemblies covering both, modality specific extrasylvian and domain general perisylvian areas. Instead, these findings indicate that lesions in fronto-parietal cortex, involving the motor system, can cause selective processing deficits independent of lesions in temporal and inferior frontal regions.

The patient sample with perisylvian, temporal or inferior temporal lesions did not differ from the two patient samples with extrasylvian lesions in their performance in any of the semantic categories, however considering their aphasia test battery performance there was at least a trend towards significance for reading comprehension to be more impaired in persiylvian/inferior temporal patients, when compared to the other two patient selections. This latter observation is in line with distributed cell assembly account of semantics, as perisylvian areas are assumed to host the word forms across different semantic word types.

Semantic Category specificity of result profiles

In order to validly interpret any of the observed accuracy effects, one must first verify their specificity. Here, the critical issue is to assure that the observed semantic category specific results cannot be attributed to deficits in more basal, non-semantic functions, like orthographic processing, visual perception or decision processes. This has been achieved by tight matching on psycholinguistic variables on the lexical and sub-lexical level between semantic categories, allowing to attribute any difference in LDT results indeed to between category differences in the semantic domain, despite the task design which would allow proper task performance purely based on lexical processing, in absence of any semantic processing. Potentially, other non-linguistic lesion induced cognitive deficits, like impaired vision, attention, or general executive function required to follow task instructions, may impair LDT performance as well and could be reflected in reduced task accuracy. However, one would expect any basal cognitive impairments to affect all semantic categories alike, given the aforementioned matching of the four different semantic categories. Hence, any of the reported differences between semantic categories, like the critical comparison of abstract or action-related categories to the non-action category of animal nouns, are still interpretable even in the potential presence of basal (non-linguistic) cognitive impairments. The same holds for any preconditions in the patients that are independent from specific lesion sites, like the general level of psychological stress, given that most patients had a brain surgery scheduled the following days after participating in the LDT and some patients even got their initial tumor diagnosis just shortly before the time of testing. This influence of these lesion site independent deteriorating effects was further controlled for by comparisons of results within and between patients groups, i.e. patients with perisylvian lesions vs. patients with dorsal/parietal or dorsal/ventral motor lesions, those non-lesion site dependent effects can be assumed to cancel each other out in these analyses. Please note that although patient samples of dorsal/parietal or dorsal/ventral motor lesions overlapped to a large degree, they were both independent of patients with perisylvian lesions or temporal lesions, thus allowing for proper between group comparisons.

Local specificity of results

The study of neuropsychological deficits was, for a long time, dominated by work with stroke patients. This was so for good reason, because the cortical tissue functionally affected by a tumors is less easily determined as is the case for an ischemic or hemorrhagic stroke. Whereas in the latter cases, the lesion can be easily delineated and any edema or penumbra areas where function is also impaired are typically in close vicinity of the lesion, the situation is more difficult for tumors, whose metastases may spread widely. For this and similar reasons, many neuropsychologists remained hesitant about strongly interpreting lesion studies with tumor patients. As brought forward by Shallice and Skrap (2011) however, the aforementioned disadvantages of tumor patient investigations also apply to patient populations of other etiologies (like e.g. strokes). Taking into account the potential drawbacks of tumor patient studies we spent much care to minimize the risk of unjustified inferences from our present patient cohort. To this end patients with more diffuse tumors (Glioblastomas or Gliomas of WHO Grade IV) were excluded from analysis and two experts in tumor surgery were consulted when delineating the exact extent of the lesions.

As most of the present tumors started growing in subcortical tissue and extend into cortical areas, rather than affecting either white or grey matter exclusively (with the exception of one patient that presented an ADEM, a focal lesion of white matter tracts), white and grey matter lesions do not occur in isolation in individual patients of the current patient cohorts investigated. Hence, the potentially different effects of white and grey matter lesions on processing action-related or abstract words can, at least in the current patient samples, not be separated from another.

An additional issue concerning local lesion specificity lies in the fact that any edemas or hemorrhages surrounding the tumor were marked as lesioned tissue included in lesion maps, although it can in general not be inferred a priori whether, or which areas within those edemas or hemorrhages cause functional impairments and which are asymptomatic instead (Karnath and Steinbach, 2011). This very liberal method of lesion definition was chosen as a precaution to prevent under-estimation of lesion tissue. This also works against the studies spatially specific hypotheses, i.e. specific contributions for motor regions to processing of concrete action-related and abstract emotion words, though in doing so the lesion profile specificity was decreased across the whole patient sample. The alternative would have been to include only those patients without surrounding edema or hemorrhages. This procedure however would have resulted only in very small sample sizes. At the same time, the other alternative would have been to disregard non-tumor tissue entirely in lesion definition, but this procedure could potentially bias results in favor of our hypothesis, depending on edema and/or hemorrhage position. We opted against these latter options, as we aimed to avoid any possible overestimation of the spatial focality when interpreting our results. Following a further consideration brought forward by Karnath and Steinbach (2011), functional reorganization of cortical and subcortical regions during (in some cases very slow) tumor growth are likely to have occurred in the patient samples. As one cannot tell whether or not specific lesioned voxels have their original function restored in remaining healthy brain tissue, a one-to-one mapping of lesion maps and functional impairment could be rendered difficult. However, following Duffau (2011), those reorganization processes are likely to not restore function to normal levels. In addition, benefits of reorganization processes should effect of all word categories applied equally and do not predict category specific differences of results. Hence, category specific impairments present in the current samples and findings for comparisons of action-related or abstract nouns to a non-action control, can indeed be soundly interpreted in terms of a functional role of modality preferential systems for semantic processing, given that specificity of lesion profiles is warranted.

Integrating category specific impairments into theory

The observed category specific deficits directly support the notion of a causal role of motor areas to processing concrete, hand action-related tool and also abstract emotion nouns. In contrast to previous neurostimulation studies (Pulvermüller at al., 2005; Willems *et al.*, 2011), the current investigation even points to a necessary (rather than merely fascilitatory) role of motor areas to semantic processing, as demonstrated by the reported dissociations in error rates between abstract emotion and tool words with animal nouns. Such effects would not be expected in case motor areas would merely hold a “coloring”, role for semantic representation and processing, unnecessary for the actual comprehension process (Mahon and Caramazza, 2008; Caramazza *et al.*, 2014). As proposed by Mahon and Hickok (2016) it could still be possible that a functional role of the motor systems is the result of entirely amodal representations which (despite their amodality) happen to be localized in the motor systems, potentially even following a pattern of effector specific semantic somatotopy. This proposal however renders a claim that is in principle un-falsifiable, given the currently available neuroscientific research methods. In order to hold validity, any theory on the nature of the neural bases of semantic representation and processing must therefore be able to explain and even predict those category specific effects, as observed in the current results.

One set of theories that provides exactly these features are those of embodied semantic representations, directly (though not exclusively) grounded in sensorimotor systems (Pulvermüller, 1999, 2005; Barsalou, 2003; Pulvermüller and Fadiga, 2010). In neural terms this could be achieved by cell assemblies spreading over multi-modal perisylvian areas and extending into modality specific systems, like the motor system. The exact structure of these cell assemblies is believed to be shaped by basic principles of correlational neural learning, Hebbian and Anti-Hebbian learning (Hebb, 1949). For a concrete tool words like ‘pliers’ or ‘screwdriver’ their usage would sometimes co-occur with actual motor performance and perception of the respective objects. Hence the linguistic sign, the word form, stored in inferior frontal and temporal perisylvian regions, would gradually be connected to aspects of its meaning in terms of respective referenced sensorimotor information. Accordingly, the underlying cell assemblies would extend from perisylvian areas into the respective motor and sensory areas, thus directly reflecting the relation of sign and reference, whereas other approaches view those modality-preferential areas to be irrelevant for genuine semantic processing and representation (Mahon and Caramazza, 2008; Caramazza *et al.*, 2014; Mahon, 2015). Once this connection has been established, other, novel concepts could be understood also from linguistic context with those grounded concepts alone, via combinatorial processes or “parasitic” learning (Harnad, 1990; Cangelosi *et al.*, 2002; Pulvermüller, 2002). However, the modality specific components would still remain a necessary and functional part of the of the underlying cell assemblies, as they allow to relate multimodal linguistic signs to their meaning via experience.

The notion of a necessary role of the motor system in semantic processing is reflected directly in the current results on category specific impairments. Results even appear to provide a level of effector specific somatotopy, as tool noun processing impairments were observed following lesions in dorsal motor and parietal areas, previously shown to be related to actual tool handling and respective action affordances. It should be noted that although only the contrast of tool vs. animal nouns yielded significant performance differences in the group of patients with dorsal motor and parietal lesions, the contrasts of animals to abstract emotion or food nouns were almost significant (with borderline significance for one-tailed testing), too. Likewise, the patient selection of predominantly ventral or dorsal motor lesions showed performance deficits to be significantly pronounced for the contrast of abstract emotion to animal nouns, but at the same time also the contrast of animals to food and tool words were almost significant. Therefore, one should remain careful to not see results of the current patient samples with predominantly extrasylvian lesions in modality-preferential motor systems as direct evidence for a pattern of effector specific somatotopy in the causal and necessary role of the motor system for semantic processing of action-related words. A possible explanation for the reported result patterns can be seen in the overlap in brain regions predicted to be of importance for processing the individual semantic word categories. For performance on tool nouns, anterior parietal and dorsal motor areas were predicted to be of relevance, as both areas have previously been shown to be involved in actual tool usage. In turn, for abstract emotion noun processing, dorsal and ventral motor areas were predicted to be of importance, as both, hand and face actions were previously discussed to be of relevance for a grounding abstract emotional semantics (see discussion below), whereas for food items, only ventral motor areas were predicted to be critical, as these areas are normally involved in face and mouth movements. Therefore it might not appear too surprising that lesions involving dorsal motor areas are associated with deficits in tool noun, as well as in abstract emotion noun processing and likewise that food words showed a tendency towards a significant performance impairment (compared to animal nouns), following lesions (in part) involving ventral motor areas. The observation of the tendency of a food word impairment compared to animal nouns after lesions in dorsal motor or anterior parietal areas (though non-significant), however, remains to be difficult to align with the level of spatial specificity in the aforementioned predictions. The reason for this may be seen by persisting lack of lesion focality within the motor system, present current patient samples. To investigate this issue further, one would need to test patients with face motor lesions and contrast their performance to those with predominantly dorsal motor or anterior parietal lesions, which was unfortunately not possible in the current investigation due to the lack of patients with predominantly ventral motor lesions.

In contrast to earlier proposals (Mahon and Caramazza, 2008), the present findings demonstrate explicitly that any role of modality specific systems (where the largest lesion overlap was observed) is not reduced solely to the acquisition process of word semantics, but instead remains predictive for, and causally involved in normal, un-disturbed processing of word meaning later on. It has been argued previously that lesion of sensorimotor systems normally only result in “subtle, rather than catastrophic” general cognitive or language deficits (Binder and Desai, 2011) and also the current effect sizes seem to support this notion, as most patients still performed well above chance in the affected categories, despite the reported category specific impairments. However, this must not be seen as evidence against the aforementioned cell assemblies and the role of sensorimotor areas, as the widespread nature of these assemblies predict a large degree of redundancy, allowing the assembly to potentially still sufficiently ignite in case some of its extrasylvian motor nodes are missing (Neininger and Pulvermüller, 2003). As the patients investigated here were either entirely a-symptomatic regarding their motor function or presented only motor impairments of mild severity, it is likely that effector specific motor components were not lesioned in their entirety. It is therefore possible that representations of some tool concepts were left largely intact in the individual case, though to a degree that still allowed for category specific performance differences in a demanding and well-controlled lexical decision paradigm. Unfortunately, standard clinical neurological and neurophysiological investigations of the patients presented here did not contain any tests that would diagnose semantic category specific deficits, however from the LDT results alone, statements about the nature of underlying neural processing of single word recognition and related semantic representations can still be soundly derived. These points apply to the observation of tool nouns being impaired after lesions in dorsal motor and parietal areas, previously related to performing actions with tools, but they also apply to the reported involvement of ventral face and dorsal hand motor areas in the processing of abstract emotion words.

Here, the corresponding cell assemblies are assumed to extend over perisylvian and limbic areas, holding their affective information, but to furthermore reach into face- and hand-related motor areas, exactly those effectors that are involved in emotion-expressing actions (Ekman *et al.*, 1969; Aviezer *et al.*, 2008). When observing and interacting with other individuals, their internal affective states are not accessible directly, to properly relate an abstract emotion sign to its meaning, as pointed out by Moseley *et al.* (2012). Hence, the emotion-expressing face and hand movements must therefore be used as a proxy for these internal states in others and in addition to one's own emotion expressing actions, as well as one's own internal affective states, provide the basis to relate an abstract emotion sign to its experiential meaning, though still leaving the possibility for further indirect grounding via learning in linguistic contexts. In native language learning during infancy, especially hand and face (and articulatory) emotion expression behavior provide means for the parent to infer the emotional state of the infant and chose the respective verbal label accordingly in implicit or explicit language teaching. From this perspective, the current observation of fronto-parietal lesions, involving, and showing highest overlap in, face and/or hand motor systems, to affect specifically abstract emotion words becomes entirely plausible and indicates again that modality specific information and corresponding substrates are not only of relevance for learning, but also for maintaining word semantics.

Comparison to results of Chapter 3

Chapter 3 presented results on two single patients with very focal lesions in the motor system, whereas this chapter investigated whole patient samples. Although the two patients of Chapter 3 were included also in the current analyses, it appears worthwhile to compare the results of both approaches, to draw conclusions in how far observations of Chapter 3 can be generalized to larger patient groups in the current chapter. For patient HS, who presented a very focal lesion directly adjacent to the hand motor tract and dorsal hand motor cortex, a relative deficit for tool nouns was reported in Chapter 3. This observation shows a good fit with results of the current chapter, as tool noun processing deficits were selectively pronounced in patients with predominantly dorso-parietal motor lesions, involving areas normally involved in tool handling. At the same time, this finding appears to contradict observations for patient CA in Chapter 3, who presented a focal lesion of the left SMA, situated in dorsal central/medial cortex and exhibited a selectively pronounced deficit for abstract emotion words. It has to be noted though, that patient CA was the only one among all patients investigated who presented a focal lesion within the SMA, an area that lacks the effector specific somatotopy of the primary motor cortex. Correspondingly, results of CA were interpreted in terms of an effector unspecific, general relevance and necessary role of the motor system for processing abstract emotion noun semantics. Largest lesion overlaps in the dorsal motor/anterior parietal patients were observed in brain areas normally involved in handling tools, thus leading to a specific impairment of semantic processing of tool nouns.

4.7 Conclusion

Category specific semantic deficits in a LDT observed in two patient samples with focal fronto-parietal lesions, including sensorimotor areas. Processing of concrete tool nouns was selectively impaired when compared to a non-action baseline category of animal nouns after lesions of dorsal prefrontal, sensorimotor and parietal areas, while fronto-parietal lesions involving dorsal and/or ventral motor areas resulted in impaired processing of abstract emotion nouns, whereas patients with predominantly perisylvian and temporal lesions and healthy age and education matched controls did not show category specificity of results. This confirms the functional necessity of extrasylvian motor areas for the processing of concrete hand action affording as well as for abstract-emotion nouns, in line with grounded approaches towards semantic processing and representation.

5. Abstract semantics in the motor system? – An event-related fMRI study on passive reading of semantic word categories carrying abstract emotional and mental meaning[2]

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[2] This chapter is based on Dreyer, F. R., & Pulvermüller, F. (*in press*). Abstract semantics in the motor system? – An event-related fMRI study on passive reading of semantic word categories carrying abstract emotional and mental meaning. *Cortex*. Author contributions**:** study concept and design (FRD and FP), material matching and selection (FRD), data collection (FRD), data analysis (FRD), manuscript drafting and artwork (FRD) and revisions (FRD, FP).

5.1 Abstract

Previous research showed that modality-preferential sensorimotor areas are relevant for processing concrete words used to speak about actions. However, whether modality-preferential areas also play a role for abstract words is still under debate. Whereas recent fMRI studies suggest an involvement of motor cortex in processing the meaning of abstract emotion words as, for example, ‘love’, other non-emotional abstract words, in particular “mental words”, such as ‘thought’ or ‘logic’, are believed to engage “amodal” semantic systems only. In the present event-related fMRI experiment, subjects passively read abstract emotion and mental nouns along with concrete action-related words. Contrary to expectation, the results indicate a specific involvement of face motor areas in the processing of mental nouns, resembling that seen for face-related action words. This result was confirmed when subject-specific ROIs defined by motor localizers were used. We conclude that a role of motor systems in semantic processing is not restricted to concrete words but extends to at least some abstract mental symbols previously thought to be entirely “disembodied” and divorced from semantically related sensorimotor processing. Implications for neurocognitive theories of semantics and clinical applications will be highlighted, paying specific attention to the role of brain activations as indexes of cognitive processes and their relationships to “causal” studies addressing lesion and TMS effects.

5.2 Introduction

Whether sensorimotor areas of the brain are involved and functionally relevant for the processing and representation of meaning and concepts has driven an intensive debate between proponents of classical amodal symbolic system approaches (Anderson, 1983; Ellis and Young, 1988), as well as neurobiologically motivated models that incorporate semantic grounding or "embodiment" (Barsalou, 1999, 2008; Pulvermüller, 1999, 2005; Glenberg and Gallese, 2012). While the former assume semantics to be represented in an amodal format, detached and independent from basal sensorimotor neural systems and therefore in *multi*-modal cortical areas alone, the latter postulate that semantic processes are carried by neuronal circuits distributed across multimodal areas, but also reaching into sensorimotor cortex. The theoretical explanation for such distributed semantic circuits comes from neurobiological theory, especially from structural cortical connectivity and functional correlational, Hebbian and Anti-Hebbian learning mechanisms (Hebb, 1949; Garagnani and Pulvermüller, 2016). Accordingly, grounded semantic circuits form as a consequence of correlated neuronal activity driven by co-occurring words and referential semantic information present in the non-linguistic environment; only after such semantic grounding of a base vocabulary, indirect ("parasitic") semantic learning can be accomplished in linguistic contexts when novel words co-occur with already semantically grounded ones (Pulvermüller, 2002). Because semantic grounding links symbols to action and perception information, it needs to involve neurons in modality-preferential sensory and motor brain systems. The distributed neuronal circuits joining together word form and semantic information are flexible insofar as their context-induced priming and task-induced preactivation of cortical areas influences their activation signatures (Pulvermüller, 2013a; Grisoni *et al.*, 2016).

In essence, the two proposals under discussion imply either the exclusive relevance of multimodal (or sometimes inappropriately dubbed "amodal") cortical areas for semantic processing, or rather the relevance of semantic circuits that draw upon these same areas and, in addition, reach into modality-preferential sensory and motor areas. In the debate on embodied cognition and action semantics, an extreme position that motor or sensory cortex are the only sites carrying meaning has been aired. However, such an extreme view has, as to the best of our knowledge, exclusively been described as a straw man in critical statements on embodiment (e.g. Mahon and Caramazza, 2008). Researchers noting the importance of grounding in semantic processing consider this straw man position as a case of "misembodiment" (Pulvermüller, 2013b) and as a "Quixotic" theoretical dead end (Barsalou, 2016). We will therefore ignore this unrealistic view here and take it for granted that concepts and words tend to activate multimodal areas in frontal, temporal and parietal association cortices (Binder *et al.*, 2009; Pulvermüller *et al.*, 2009; Binder and Desai, 2011).

At this stage, the most critical question is whether modality-preferential sensorimotor areas make additional contributions to semantic processing and representation. Lesion studies and work investigating the causal influence of local cortical activity changes might be seen as most appropriate for addressing this issue. However, as we discuss below, in the recent history of cognitive neuroscience, important clues came from neuroimaging experiments looking at brain activity to linguistic stimuli with different meanings. Together, the correlational (imaging) and causal (lesion or neurostimulation) studies can provide a good picture of the role of cortical areas in semantic processing. This question is not only of relevance in the context of general theories of language comprehension, but also for clinical applications, like aphasia therapy. Here, traditional approaches that apply for example confrontation naming (e.g. Howard *et al.*, 1985), focus predominantly on word and language training in isolation, as it would be sufficient following the implications of aforementioned amodal symbolic system theories. In contrast, alternative therapeutic approaches, as constrained induced language action therapy (CIAT; Pulvermüller *et al.*, 2001) or the intensive language action therapy (ILAT; Difrancesco *et al.*, 2012), also consider an involvement of action-related brain areas in language comprehension and especially stress the importance of an action-embedded context for language training.

Brain correlates for semantic grounding of concrete semantics

From a neuroscientific perspective, a range of results confirmed the involvement of sensorimotor areas in, and even their relevance for, semantic processing. For example, words used to speak about objects characterized primarily by visual, olfactory, gustatory and auditory information specifically activated the corresponding sensory areas (e.g. Barrós-Loscertales *et al.*, 2012; González *et al.*, 2006; Kiefer *et al.*, 2008). In the domain of action semantics, primary- and pre-motor areas were shown to become active and to index the body part with which the action denoted by an action verb is typically executed, as well as the body movements afforded by objects such as tools or food items (e.g. Martin *et al.*, 1996; Hauk *et al.*, 2004; Carota *et al.*, 2012). Further research showed that sensorimotor activations reflecting semantic aspects of symbols occur even when subjects do not attend to the incoming symbols, thus demonstrating a degree of automaticity of semantic activations (Pulvermüller *et al.*, 2005b; Shtyrov *et al.*, 2014). In addition, the early emergence of these sensorimotor activations, which are as early as the earliest semantic brain indexes known to date (ca. 100-200 ms), suggest their semantic status and make it unlikely that they resemble epiphenomenal post comprehension processes. Furthermore, behavioural paradigms (Witt *et al.*, 2010; Connell *et al.*, 2012; Shebani and Pulvermüller, 2013), neurostimulation approaches (Pulvermüller *et al.*, 2005a; Willems *et al.*, 2011), as well as studies in neurological patients (Bak *et al.*, 2001, 2006; Neininger and Pulvermüller, 2001, 2003; Pulvermüller *et al.*, 2010; Arevalo *et al.*, 2012; Bonner and Grossman, 2012; Kemmerer *et al.*, 2012; Trumpp *et al.*, 2013; Mårtensson *et al.*, 2014), though with varying degree of specificity, add to the correlational results from neuroimaging studies, by also demonstrating the functional relevance of sensorimotor systems for semantic processing. Most recent reports showed category specific semantic deficits as a consequence of minimal motor lesion (Dreyer *et al.*, 2015) and motor system activation reflecting semantic priming, which is a widely established index of meaning processing (Grisoni *et al.*, 2016), thus accumulating further evidence for a crucial and semantically specific role of sensorimotor cortex. Furthermore, although some reports suggest multimodal areas as the only substrate of semantic similarity processing (Fairhall and Caramazza, 2013), recent representation similarity analysis results could also demonstrate the motor system's role (in conjunction with left inferior frontal and left middle temporal areas) in computing semantic similarities between words and thus an indicator of genuine semantic processing (Carota *et al.*, 2017). Explicit formal neurobiological models of symbolic processing, which implemented structural neuro-anatomical connections between areas of the human cortex as revealed by tractography studies (see Rilling, 2014), were able to explain category specific semantic activations documented by neuroscience research along with the context- and task-dependent flexibility of the activations of distributed lexical and semantic circuits (Garagnani *et al.*, 2008; Garagnani and Pulvermüller, 2016; Pulvermüller and Garagnani, 2014).

The challenge posed by abstract concepts

In the vast majority, the studies in support of grounded action perception semantics applied concrete words and sentences normally used to speak about objects, scenes or human actions. Proponents of the "amodal" symbolic approach therefore suggested that grounding theories may not be capable of explaining the representation of abstract words and concepts (Mahon and Caramazza, 2008; Dove, 2016). In contrast, a critical claim immanent to some grounded models is that modality-preferential information is also recruited in the processing of abstract semantic information (Barsalou *et al.*, 2005), although, depending on the task, semantic priming and other aspects of context strongly influence the specific meaning aspects retrieved in any particular usage of an abstract symbol. Similar to concrete words, abstract concepts would accordingly be grounded in modal experience of instances of objects, actions, frames and scripts. A crucial difference to concrete concepts may exist with regard to the similarity and feature overlap between different instances of a concept, as context-dependent meanings are typically more variable and more complex than concrete ones (Pulvermüller, 2013a; Wilson-Mendenhall *et al.*, 2013). As proposed by some authors (Borghi and Cimatti, 2009; Borghi and Binkofski, 2014) a further difference between both kinds of words can be seen in the relevance of linguistic information for the respective acquisition processes, which is assumed to be of higher importance for words of abstract than for concrete semantics (see also Discussion below).

Nevertheless, assuming that knowledge about semantically related action and perception knowledge is in part processed by neurons in sensorimotor brain systems, these theories would propose that, despite their variable relationships to concrete actions, objects and scenes, the retrieval of abstract mental meanings might still call upon modality-preferential systems, in addition to multimodal brain areas.

Previous research on abstract symbols

Previous research outcomes do not conclusively distinguish between the theories presented above. Behavioural results, as well as results from TMS induced motor evoked potentials (MEPs), indicate that the processing of abstract concepts is indeed functionally linked with motor systems, as sentences that described the transfer of abstract information (example: “Anna delegates the responsibilities to you”) were shown to modulate activity within hand and arm motor systems (Glenberg *et al.*, 2008b). This interplay between processing of abstract semantics and motor systems was also shown for the reverse direction, with response times of sensibility judgments on abstract sentences being affected by previous movements of the hand and arm (Glenberg *et al.*, 2008a). Likewise, through a series of implicit association behavioral tasks, Casasanto (2009) and Casasanto and Chrysikou (2011) showed that motor experience and handedness play a role in processing abstract emotion concepts. Furthermore, a specific involvement of face motor systems for abstract over concrete words was recently reported by Borghi and Zarcone (2016) in a semantic decision task, as demonstrated by an interaction effect in reaction times of word semantics (i.e. abstract or concrete) and responses given via the mouth or hand.

In contrast, most of previous neuroimaging studies did not present direct evidence for an involvement of sensorimotor areas in abstract word processing. For example, Binder and colleagues (2005) concluded that left dorsolateral and inferior prefrontal areas, in addition to the superior temporal gyrus, activated more strongly for abstract words than for concrete words when these were presented in a lexical decision task. However, we note that, although these authors primarily highlight prefrontal cortex, a multimodal site, their most prominent activation cluster, a large premotor and prefrontal cluster, covering modality-preferential areas, was revealed to produce stronger activation for abstract than concrete words, too. Using a synonym judgement task, Noppeney and Price (2004) found the left posterior inferior frontal lobe, along with the temporal and middle frontal gyri, to show a preference for abstract over concrete words, whereas Vigliocco and colleagues (2014) found the rostral part of the anterior cingulate cortex (rACC) in both hemispheres to be the only region activating more strongly for abstract words than for concrete ones. Two meta-analyses (Binder *et al.,* 2009; Wang *et al.,* 2010) summarized a set of fMRI and PET studies (overall 25) on the processing of abstract words and sentences. Results revealed that, across studies, the left inferior frontal gyrus and the medial temporal gyrus became more strongly involved during processing of abstract words or sentences as compared with matched stimuli with concrete semantics. A prominent role of modality-preferential brain areas in abstract semantic comprehension however was in most cases not highlighted.

It is important to relate these experimental findings to grounded and amodal theories of language comprehension. Please note in this context that both meta-analyses and many of the single studies were designed to identify local brain activation patterns whose strengths *differed between* concrete and abstract words, a strategy that had been motivated by previous findings suggesting processing differences between concrete and abstract stimuli in behavioral paradigms (James, 1975; Kroll and Merves, 1986; see also Kousta *et al.*, 2011). However, the between-category contrast of course misses any neural patterns and local activations shared between concrete and abstract semantics, along with topographically specific modulations of activity indexing more fine-grained semantic differences. This is a crucial issue, especially because models of grounded semantics do not posit that abstract words activate the sensory or motor systems of the brain more strongly than object and action-related symbols with concrete meaning. For example, one study indeed showed that the degree of motor system activation was comparable between concrete action words and abstract emotion words (Moseley *et al.*, 2012). Therefore, in order to address the critical theoretical issue, it is necessary to focus not only on between-category differences in activation, but also on the activation patterns shared by abstract and concrete meaningful language. Furthermore, by looking at fine grained subtypes of both abstract and concrete meaningful items, it may become possible to reveal semantic activation signatures of more specific semantic features.

We also note that some of the previous results about local brain activations related to abstract meaning processing were quite variable (reporting, for example, dorsolateral vs. inferior frontal activations) and some of this variance might be explained by the selection criteria for abstract stimuli. In most of the previous studies, low ratings of concreteness and/or imageability scores were the only semantic criteria for selecting abstract words or sentences, so that more fine grained subtypes of abstract meaning related, for example, to modality-specific information, were not considered (see also Connell and Lynott, 2012). When looking at abstract words as a whole, it is indeed immediately obvious that there are quite different subtypes of abstract symbols. Abstract emotion words such as ‘fear’ relate to emotional states, whereas number words such as ‘four’ are used to speak about mathematical abstractions, and mental words like ‘thought’ can indicate cognitive states or processes that are typically not observable but hidden within the cognitive machinery of the brain (for additional abstract semantic sub-classes, see Della Rosa *et al.*, 2014). As previous work on concrete words and sentences has shown topographical brain activation differences for specific subtypes of action-related (Hauk *et al.*, 2004) and object-/visually-related words (e.g. Pulvermüller and Hauk, 2006; Pulvermüller *et al.*, 2009; Carota *et al.*, 2012), differences in topographical patterns of activation may also exist for subtypes of abstract words. Similarly, the general “abstract words” category may include subtypes that produce locally specific activations, which, to a degree, cancel each other out when investigating the large heterogeneous category of abstract items. Indeed, some previous research encouraged this abstract sub-categorization perspective. The already mentioned study by Moseley and colleagues (2012) specifically investigated the subclass of abstract emotion words (e.g. ‘love’ or ‘hate’) and revealed that, in addition to different parts of the limbic system (insula, basal ganglia and anterior cingulate cortex), the left inferior frontal gyrus as well as precentral hand- and face motor areas were recruited in passively reading these items. In a similar vein, Tschentscher *et al.* (2012) found motor system along with anterior parietal cortex activation specifically to number words and numbers, but little limbic system involvement. Using a word-picture matching task, Wilson-Mendenhall and coworkers (2013) showed activation preferences for the abstract word ‘convince’ in modality-general areas previously identified to be involved in mentalizing and social cognition processes, including medial prefrontal-, posterior cingulate- and the orbitofrontal cortex, and furthermore in superior temporal sulcus. Instead, the abstract concept ‘arithmetics’ activated anterior parietal areas previously shown in number and action processing (Dehaene *et al.*, 2003; Rizzolatti and Craighero, 2004). In a most recent study looking at different sub-classes of abstract meaningful language, Ghio *et al.* (2016) found differences in perisylvian cortex but not in modality-preferential pre- and post-central gyri when comparing local multi voxel patterns elicited by sentence with abstract arithmetic, emotional and mental meaning. Ghio and colleagues (2013) posit that the use of sentences makes it possible to provide syntactically and semantically well-controlled linguistic contexts for noun and verb semantic processing, as opposed to single word presentation, where, in their view, aspects of semantic processing related to argument assignment and meaning indeterminacy are difficult to control. However, most sentence processing studies, including that of Ghio and coworkers (2016), used variable words into their sometimes long sentences, most of which are not matched for crucial psycholinguistic factors, thus adding uncertainty to the causes of any sentence-elicited brain activity patterns. Furthermore, lack of control of the predictability of semantically critical words and their cloze probability may add further uncertainty as to the causes of brain activity during sentence processing. As these previous studies vary in their results on modality-preferential sensorimotor system activation in abstract symbol processing, it appears important to address this issue in the processing of different subtypes of abstract words well-matched for relevant psycholinguistic variables.

The current approach

The current study uses a classic univariate approach to shed light on abstract semantic processing. As large semantic categories may not reveal important brain correlates of facets of semantic processing, more fine grained semantic types are being targeted. To avoid the complex and possibly confounding influence of multiple contextual factors (phonological, syntactic and semantic priming, close probability and mutual information etc.) on the results, we investigated single words well matched for a range of physical and psycholinguistic variables. At the same time, extensive semantic ratings confirmed that, when words were presented in isolation, different subjects gave comparable ratings of their meaning features, thus arguing against the possibility of out-of-context “meaning indeterminacy”. This issue is of particular importance, as especially the meaning of abstract words has been shown to be sensitive to linguistic context (e.g. Schwanenflugel and Shoben, 1983). To address the critical question in the grounded cognition debate, we used a passive reading paradigm where modality-related semantic processes (e.g. visual imagination when monitoring for ‘kitchen utensils’) were not encouraged, so that any activations can be related to word semantics but not to task induction. Mental/cognitive abstract nouns such as ‘logic’, whose meaning does not carry emotional information, appear to be the ideal test case for words that are classically seen to be “disembodied” and to investigate the limitation of semantic grounding (Shallice and Cooper, 2013; Dove, 2016). These items, which we here call *abstract mental nouns* were contrasted with abstract emotion nouns such as ‘disgust’. In addition to abstract nouns, action-related nouns of the food and tool categories were probed, as those had previously been shown to differentially activate motor regions involved in controlling the face and hands/arms (Carota *et al.*, 2012). We expected that, in addition to modality general perisylvian cortex activation, activity in sensorimotor cortex will distinguish not only between subtypes of concrete action words, but likewise between abstract emotion and mental symbols. Some authors have stated that linguistic information is more important in semantic learning for abstract words compared with concrete ones (Borghi and Cimatti, 2009; Borghi and Binkofski, 2014). This position predicts that articulatory and face motor systems are more strongly activated by abstract mental words than other motor fields. A different argument has been put forward for abstract emotion words. As many emotions are typically expressed by bodily actions involving face and arms and such emotion expression provides a prime opportunity to semantically ground emotion words, Moseley and coworkers (2012) argued that broad ventral motor activity spanning face and arm areas might reflect the semantic grounding of emotion words in bodily action. Following these proposals, we predicted that abstract mental words will activate face motor cortex more strongly than hand motor areas, whereas abstract emotion words spark both hand and face motor areas to similar degrees. Current “amodal” theories attributing semantic processing to a symbolic system do not predict such topographical specificity in the motor system.

5.2 Methods

Participants

Thirty-three healthy native speakers of German participated in the fMRI study. All participants had normal or corrected-to-normal vision, reported no history of neurological or psychiatric disease and provided written informed consent before testing. Data from five participants had to be excluded from analysis, due to anatomical anomalies found during structural scanning (1), insufficient eye-sight correction (1) and excessive head movements during the reading paradigm and/or general lack of task compliance (3). The remaining 28 participants (16 female) were 23.7 years of age on average (*SD* = 5.3 years) and strongly right handed, according to handedness scores (mean laterality quotient = 93, *SD* = 12.4) of the Edinburgh Handedness Inventory (Oldfield, 1971). All procedures were approved by the ethics committee of the Charité University Hospital, Campus Benjamin Franklin, Berlin, Germany.

Stimuli

Material consisted of 160 experimental nouns, along with 120 hashmark strings that served as a visual baseline and 320 filler words to disguise the studies purpose and to increase the variability of word meanings to be processed. The 160 nouns of interest were made up of 40 stimuli from 4 semantic categories. These were words referring to concrete objects, including tools (e.g. 'Säge', saw) and food items (e.g. 'Apfel', apple), as well as abstract nouns with emotional (e.g. 'Angst', fear) and non-emotional, mental-cognitive meaning (e.g. 'Logik', logic).

All non-filler noun groups were matched for a range of lexical and sub-lexical psycholinguistic variables, as determined by the dlex corpus (Heister *et al.*, 2011). Matching was achieved for word length, number of syllables, normalized lemma frequency, character frequency, character bigram frequency, character trigram frequency and word initial character-, word initial bigram- and word initial trigram frequency. F/t tests did not reveal any differences between semantic category groups for any of these psycholinguistic variables (all $p > .05$). Descriptive statistics of psycholinguistic variables and matching details are depicted in Table 5.1.

Table 5.1: Psycholinguistic characteristics of experimental noun categories. *P* values denote results from a one-way analysis of variance with the factor semantics for the respective variables.

	Abstract Emotion		Abstract Mental		Foods		Tools		
Variables	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*p*
Lemma Freq./Mio.	8.23	6.06	8.93	7.73	8.22	9.65	8.02	7.51	0.96
Length	6.75	1.66	7.15	1.61	6.83	2.12	7	1.83	0.76
Number of Syllables	2.18	0.5	2.15	0.48	2.1	0.63	2.15	0.36	0.93
Character Freq./Mio.	1879103	590078	1767403	632999	1774341	715398	1974291	559659	0.41
Character Bigram Freq./Mio.	257845	121172	216863	135797	257169	161294	290025	138413	0.14
Character Trigram Freq./Mio	139288	80408	99588	60939	135156	95621	139851	92606	0.1
Initial Character Freq./Mio	12527	5392	15076	5818	14775	6232	13730	6866	0.24
Initial Bigram Freq./Mio	2278	1833	3511	2747	2351	2074	2602	2246	0.06
Initial Trigram Freq./Mio	415	954	1037	1707	787	1686	883	1711	0.32

To empirically evaluate the semantic properties of the word stimuli, semantic ratings were collected from 29 healthy participants (native speakers of German, aged 18-32 years, 17 females) before the main experiment. Similar to previous studies (Pulvermüller *et al.*, 2001; Hauk and Pulvermüller, 2004; Moseley *et al.*, 2012), semantic ratings were expressed on a Likert scales ranging from 1 (no relation) to 7 (strong relation). Each word was rated for its semantic relatedness to hand/arm-, face/mouth-, leg/foot actions, to visual, olfactory, gustatory, and haptic/tactile perceptions, as well as to emotions and mental processes. Ratings of concreteness and word familiarity were also obtained. The concreteness scale was designed with the poles of high abstractness (1) to high concreteness (7). For inclusion into an effector-specific action word category (tool/ food nouns), words had to achieve an average rating above the neutral mid-point of 4 for the related question while being rated lower on all other action semantic scales. Abstract words had to fulfil the criteria of ratings < 4 on all action scales, on concreteness and all perceptual scales, but > 4 on the scale for relation to mental processes. In addition, abstract emotion words were chosen to show strong emotional connotations whereas abstract mental words where lacking such a connotation, while still maintaining the high relatedness to mental processes. In the semantic rating study, many more stimuli than the chosen ones had been included (see Chapter 2 for details) and an important criterion for inclusion in this study was low variance of semantic ratings across raters, thus reducing possible meaning indeterminacy when words are presented in isolation, in the absence of further linguistic context. Please note that the confidence intervals of our semantic ratings were comparable between our abstract and concrete words, thus arguing against a principal difference in semantic variability of single abstract and concrete words presented out of context, at least for our present word selection. An overview of semantic ratings for all experimental categories is shown in Fig. 5.1.

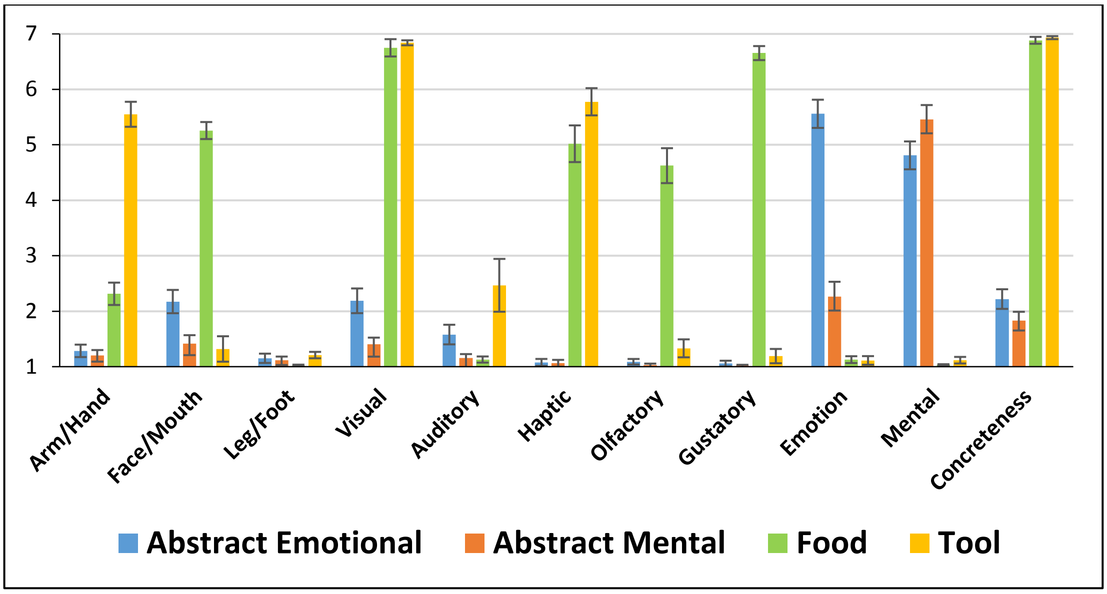

Figure 5.1: Average semantic ratings for experimental categories of abstract emotion, abstract mental, food and tool nouns. Ratings for arm/hand, face/mouth and leg/foot action-relatedness, as well as visual, auditory, somatosensory, olfactory, gustatory, emotion and mental process relatedness were given on a scale from 1 (no semantic relation) to 7 (very strong semantic relation). The concreteness scale was designed with the extrema of 1 (high abstractness) and 7 (high concreteness). Error bars 95% confidence intervals of the mean.

Procedure

The study's design parameters were chosen to match those of the Moseley *et al.* (2012) study. Participants were asked to passively and silently read the words presented tachistoscopically one by one, each presented for 150 ms. Short, tachistoscopic presentation was chosen to avoid directed eye movements and any associated motor activity during reading. The inter stimulus interval had a jittered duration of 2350 ms on average, randomly varying between 2100 ms and 2500 ms, in which a fixation cross was shown in the center of the screen. All stimuli were printed in white letters on black background, using monospaced Courier New font and were spanning a maximum of 2° horizontal and .6° vertical visual degree.

The reading paradigm performed in the scanner was divided into four blocks of eight minutes. Each block started and ended with a baseline phase of 15 seconds in which a central fixation cross was presented. A motor localizer task was performed after the reading task, while subjects were still lying in the scanner. This task was not announced previously to the participants to avoid a possible bias towards motor semantics in the stimuli. Hence instructions for the motor localizer were given by short video clips inside the scanner to directly demonstrate the movements in question. Participants were asked to repetitively move different body parts, including the lips, tongue, fingers of their right hand, or were asked to grin, using only the mouth musculature, or to frown, using only the forehead muscles. Each type of movement had to be performed continuously for twelve seconds of a miniblock; there were four mini-blocks per movement type. The sequence of these blocks was pseudo-randomised and a twelve second resting period was introduced in between any two mini-blocks. Visual cues, consisting of only two letters to avoid extensive visual processing, indicated the target movement of a trial. Throughout the passive reading and the motor localizer task a video camera was used to monitor participants' task compliance. Following the motor localizer task, a T1 weighted Magnetization Prepared Rapid Acquisition Gradient Echo (MPRAGE) scan was collected for approximately 5 minutes while the participants lay still with their eyes closed to obtain a structural MRI at grain size of 1 mm^3 voxels. To test for their attention and task compliance during the passive reading task, participants were asked to perform a previously unannounced word recognition test immediately after scanning. This test included 40 novel and 40 words they had previously been presented with in the reading paradigm (balanced for semantic conditions and time of presentation in the reading task). This task was not announced previously to the participants to avoid a possible bias toward the application of memory strategies during reading.

5.3 Data Analysis and Imaging Methods

Stimulus Validation

To test whether stimuli show the desired dissociations in semantics, repeated measures (RM) ANOVAs and post hoc t-test were performed on face/mouth and arm/hand scores and relatedness to mental processes or emotions for semantic categories.

Scanning and Data Analysis Parameters

Scanning was performed with a 3 Tesla Siemens Tim Trio magnetic resonance device using a 12 channel head coil. Functional images were acquired in echo-planar imaging (EPI) sessions with a time repetition of 2000 ms, time echo of 30 ms and a flip angle of 78°. Scans consisted of 32 slices, acquired in descending order, with a voxel size of 3 mm x 3 mm x 3 mm and an interslice distance of .75 mm. Data preprocessing and analysis was performed using SPM8 (Wellcome Department of Imaging Neuroscience, London, UK). Before analysis, images were corrected for slice timing and realigned to the first image using sinc-interpolation. As a next step, EPI images were coregistered to the structural T1 images, which were normalized to the 152 subject T1 MNI template, and the resulting transformation parameters were applied to the coregistered EPI images. Images were resampled with an interpolated spatial resolution of 2 mm x 2 mm x 2 mm and spatially smoothed with an 8-mm full-width half-maximum Gaussian kernel. First and second level general linear models were derived on the basis of the canonical hemodynamic response function, using a highpass filter of 128 s to reduce low-frequency noise. In the first level models, the onset times of all words from a given semantic category were modeled as separate events of the same type. There were stimulus type regressors for all semantic categories and fillers, one for the visual baseline, and 6 to account for subject movements and head rotations, separately for all blocks of the reading paradigm. Likewise, for the motor localizer task, onset times for each movement were modeled as separate events of 12 s length each. As the current studies hypotheses concerned left hemispheric brain areas, the right hemisphere was excluded from first level analysis, to decrease the beta-error rate for left hemispheric activations. In addition, a gray matter mask, defined by voxels with a gray matter probability > .3 in the Statistical Parametric Mapping (SPM) template, was applied to further increase statistical power of the analyses. At the second level, group data were analyzed using random-effects analysis. To this end, activity elicited by all noun categories taken together was compared against the visual baseline**,** to reveal the general network underlying noun processing in the passive reading paradigm. In addition the four noun categories of tools, foods, abstract emotion and abstract mental items were each contrasted against the visual baseline separately. As the study's hypotheses predict dissociations between, and different activation topographies for, specific semantic word types in the motor system, a further mask was applied to these category specific contrasts consisting only of those areas with significant false discovery rate (FDR) corrected ($p < .05$, peak-level) activation in the hand- or face-motor localizer tasks within precentral and rolandic motor areas, as defined the Wake Forest University pick atlas (Maldjian *et al.*, 2003).

ROI definition and analysis

Category specific activations were calculated for three sets of region of interest (ROI) analyses, with raw average ROI parameter estimates being extracted using the marsbar toolbox (Brett *et al.*, 2002) in SPM 8.

The first “semantic” set of 10 ROIs were previously reported to be involved in semantic processing by a meta-analysis (Vigneau *et al.*, 2006). As only inferior frontal temporal regions from the “semantic” ones showed significant between word category differences (see results in Supplementary Material), two ROIs with the largest signal strength, one in inferior frontal (IF), the other in middle temporal (MT) cortex, thus spanning over “classical” inferior frontal and temporal language areas, were selected for direct comparison with the motor localizer ROIs. In this second analysis, the two selected “semantic” ROIs were analyzed together with activity in face and hand motor regions as determined by the localizer tasks. A further analysis looked at areas with local activation peaks in our all-words-against-baseline contrast, defining the ROIs in a data-driven manner (see Supplementary Material for details). All ROIs were defined as spheres of 5 mm radius around the local activation peak, either reported in the literature (Vigneau *et al.*, 2006), or delivered by the group level motor localizer contrasts (lip, tongue, frowning and grinning movements or finger movements vs. rest). The rationale behind the inclusion of these semantic and motor ROIs in a single analysis was to investigate, whether differential activations between semantic classes are present in general semantic and/or motor systems. To test for those dissociations between semantic subclasses across ROIs, a first 4 (ROIS: IF/MT/Hand motor/Face motor) X 4 (Semantics: abstract emotion/abstract mental/foods/tools) RM ANOVA was performed. This analysis allowed to test whether the selected ROIs did indeed show differential activations between ROIs for the semantic classes. In case these analyses revealed significant effects, follow up ANOVAs focused on semantic and motor areas separately, to pin down the origin of any main- or interaction effects.

To this end, 4 (Semantics: abstract emotion/abstract mental/foods/tools) X 2 (ROIs: Hand/Face or IF/MT) RM ANOVAs were performed, which, in case of further significance, were reduced to 2 X 2 analyses focusing on either action or abstract words only. Finally, post hoc t-test were applied to disentangle any interactions and main effects for the within abstract- or concrete classes ANOVAs.

To potentially improve the accuracy of motor activity estimation in individual subjects, a third set of analyses were performed, now defining motor ROIs in a subject-specific manner. In this case, 5 mm sphere ROIs where centered on activation peaks of first level contrasts in the motor localizer tasks, obtained separately for each participant, thus taking into account individual differences of motor processes/representations. On these individual motor ROIs, the same 2 (ROIs: Hand/Face motor) X 4 (Semantics: abstract emotion/abstract mental /foods/tools) RM ANOVA and, in case of significant effects, subsequent 2 (Hand/Face motor ROIs) X 2 (Semantics: specifically for abstract emotion/abstract mental or foods/tools) RM

ANOVAs, along with pairwise motor and abstract word type comparisons, were performed as it was the case for the motor ROIs in the aforementioned group level approach. Note that all ROI defining procedures, for the group level, as well as for the subject specific approach, were entirely orthogonal to the contrasts of interest (i.e., abstract emotion vs. abstract mental words and face vs. arm-related words), therefore avoiding any perils of “double dipping” (Kriegeskorte *et al.*, 2008).

5.4 Results

Behavioural results

Results of the unannounced word recollection test performed directly after the fMRI experiment, approximately 20 minutes after the end of the reading paradigm, indicated poor task compliance in the reading paradigm in three participants (D-prime < .2), which were hence excluded from analysis (see Methods). For the remaining 28 participants, an average D-prime of .87 ($SD = .49$) was obtained, thus indicating acceptable attention to and processing of the word stimuli presented in the reading paradigm.

Semantic ratings

The concrete categories of foods [$F(1, 39) = 539.7$, $p < .001$, *partial* $\eta2 = .93$] and tools [$F(1, 39) = 817.2$, $p < .001$, *partial* $\eta2 = .96$] both showed a significant main effect across motor features (arm/hand- and mouth/face-relatedness). Post hoc tests confirmed the relatively greater hand action-relatedness for tools [$t(39) = 28.6$, $p < .001$, Cohen's $d = 6.8$] and likewise the relative dominance of face action-relatedness for food words [$t(39) = 23.2$, $p < .001$, Cohen's $d = 5.71$]. Interestingly, effector specific dissociations in semantic relatedness were also observed within the subclasses of abstract emotion [$F(1, 39) = 65$, $p < .001$, *partial* $\eta2 = .62$] and abstract mental items [$\mathrm{F}(1, 39) = 7.62$, $p < .01$, *partial* $\eta2 = .16$]. Post hoc tests for both abstract classes revealed a stronger relation to face actions compared to arm actions [abstract emotion: $t(39) = 8.06$, $p < .001$, Cohen's $d = 1.71$; abstract mental: $t(39) = 2.73$, $p < .01$, Cohen's $d = .51$].

Consistent with the semantic pre-evaluation of the stimuli, semantic ratings of face and hand relationship revealed a double dissociation for food and tool nouns manifest in a significant interaction effect in a 2 (noun category) X 2 (arm/face action-relatedness) repeated measures ANOVA [$F(1, 78) = 1356$, $p < .001$, *partial* $\eta 2 = .95$], based on the aforementioned higher face ratings than arm ratings for the former and the reverse for the latter. Similarly, a dissociation between abstract emotion and mental nouns was manifest in an interaction effect when considering ratings of emotional and mental semantic ratings in a 2 (noun category) X 2 (relatedness to emotions/mental processes) ANOVA [$F(1, 78) = 294.4$, $p < .001$, *partial* $\eta 2 = .79$]. As expected, relatedness to emotions was more pronounced than to mental processes [$t(39) = 4.69$, $p < .001$, Cohen's $d = 1.14$] for abstract emotion nouns, while the reverse was observed for their abstract mental counterparts [$t(39) = 19.32$, $p < .001$, Cohen's $d = 4.71$]. Unexpectedly, abstract nouns showed a significant interaction in a 2 (abstract emotion/mental nouns) X 2 (hand/face action-relatedness) ANOVA [$F(1,78) = 24.8$, $p < .001$, *partial* $\eta 2 = .24$], due to abstract emotion nouns being more face action-related than abstract mental nouns [$t(70.62) = 5.91$, $p < .001$], while the two abstract noun classes did not differ in terms of hand action-relatedness [$t(78) = 1.19$, $p = .27$], although it should be noted that even for abstract emotion nouns face-relatedness was very low on average (2.1 on a scale from 1-7). In sum, semantic ratings indicate that stimuli met the intended action- and emotion-relatedness characteristics of all noun categories.

Imaging results

Left hemispheric activations

At a FDR corrected significance level of $p < .05$ (peak-wise), the contrast of all noun categories against the visual baseline revealed activation of classic perisylvian language areas, the visual word form area, as well as that of extrasylvian sensorimotor areas in the left hemisphere. Activated clusters were spread across the left inferior frontal and posterior temporal cortex in addition to pre- and postcentral areas (see Table 5.2 and Figure 5.2A for details). These results agree with activation patterns reported in previous passive word reading studies (e.g. Moseley *et al.*, 2012; Carota *et al.*, 2012; Moseley and Pulvermüller, 2014), confirming sufficient processing of presented word stimuli across participants and demonstrating good signal-to-noise ratios in these regions. Activations of specific semantic classes for contrast against the hashmark baseline are presented in the Supplementary Material. However, as the mere contrast to visual baseline is confounded by a range of psycholinguistic processes, we want to stress that statements about semantic processing are hence difficult to derive from those individual contrasts, so that these results serve illustrative, rather than inferential purposes. For the motor localizer task, contrasts of face movements (consisting of lip, tongue, frowning and grinning movements) against rest showed strongest signals in ventral motor and premotor areas whereas hand movements showed strongest signals in more dorsal motor, premotor and somatosensory areas (see Figure 5.2B for an overview of respective clusters).

Table 5.2: MNI coordinates for activation peaks of the contrasts of all nouns against a visual hashmark baseline. Coordinates are plotted at a false discovery rate corrected *p* < .05 (peak-wise), with indented coordinates reflecting coordinates which arose as part of a larger cluster and are given in mm in Montreal Neurological Institute space.

All Nouns vs visual baseline					
Cluster Size	MNI Coordinates			*t*	*p*
	x	y	z		(FDR corrected)
2140	-42	32	-2	5.68	.027
	-54	-8	44	5.07	.027
	-52	14	-10	4.94	.027
162	-56	-18	18	4.72	.027
19	-30	-36	0	3.92	.031
54	-22	0	-4	3.85	.031
96	-42	-52	-14	3.81	.032
24	-32	-18	-10	3.78	.033
	-24	-10	-10	3.24	.047
28	-6	-16	70	3.41	.042
	0	-10	64	3.22	.048
6	-60	-38	16	3.41	.042

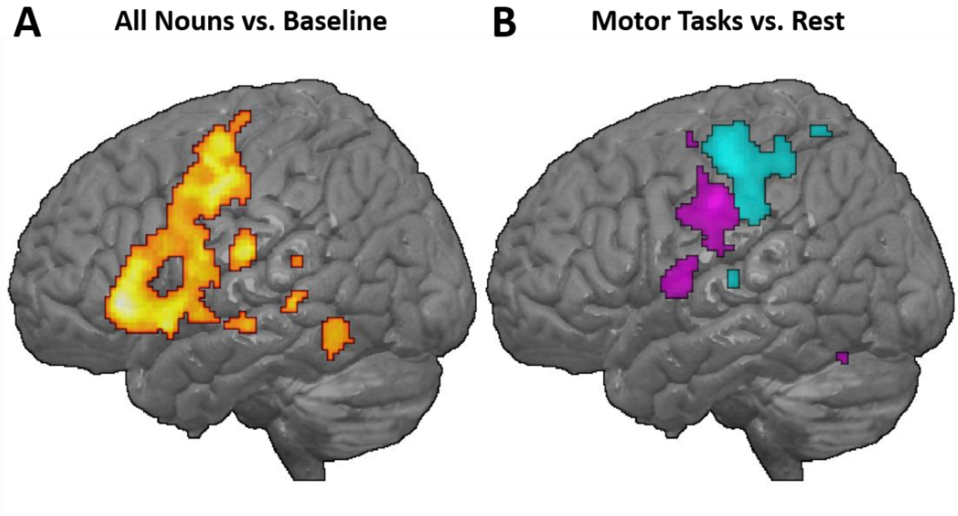

Figure 5.2: A: Left hemispheric activation clusters in gray matter for the comparison all nouns pooled together against a low level visual baseline, thresholded at *p* < .05, FDR corrected (peak-wise). **B:** Left hemispheric activation clusters in gray matter for contrast of face- (depicted in purple) and hand movements (depicted in cyan) against rest, thresholded at *p* < 1e-6, family-wise error rate (FEW) corrected (peak-wise).

ROI Analyses

Group level ROIs

Analysis of Semantic ROIs as derived from Vigneau *et al.* (2006) revealed a significant main effect for ROIs [*F*(9,243) = 2.95, *p* = .02, *partial η2* = .1], but only a tendency towards significance for the main effect of Semantics [*F*(3,81) = 2.63, *p* = .055, *partial η2* = .09] and also the interaction between ROIs and Semantics was not significant [*F*(10.6, 284.9) = 1.4, *p* = .18, *partial η2* = .05] (see Supplementary Material for further details of this analysis).

ROIs considered in the second set of ROI analyses are depicted in Figure 5.3. The motor localizer showed most prominent activation for the face tasks centered in the ventral motor cortex (MNI X = -62 mm, Y = -14 mm, Z = 38 mm), whereas the hand motor task activated more dorsal motor cortex (MNI X = -34 mm, Y = -22 mm, Z = 52 mm), which each provided the center of a 5 mm radius sphere defining the motor system ROIs.

A 4 (ROIs: IF/MT/ Face motor/Hand motor) X 4 (Semantics: abstract emotion/abstract mental/foods/tools) RM ANOVA revealed no significant main effect for ROIs (*F*(3,81) = 1.75, *p* = .16, *partial η2* = .06) but a significant main effect for Semantics [*F*(3,81) = 3.33, *p* = .024, *partial η2* = .11], and, crucially, the interaction between ROIs and Semantics was significant [*F*(7.3,152.1) = 2.14, *p* = .038, *partial η2* = .07]. To further investigate this interaction two 2x2 ANOVAs were conducted, for "semantic" ROIs and motor ROIs, respectively. A 2 (ROIs: IF/MT) X 4 (Semantics: abstract emotion/abstract mental/foods/tools) RM ANOVA showed a significant main effect for semantics [*F*(3,81) = 4.3, *p* = .007, *partial η2* = .13], whereas the main effect for ROIs and the ROI*Semantics interaction were not significant (*F*s < 1.1). A further ROI analysis, based on data driven perisylvian ROI definitions, rather than on previously reported semantic nodes, confirms this observation of a non-significant ROI*Semantics interaction and is presented in detail in the Supplementary Material. In contrast, within the motor ROIs, a 2 (ROIs: Face/Hand motor ROI) X 4 (Semantics: abstract emotion/abstract mental/foods/tools) RM ANOVA showed no main effects for ROIs or Semantics (Fs < .8), but a significant ROI*Semantics interaction [*F*(3,81) = 3.5, *p* = .019, *partial η2* = .11], thus indicating differential activation for the semantic classes within the motor system. This complex interaction was broken down to separately test for effects for abstract and concrete word types. When motor ROI activation patterns were analyzed separately for abstract and concrete words, a 2 (ROIs: Face-/Hand motor) X 2 (Semantics: abstract emotion/abstract mental) repeated measures ANOVA revealed a significant ROI*Semantics interaction [*F*(1, 27) = 5.9, *p* = .022, *partial η2* = .179], but no significant main effect for neither ROIs, nor Semantics (Fs < .12). Post hoc paired samples t-tests on abstract noun activity in the motor ROIs revealed a significant difference of abstract mental nouns between face and hand ROI activations to underlie the observed interaction [*t*(27) = 2.07, *p* = .048, Cohen's *d* = .55]. The ROI*Semantics interaction did not reach significance when comparing motor activations elicited specifically by food and tool words [*F*(1, 27) = 2.66, *p* = .115, *partial η2* = .09] and also the main effects were not significant (*F*s < 1.7) in this analysis.

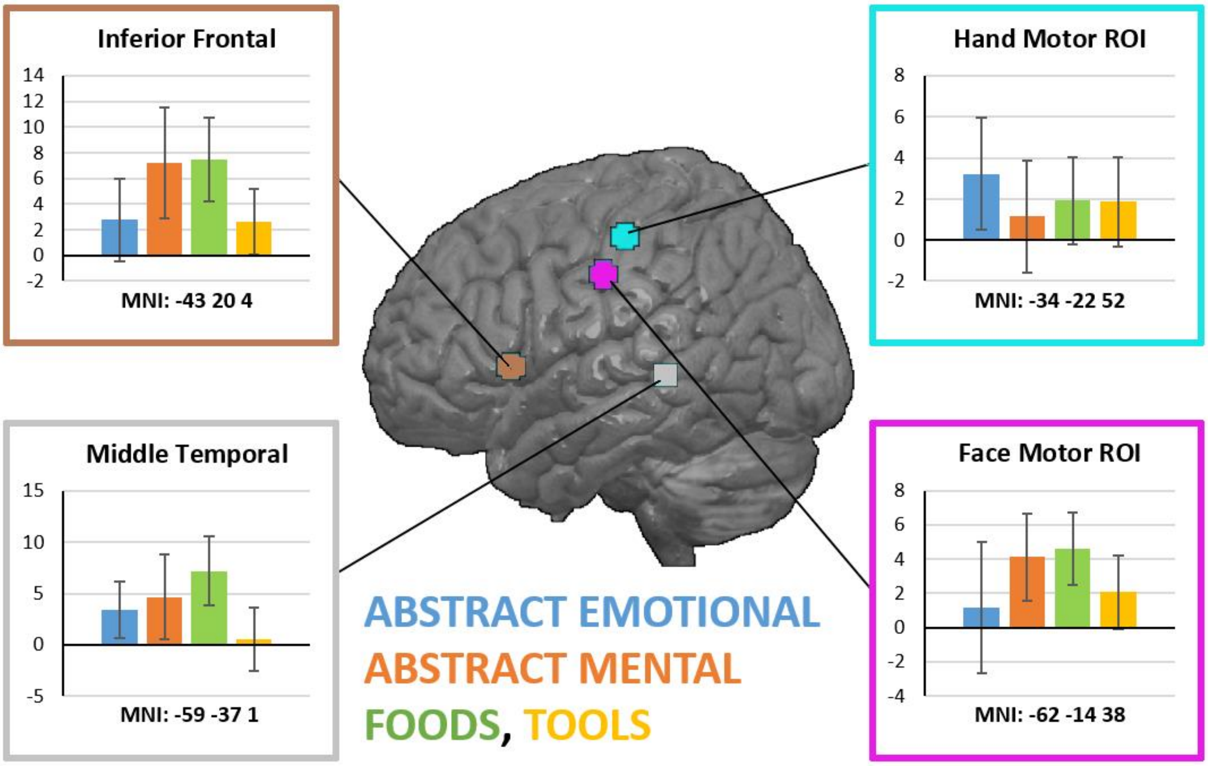

Figure 5.3: Overview of group level Regions of interest (ROIs) on semantic network nodes (Vigneau *et al.*, 2006) in inferior frontal (shown in brown) and middle temporal cortex (shown in gray), as well as motor ROIs for face (magenta) and hand movements (cyan, each presented with the respective ROI center mm MNI coordinate. Bar graphs represent raw parameter estimates of noun categories against baseline in these ROIs, with bars denoting 95% confidence intervals of the mean, corrected for between participant variance (Morey, 2008). Blue bars depict results for abstract emotion nouns, red bars for abstract mental nouns, green bars for food nouns and yellow bars for tool nouns.

Subject specific motor ROIs

The left panel of Fig. 5.4 depicts a summary of participants' individual peaks in the hand and face motor localizer task, which served as centers for subject specific motor ROIs areas, defined as spheres of 5 mm radius. One participant was excluded from this analysis due to atypical activation peaks in the motor localizer task (note however that the overall pattern of results did not change, when this participant was included in analysis). The remaining individual motor foci still showed a considerable amount of variation between participants, with an average Euclidean between-focus distance of 11.8 mm (*SD* = 5.6 mm) for face- and 12.2 mm (*SD* = 5.6 mm) for hand motor foci. Data extracted from these ROIs for the contrast of noun categories against hashmark strings are shown on the right panel of Figure 5.4. A 2 (ROIs: individual Face/Hand motor peaks) X 4 (Semantics: abstract emotion/abstract mental/foods/tools) RM ANOVA revealed a significant ROI*Semantics interaction

[F(1.8,45.7) = 3.87, p = .03, *partial η2* = .13], with main effects being insignificant (all *F*s < 1.3). Post hoc ANOVAs to disentangle contributions of abstract and concrete nouns to this interaction effect showed significant ROI*Semantics interactions for both the abstract [*F*(1,26) = 6.88, *p* = .014, *partial η2* = .21] and the concrete action-related nouns [*F*(1,26) = 7.52, *p* = .011, *partial η2* = .22], whereas all main effects were not significant (all *F*s < 2.8). For abstract nouns the interaction was driven by relatively stronger activation of face motor ROIs compared with hand motor ROIs to mental words [*t*(26) = 2.34, *p* = .027, Cohen’s *d* = .64], while for concrete nouns a selective preference of the face-motor-ROIs for foods over tools [*t*(26) = 2.71, *p* = .012, Cohen’s *d* = .74], was confirmed as the basis of the observed interaction. This pattern of ROI*Semantics interactions, for abstract and concrete semantics, was observed to not change when data were normalized within each ROI before being included in the respective ANOVAs.

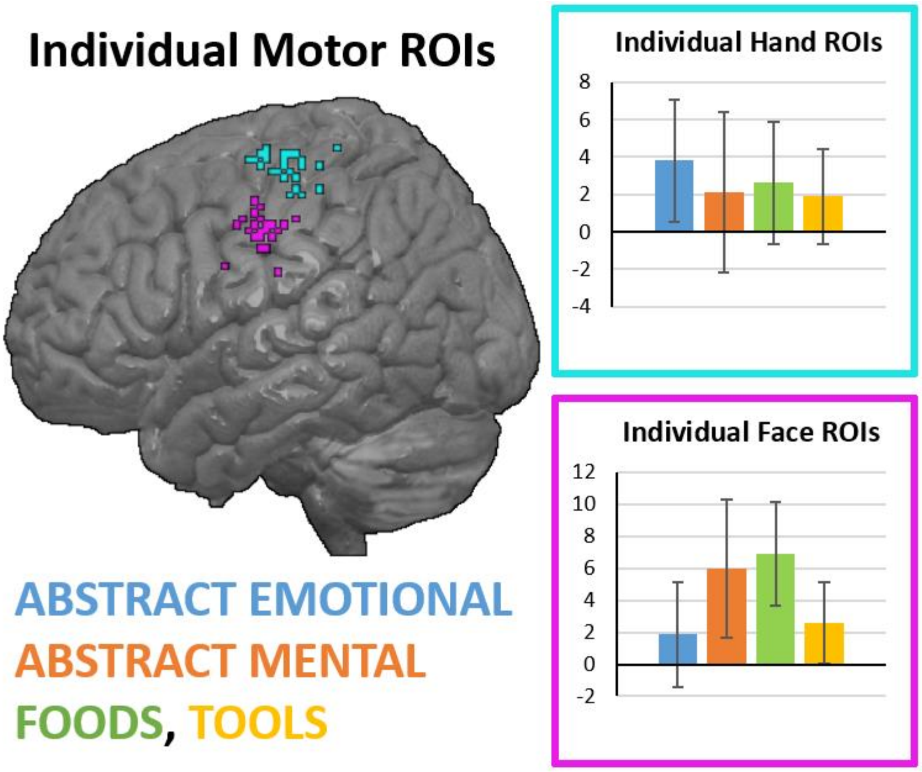

Figure 5.4, left Panel: Overlay of individual motor peaks for face (depicted in magenta) and hand (depicted in cyan) movements across participants. Each dot represents the signature motor activation voxel (maximal *t* in the contrast movement vs. rest) of one participant. **Right panel:** Category specific activation vs. baseline in individual face and hand motor ROIs. Bar characteristics and colour coding as in Fig. 5.3.

5.5 Discussion

Compared with a low level baseline, we found neural activation in classic left-perisylvian language areas and extrasylvian precentral regions when subjects passively read nouns with abstract and concrete meaning while refraining from any motor movements. These activations included foci in inferior frontal Broca's region, in posterior middle and inferior temporal gyrus along with fusiform gyrus, and in precentral cortex. Region of interest analyses demonstrated specific somatotopic dissociations in hemodynamic activity within the motor system, in particular in motor areas controlling face/mouth and arm/hand movements, as identified by motor localizer tasks, which was absent in perisylvian and temporal areas, classically identified to be involved in semantic processing (Vigneau *et al.*, 2006). Significantly greater activity to food words affording mouth actions were found in face motor areas, relative to hand action affording tool words, thus replicating previous results on English food nouns (Carota *et al.*, 2012). Interestingly, similar to the patterns elicited by action-affording object nouns, the passive reading of different types of abstract words led to activity dissociations in motor areas, which became manifest in significant interactions of motor ROI and semantic word type factors. In particular, for abstract mental words such as 'logic', relatively stronger activation in face motor regions was found, whereas abstract emotion words activated the different motor ROIs to the same degree.

These results provide the first neuroimaging evidence that patterns of motor cortex activation do not only reflect aspects of the meaning of words with concrete semantics, but that, in addition, different types of abstract meaning are associated with their own specific activation signatures across the sensorimotor system. In the paragraphs below, we will discuss our present results in the context of pre-existing evidence and in that of theories of "amodal symbolic" and "grounded/embodied" semantic and conceptual processing.

Support for semantic grounding of abstract words

Apart from semantic processing, activation in motor areas, as observed in the current study, has previously been associated with basal phonological- (Fadiga *et al.*, 2002; Pulvermüller *et al.*, 2006; D'Ausilio *et al.*, 2012; Schomers *et al.*, 2015) and morphological processing (Pulvermüller and Shtyrov, 2009; de Zubicaray *et al.*, 2013). Therefore, contrasts of all experimental categories against a non-linguistic low-level baseline are not strictly informative about semantic processing, as they might reflect various psycholinguistic processes (including morphology and phonology) brought about by word and non-word stimuli. Still, our hashmark control condition allowed us to subtract out unspecific effects of visual stimulation due to strings of visually displayed signs of similar physical makeup. Any conclusions on semantic processing must therefore rest on comparisons between activation patterns elicited by meaningful symbols of different semantic types. Interestingly, our main result was that there were such topographical differences in word-elicited brain activation in sensorimotor systems for both concrete action-related words and different subtypes of abstract terms too.

Before any conclusions from the present results on theories of cognitive and brain function can be drawn, it is necessary to consider the hypothesis space to which our results can be applied. This is important, because, in recent discussions, this hypothesis space has been substantially widened and the original driving force behind many neuroscience studies of semantic processing – to decide between grounded and modularist theories of conceptual processing – therefore became obsolete. Today, it seems widely accepted that an encapsulated module for semantic and conceptual processing cannot explain that sensory and motor systems are recruited in some symbol processing tasks – at least by some symbols – and why activation changes in sensorimotor systems can have a causal influence on symbol processing (Pulvermüller, 2005; Barsalou, 2008; Glenberg *et al.*, 2008a; Binder and Desai, 2011; Pulvermüller, 2013a; Kemmerer, 2015). As the pre-existing evidence had been accepted to falsify encapsulated modularism, in particular an encapsulated conceptual "meaning box" (for discussion, see Pulvermüller, 2005) – a new type of "hybrid model" was proposed according to which the abstract symbol processing mechanism can interact with sensorimotor systems when needed, that is, when the task or context requires such interaction (see, for example, Mahon and Caramazza, 2008). Our passive task did not encourage, and certainly did not require, such sensorimotor interaction and, therefore, the results are open to interpretation in terms of word-induced semantic processes driving any differences in brain activation patterns.

After reshaping the space of available theories, the major claim of one version of an amodal symbolic semantic account seems to be that "modality-independent neural systems" – understood as *multimodal* areas in frontal, parietal and temporal cortex – carry concepts and meanings (Bedny and Caramazza, 2011). This type of model predicts that meaningful words activate multimodal areas but not motor systems. A modification thereof (Mahon and Caramazza, 2008) posits interaction between multimodal and motor systems in the processing of action verbs under certain conditions (e.g. under heavy task constraints) and this view may also be applied to action-affording nouns. However, this approach does not predict or imply specific patterns of motor system activation brought about by different types of abstract words.

In case of such evidence, the proposal might be up for still another revision. In contrast, semantic grounding models imply storage of and access to semantic action features in the motor system (Pulvermüller, 2005), in addition to semantic mechanisms in perceptual and multimodal brain areas. They predict that semantic aspects of action-affording words (presented in passive tasks and out of contexts that could prime their semantic representations) are reflected by activity patterns in the sensorimotor system. In addition, grounded representations of abstract words (Barsalou *et al.*, 2005) predict sensorimotor activation to these items, although being potentially weaker than that to concrete ones (Pulvermüller, 2013a). In this perspective, differences in meaning between sub-types of abstract words may in part be manifest in different sensorimotor system activations.

The main result of the present study is that different sub-categories of concrete and abstract words activated the motor system in different ways, in part reflecting aspects of their meaning. We certainly do not claim that the motor system is the sole locus for differential semantic processing of those abstract and concrete subclasses, despite the absence of an interaction between ROIs and semantics in domain general semantic nodes. Still, as a main effect of Semantics but no significant interaction of this factor with the region of activation was present in classic semantic areas, this main effect could always be explained, in theory, by a modulation of general processing demands, rather than specific semantic feature processing. Instead, the motor systems revealed significantly different activation signatures for abstract mental and abstract emotion words, which cannot be explained by general activity modulation but strongly suggest semantically-specific activation signatures across areas. These results provide evidence that the motor system, possibly in addition to established semantic nodes, is specifically involved in the processing of abstract and concrete meaningful symbols.

Note that this interpretation does not rest on comparisons with our low level baseline condition (hashmarks), but rests on significant interactions seen for across word classes and cortical areas. Any baseline activation common to all compared conditions falls out of such analysis, as it represents a contrast orthogonal to the relevant comparison between semantic classes. Furthermore, we put a focus on the finding that well-matched words with clearly-defined and experimentally-confirmed semantic differences activated cortical regions *differentially*. This was the case for both the concrete action-affording items as well as for the words related to different types of abstract concepts. The current ROI results, from both, the group level ROIs approach, as well as the one that takes into account individual differences in motor localizations, showed activity dissociations in the hand or face sensorimotor areas to both concrete and of abstract words, with activation for abstract mental nouns being more prominent in the face-motor area than in the hand-motor area, while such a within motor system dissociation was not observed for abstract emotion words (see also Moseley *et al.*, 2012).

Our neuroimaging results are consistent with previous behavioural studies suggesting a degree of involvement of face/mouth muscles when processing abstract mental symbols (Borghi *et al.*, 2011; Granito *et al.*, 2015; Borghi and Zarcone, 2016). These current and previous findings are in line with grounded cognition accounts and in particular specific proposals about the neurobiological basis of symbolic meaning. They call for revisions of current amodal and hybrid models of semantic processing.

One more remark on hypothesis space: Our results are interpretable in case one accepts that grounded semantic models predict sensorimotor activation but "amodal" ones do not. Recent extreme widening of the hypothesis space of the latter now even include statements that abstract amodal meaning processing could be reflected in the motor system (Mahon and Hickok, 2016). We agree that such proposals cannot be falsified by specific sensorimotor processing in abstract semantic category processing. However, we are concerned that such extreme hypothesis space widening might result in generally unfalsifiable neurocognitive approaches to concepts. Therefore, we will not consider this proposal in light of our results.

Concrete word meaning and the motor system

Our results show differential activation of motor systems to action-affording nouns resembling those of previous studies, although they exhibit some specific differences. For example, the ROIs defined based on the group averages of the localizer tasks just led to near-significant activation dissociations manifest in a ROI by Semantics interaction, whereas previous work had shown a full double dissociation (Carota *et al.*, 2012). As our second analysis using ROIs defined separately for each individual confirmed the full significance of this critical interaction, a tentative conclusion is that inter-subject variability in cortical motor representations plays a significant role in studies on semantic and action processing, a suggestion also bolstered by a range of previous works (Aglioti *et al.*, 2008; Lyons *et al.*, 2009; Willems *et al.*, 2010; Hauk and Pulvermüller, 2011). Looking more closely at the result pattern obtained here, the two types of action-affording words elicited significantly different activation levels in the face motor region, but comparable motor activations in the hand ROI. However, we note that an enhanced tool word related motor activity was observed in precentral-/premotor areas (see Supplementary Material), just anterior to the finger-localizer defined ROI. We do not have an explanation for this slight anterior shift but suggest that it may be the reason why, in the present study, there was no activation difference in the dorsolateral hand motor ROI, as this ROI might have been set on pre- rather than primary dorsal motor areas. Nevertheless, the confirmation of the significant interaction between the factors Semantics and Motor ROIs (here based on a single rather than a double dissociation) is crucial for the conclusion on word type specific topographies of motor system activation. This interaction was not only significant in previous studies reporting specific motor activations to action verb categories (Pulvermüller *et al.*, 2001, 2005; Hauk *et al.*, 2004; Shtyrov *et al.*, 2014), it also emerged in a re-analysis of data from a study originally reporting a replication failure (Postle *et al.*, 2008; re-analysis report in Pulvermüller and Fadiga, 2016). Although we do not claim that the present results and in general all aspects of semantic motor system activations can be replicated in each study, there is by now a broad basis of evidence for semantically related modulation of neural activity in the motor system (Carota *et al.*, 2012; Kemmerer, 2015).

We also note that there are a range of other features that could account in part for differences between this and earlier studies. These features include the experimental language (here German, previously English, Italian, Finnish, Russian etc.) and the psycholinguistic properties of the words and sentences selected. For example, in the current study, we included relatively long (2-3 syllables) words many of which were morphologically complex. It has previously been found that addition of grammatical morphemes diminishes language-induced semantically-related brain activity, both in the motor system and in multimodal areas (Pulvermüller *et al.*, 2012).

Similar to the present study, the very recent fMRI study by Ghio and coworkers (2016) investigated the processing of different types of abstract sentences. These authors did not report any significant activation differences in sensorimotor areas. In their study, perisylvian cortical areas, but not modality-preferential pre- and post-central gyri, allowed for discrimination and classification of multi voxel patterns elicited by sentences with abstract mathematical, emotional and mental meaning. Note that these results are almost the opposite of our own findings, where (perisylvian) semantic areas did not produce somatotopic category differences, whereas sensorimotor systems did. One reason for the absence of successful classification outside the perisylvian cortex may lie in the fact that it is crucial to focus on regions where stimuli elicit reliable activity, in order to perform successful multivariate pattern analysis (MVPA) and discrimination. As our present results and those of others show, however, specific concrete and abstract symbol types may not consistently activate all motor regions. For example, our results indicate that abstract mental words do not activate dorsolateral sensorimotor cortex to a great extent and, according to Tschentscher *et al.* (2012), mathematical number words activate the dorsolateral hand motor cortex but not the ventral face areas. In addition, functional localizers of motor, affective, arithmetic and mental/cognitive functions were acquired from a different group of participants than the reading data in the approach by Ghio and coworkers (2016). Given the current findings on individual differences in localizations of motor representations, this procedure could have added noise to the analysis procedures. A further critical issue is their use of sentences in third person singular form, which is known to reduce motor activation relative to first person perspective (Brunyé *et al.*, 2009; Gianelli *et al.*, 2011). In sum, it does not seem surprising that Ghio *et al.* (2016) did not show sensorimotor discrimination of abstract or concrete language. In contrast, a recent study that applied MVPA on data for single word, rather than more complex sentence stimuli could indeed show left precentral motor areas, in concert with left inferior frontal and posterior middle temporal regions, to be involved in processing semantics similarity (in a distributional sense) among action-related words (Carota *et al.*, 2017).

Understanding abstract word comprehension in terms of neuronal assemblies

Grounded models of meaning in the brain propose that word meanings are represented in terms of contextual and situational sensorimotor information inherently linked with a word's usage. Therefore, in the typically developing language learner, the meaning of at least some concrete words such as 'hammer' would arise, at least in part, from sensorimotor information, including the visual, somatosensory and action-related features inherent to seeing, touching and using hammers. Such semantic grounding of at least a base vocabulary, or "grounding kernel", of concrete terms is in fact necessary to solve the so-called symbol grounding problem (Searle, 1980; Harnad, 1990) and would provide a necessary basis for subsequent semantic learning by (linguistic) context, which may lead to the "handing over" of grounded semantic features between signs (Cangelosi *et al.*, 2002; Pulvermüller, 2002; for review, see Kiefer and Pulvermüller, 2012).

A neurobiological mechanism for semantic grounding is provided by Hebbian learning (Hebb, 1949) of the correlation structure of words and actions/perceptions, leading to the formation of distributed semantic circuits (Pulvermüller 1999, 2013a; Pulvermüller and Fadiga, 2010). Likewise, the handing over of semantic features between circuits in contextual learning is equally explained by correlation learning. Learning of the correlation structure of words with other words and with sensorimotor semantic features jointly entails the formation of distributed circuits spread across perisylvian language areas, modality-specific sensorimotor areas where semantically relevant object and action information is present, and, in addition, connector hub areas linking together the latter two types of areas.

For abstract words which lack transparent external referents, but are used to speak about emotions or mental processes, such direct linking to modal experience appears to be impossible. Therefore, one could feel tempted to conclude that semantic grounding generally should fail to account for abstract words and concepts. If this position were true, the aforementioned symbol grounding problem would still apply to abstract words, even after grounding of concrete object related words has been achieved.

A tentative solution for the abstract symbol grounding problem has been offered by the formula that abstract meaning is grounded in emotion (Kousta *et al.*, 2011; Vigliocco *et al.*, 2014). However, a first principal problem of this approach lies in the fact that not all abstract terms semantically relate to emotion (see discussion below). A second difficulty arises because emotion does not offer a possibility for semantic grounding in the same sense as grounding can apply to actions and objects. No criteria exist for correct use of a word in the context of specific emotional states per se. The criteria for the presence of an emotion state come from the typical expression of the emotion in action (Wittgenstein, 1953; Moseley *et al.*, 2012). Specifically, Moseley *et al.* (2012) argued that contributions of face and hand motor areas to abstract emotion word processing are in line with the observation that the expression of emotions in the early infant’s learning of emotion words may be important for linking meaning and word form. These emotions are expressed primarily through face and hand movements (e.g. Ekman *et al.*, 1969; Aviezer *et al.*, 2008) and this could underlie the observed specific motor activations. Consistent with this position, the subset of abstract emotion words activated emotional-limbic areas, including anterior insula and anterior cingulate cortex, in conjunction with activity in the motor system, including hand and face-related precentral gyrus (Moseley *et al.*, 2012). The specific explanation for this observation is that emotions are typically expressed by face and arm movements and semantic grounding of (at least a base vocabulary of) abstract emotion terms occurs by way of the expression of emotion in action. The child’s emotion expression puts the adult in the position to select an appropriate emotion word so that emotion-semantic grounding can take place. A role for the motor systems is furthermore supported by work of Moseley and coworkers (2013; 2015), who demonstrated populations with a deficit in expressing emotion in action, in particular subjects with an autism spectrum condition, to activate motor systems in emotion and action language processing and likewise seem to have problems in speaking about emotion and in processing other action-related word. The comparable activation of face- and hand-related motor areas for abstract emotion words was first reported by Moseley *et al.* (2012) and replicated in the present study. Therefore, the lack of a dissociation between hand and face motor activations for abstract emotion words, seems to be consistent with this model of abstract semantic learning by emotion expression.

However, this emotion-centered explanation does not answer the question about the "meaning" of the face motor activation spot seen for abstract mental words, as it is not clear whether a similar point can be made for abstract mental words. The relevance of emotion is unclear for abstract mental words such as 'logic'. This is not to doubt that everyone may have non-semantic associations between the word 'logic' and either positive or negative experiences in their lives; however, there does not appear to be any systematic, that is, *semantic*, linkage characteristic between abstract mental words and emotional information in abstract language use that could be generalized across individuals. Whether one likes or dislikes logic is not a critical semantic feature of this word, and does not appear in typical explanations of its meaning. The small (if at all existent) role of emotion-semantics is reflected in semantic ratings (Figure 5.1), as not only the concreteness- and action-/sensory-relatedness, but also emotion-ratings were very low ($M < 2.3$, $SD = .8$, on a scale from 1-7) for abstract mental words. Therefore, the question arises why these non-emotional abstract symbols might activate part of the sensorimotor system, especially those areas related to face movement and articulator control.

A potential explanation can once again be built on Wittgenstein's established anti-solipsist argument: As you cannot a priori know which of your internal states relates to which to-be-learnt word, action-related behavioural criteria are necessary. In the aforementioned case of abstract emotion words, the expression of emotions using face and hands plays a primary role as behavioural criterion, which can explain previous (Moseley *et al.*, 2012) and current results on the comparable activation of the corresponding motor regions. Similarly, one may postulate that mental states such as 'thought', 'decision' or 'conclusion' can sometimes be 'read' from face (but not so likely hand) expressions, thus providing a putative semantic grounding explanation for mental words in face motor cortex. The bright look on the child's face may function as a cue for adults to initiate the mental word grounding of words such as 'thought', 'idea' and 'decision', and possibly other abstract mental words. Although this word-world grounding proposal may work for some mental words, it is difficult to see how our example 'logic', and likewise 'justice', 'truth' and 'syllogism', might fair if such a grounding in basic actions was the only pathway offered. For these abstract mental words, the criteria for appropriate application involve more complex social actions and interactions, including the expression of thoughts in verbal language as a key component. Grounding of a word like 'logic' is only possible if complex action patterns of drawing conclusions from premises, consistency testing and fallacy recognition are possible, as it is provided in social discourse or other forms of linguistic communicative context. A sequence of statements may provide typical grounding, such as ‘all men are mortal’, ‘Aristotle is a man’, ‘thus, Aristotle is mortal’. From individual statements, general verbal inference schemas (e.g. “all x are P”, “A is an x”, “thus A is P”) may be inferred. Thus, grounding in basic actions involving the face (e.g. thoughtful face) and grounding in verbal communication (e.g. syllogistic action sequence) provide two avenues for different kinds of abstract mental words.

As abstract mental words may be more difficult to relate to concrete objects and actions than concrete ones, it has been argued that grounding by verbal explanation might be especially relevant for this word category (see Borghi and Cimatti, 2009; Borghi and Binkofski, 2014). The word ‘logic’ is sometimes explained by a sentence such as "a tool to derive reasonable conclusions based on given information", and may be seen as a basis of semantic learning. Note that this view rests on the possibility to directly or indirectly ground other relevant terms in action and perception. Otherwise, definition circularity and Harnad's “merry-go-round” could not be avoided (Harnad, 1990; Cangelosi *et al.*, 2002). This approach (which can be seen as “grounded” but likewise fits into a symbolic explanatory strategy) states that semantic learning draws upon interlinking verbal material with other verbal material (“word-word”, rather than “word-world”, learning). From a brain perspective, language processing in perisylvian areas and articulatory cortex would be involved. A different mechanism of word-word correlation learning possibly underlying the observed grounding of abstract semantics in face motor systems can also be derived from knowledge about the co-occurrence properties of words (Landauer and Dumais, 1997; Andrews *et al.*, 2009). In essence, all four proposals that may be relevant for learning the meaning of abstract mental words – (1) grounding in basic actions, (2) grounding in verbal-communicative sequences, (3) semantic learning by verbal explanation and (4) distributional learning of word-word correlations from texts – are in line with the notion of neurobiological circuits underpinning these words interlinking with neurons in face-related and articulatory motor cortex, thus motivating the prediction that they activate face and articulatory motor cortex more than other motor fields. The verbal proposals (2) – (4) share the additional implication that perisylvian language regions, including inferior frontal and superior temporal cortex, share the activation pattern with articulatory motor cortex. As we found the latter combination of results – mental words strongly activating face/articulator (but not hand/arm) motor cortex and similar dynamics in inferior frontal and superior temporal cortex – we submit that our results are consistent with all the above proposals ((1) – (4)) but best fit models (2) - (4).

In summary, we believe that the topographically specificity of motor system activation brought about by abstract word processing can be explained by a grounding model, especially by considering the semantic criteria applied when teaching the naïve language learner such abstract concepts and words. In contrast, it is not obvious how an entirely disembodied amodal semantic system could explain the differential activations observed. Let us be very clear about what we mean here: We do not mean that such an amodal approach could not be extended by stipulating that "In passive reading, abstract emotion and mental words dynamically and flexibly activate, respectively, either hand and face motor cortex to similar degrees or face motor areas more strongly than hand motor ones". Such an ad hoc statement following recent data is possible within any theoretical framework, and therefore also in the amodal tradition. What we mean is that this approach – as it has been outlined so far in the literature – cannot, as to the best of our knowledge, provide an explanation for the unexpected results on category specific abstract word processing presented in this study.

Causal role of motor systems in semantic processing

In light of previous fMRI results on semantically grounded language processing, one could argue that any observed modal activation in precentral cortex could in fact only index a post-comprehension epiphenomenon that is not causally involved in the actual understanding process (see, for example, Mahon and Caramazza, 2008). However, in the domain of concrete action verbs, this view has been challenged by results of neurostimulation approaches (Pulvermüller *et al.*, 2005b; Willems *et al.*, 2011; see also Schomers *et al.*, 2015) and by lesion studies (Bak *et al.*, 2001, 2006; Neininger and Pulvermüller, 2001, 2003; Kemmerer *et al.*, 2012), demonstrating that motor areas indeed hold a causal role in language comprehension, at least for concrete action-related words. Although some have argued that much of this evidence is confounded by lexical variables, in particular the noun-verb difference, results of Chapter 3 demonstrated that minimal lesions just underlying the motor cortex's hand representation can lead to specific processing deficits for nouns related to objects with action affordances, whereas control noun processing was impaired less. This observation was replicated in larger patient samples in Chapter 4, though with reduced lesion focality. This is clear evidence for a causal role of motor systems for processing words semantically linked to action. Furthermore, results of Chapters 3 and 4 also provide some of the first lesion data for a necessary role of sensorimotor areas in the processing of abstract words. Selective deficits in processing abstract emotion nouns were present in a patient with a focal lesion of the left supplementary motor area

(SMA) in Chapter 3 and in a group of patient with predominantly dorsal and or ventral motor area lesions thus confirming a causal role of the motor system in the processing of abstract (emotional) words. We conclude that the activations of motor systems during word, phrase and sentence processing cannot all be epiphenomenal to semantics.

5.6 Conclusion

Passive reading of different types of abstract words was found to activate motor regions and differences in meaning between these abstract types was reflected in different topographies of motor system activation. Whereas abstract emotion words such as ‘love’ and ‘disgust’ activated hand and face motor cortex to similar degrees, mental non-emotional abstract words that relate to cognitive states and processes like ‘logic’ or ‘intellect’ elicited activation preferences in face over hand motor areas, especially when individual differences in the cortical localization of motor representations were taken into account. Similar differential semantic modulation of motor system activation was found for concrete food and tool words, which relate to objects affording hand and mouth actions. These results are consistent with brain language theories postulating semantic grounding of both concrete and abstract symbols in the sensorimotor system.

6. General Discussion

To begin the discussion of my dissertation I will first give a brief summary of the three research projects presented, before I turn to their implications for neural models of language in general and for cognitive and neural approaches towards an embodiment of abstract word semantics, in addition to their limitations and perspectives for future research.

6.1 Summary of Chapter 3

Previous evidence on an involvement of motor areas in the processing of abstract and concrete word semantics, the first dissertation project aimed at validating, whether this contribution was of mere epiphenomenal or of causal and functional nature. To do so, two neurological patients, HS and CA, were tested in a lexical decision paradigm, in addition to subtests of a standardized aphasia test battery. Results in both patients revealed no general aphasic symptoms but the lexical decision paradigm showed selectively pronounced accuracy deficits for specific semantic categories. For patient HS this was observed for tool words, which showed less accuracy than the other word categories applied, especially the non-action category of animal nouns. Investigations of HS' lesion revealed a very focal lesion (18 mm in diameter) caused by a mono-focal acute disseminated encephalomyelitis, situated directly in white matter inferior to left hand motor cortex. The finding of a focal lesion in hand motor systems resulting in specific processing impairments for hand action-related tool nouns directly supports a causal role of the motor system in processing concrete words even in an effector specific, somatotopic fashion. This observation thereby matches predictions of embodied and grounded approaches towards the neural bases of semantics (e.g. Pulvermüller, 1999, 2005; Pulvermüller and Fadiga, 2010). For patient CA a focal metastasis in the left supplementary motor area was associated with accuracy deficits across all categories applied, when compared to performance of healthy controls, but the deficit was selectively extreme for abstract emotion nouns. The SMA does not present a similar effector related somatotopy as the pre- and primary motor areas, as specific subparts of the SMA do not correspond to specific motor effectors (Roland *et al.*, 1980; Fried *et al.*, 1991). Therefore, contributions of different effectors to abstract emotion noun semantics could not be disentangled. Instead, this finding highlights a general functional role of the motor system which is not exclusive for concrete word semantics but can also be found for the processing of abstract terms. In contrast to previous patient approaches, performance was compared in each case between words of the same grammatical class that were in addition matched for a whole range of psycholinguistic variables on a lexical and sub-lexical variables, so that the observed category specific processing impairments cannot be interpreted in terms of deficits on these un-semantic psycholinguistic properties. Furthermore, the etiology and focality of lesions allows to infer an involvement of the motor system in semantic processing, even when classical perisylvian areas remained intact, which again has not been possible in the majority of earlier investigations of clinical populations.

6.2 Summary of Chapter 4

The fourth chapter aimed at expanding at the results of Chapter 3 by applying the same paradigm to a larger set of patients. Forty-one tumor patients were tested and screened for specific lesion characteristics, according to predictions derived from grounded models of semantic representations. To this end, a sample of patients (n = 8) was identified to have lesions in areas previously involved in tool-handling, i.e. in dorsal motor and anterior parietal cortex, but showed no lesion in perysilvian inferior frontal or temporal areas. Lexical decision results for this selection indicated accuracy for tool nouns to be specifically impaired in contrast to non-action control animals. Another grouping of patients, with fronto-parietal lesions involving dorsal and/or ventral motor areas, showed such a specific deficit for abstract emotion nouns. In contrast, a third group of patients, with lesions not prominent in motor areas but instead in inferior frontal and temporal regions revealed no such specific deficit in comparison to animal nouns, but comparable impairments across all categories. Furthermore, also a group of matched healthy controls did not show any hints of performance differences between semantic categories. This pattern of results directly corresponds to predictions of grounded theories on the neural bases of semantic representation, as specifically lesions in areas involved in hand actions and tool manipulations were associated with impairments of tool noun processing. Likewise, results indicate also a functional role of hand and face motor areas for the processing of abstract emotion words and directly replicate and extend on earlier fMRI findings on the same matter. Chapter 4 therefore allowed the conclusion that the observations in Chapter 3 on a necessary role of the motor system in general for processing of concrete and abstract word semantics are not based on extreme outlier cases, but can be replicated in larger patient samples. Hence, the motor system is of functional relevance for processing concrete and abstract words and its contribution can likely not be attributed to mere epiphenomena of semantic processing and representation.

6.3 Summary of Chapter 5

After Chapters 3 and 4 established a causal role of the motor system (SMA in Chapter 3, dorsal/ventral motor areas in Chapter 4) also for abstract emotion words, Chapter 5 aimed to investigate whether an involvement of the motor system in processing abstract semantics is exclusive to abstract emotion words or whether it can also be found for abstract words that do not contain emotional information and are hence even more disembodied, i.e. detached from transparent experiential referents. To test this, abstract mental words, like ‘thought’ or ‘logic’ were included in a stimulus list with a similar setup as in Chapters 3 and 4 and applied in a passive reading fMRI paradigm. Results indicate a specific contribution of face over hand motor areas in processing of abstract mental words, whereas processing of abstract emotion words did not result in activation differences between face and hand motor areas. Likewise, also food words were found to activate face motor areas more strongly than hand motor areas. Importantly, similar category specific dissociations were not observed between classical perisylvian inferior frontal and temporal areas. Findings on abstract mental nouns demonstrate that the motor system involvement does not occur as a function of emotional valence, but can occur even when neither transparent motor nor emotional semantics are present. These findings indicate that dissociations in motor system activity is not only informative about concrete, but also about abstract word semantics and thus demonstrate that grounding in the motor system occurs even for some of the most abstract or “disembodied” words.

6.4 Interpretability of results in semantic terms

In order to properly discuss the implications of the findings presented in Chapters 3-5 for theories on semantic representation and processing in the brain, it has to be assured that the observed effects are indeed informative about semantics. While this has been touched upon already in the individual chapters, I will briefly summarize the most important considerations here, before interpreting the results in the context of neural models and theories of semantics.

Although the lexical decision paradigm, as applied in applied in Chapters 3 and 4, has previously been shown to be sensitive to manipulation of semantic content (James, 1975; Chumbley and Balota, 1984; Kroll and Merves, 1986; Jin, 1990; Samson & Pillon, 2004), it does, at least technically speaking, not resemble a genuine semantic task. The main motivation for the choice of the LDT was that it conveniently allowed to test for the processing of a whole range of different semantic word classes, even abstract ones, in parallel. In contrast, alternative tasks which demand semantic processing directly, like semantic decision paradigms, would classically allow to test only for one or two semantic categories simultaneously. Here, participants are asked to evaluate via button press whether stimuli fit into predefined categories (e.g. “objects” or “animals”, see Moseley *et al.*, 2013) or show specific semantic features. In principle, semantic decision paradigms could be extended to test for more than two categories at once, by increasing the number of response keys, e.g. to four response keys corresponding to four individual semantic categories or properties. Such a setup would however come to the cost of increased complexity and executive or attention task demands, compared to only two response keys. This could prove to be challenging especially for patient populations and hence potentially yield increased error rates independent of semantic processing impairments. Alternatively, the semantic decision paradigm could also be conducted in separate sessions, with the task instructions and exact semantic judgements changing between sessions, in order to test multiple categories without the need of complex response key arrangement. This setup however would result in significantly prolonged overall experiment duration, which again would be not beneficial especially when neurological patients are considered as participants, as they may be more prone to exhaustion compared to healthy populations. Furthermore, separate semantic decision sessions could also result in the need to include a higher number of stimuli in the experiment which renders proper stimulus selection more challenging.

Although lexical decision tasks instructions ask participants to decide whether or not a word is meaningful, this task can be completed on the lexical level alone, without the need to access word specific semantics. In order to interpret results in the lexical decision tasks in terms of semantic processing, all words applied were closely matched on lexical and sublexical psycholinguistic features, so that any performance difference between semantic classes can at least not be attributed to differences in these non-semantic dimensions. One may argue however, that despite this close matching, results may still be confounded by other non-semantic psycholinguistic properties, that were not taken into account during stimulus matching, like phonological or morphological complexity features. With regards to the morphological properties, a post hoc comparison in the amount of morphological complex items (i.e. words containing either derivational or compound morphology) indeed revealed statistically significant differences between noun categories (see Fig. 8.1.1 in the Supplementary Material). At the same time, the critical comparisons of individual categories to the non-action control, animal noun category revealed no significant differences in morphological complexity. Results of contrast between individual noun categories and animal nouns, as presented in Chapter 3 and 4, are therefore not confounded by differences in morphological complexity. For phonological features (and respective phoneme-frequency measures), this comparison was not as easily available, as the dlex corpus unfortunately does not provide information on phonology. Another text corpus, popular in psycholinguistic literature, the CELEX (Baayen *et al.*, 1995) provides these measures, but unfortunately has only a very small size (6 million tokens for the German CELEX version, compared to 100 million tokens in the dlex) and is in addition quite dated, so that numerous types (and lemmas) were not represented in the corpus. Therefore, phonological properties had to be approximated by word-initial and general bi- and trigram measures on the orthographic dimension(see stimulus details of Chapters 3-5), thus leaving, at least strictly speaking, the possibility for phonological confounds between semantic noun categories.

When considering the relative performance difference between categories, as it has been done in both Chapters 3 and 4, also any influence of lesion induced non-linguistic basal cognitive deficits in domains relevant for unimpaired task performance, like impairment of executive function or attention, can be ruled out to underlie these selective deficits, as those basal cognitive functions would be assumed to affect performance for all words, irrespective of semantic categories. Furthermore, the sensitivity of lexical decision paradigms to semantic properties of words has successfully been shown already in earlier approaches (e.g. Chumbley and Balota, 1984; Neininger and Pulvermüller, 2001, 2003). In addition, fMRI results by Binder *et al.*, (2003) directly indicate that the LDT employs semantic processing of target words, rather than “pure”, a-semantic lexical access, as the number of orthographic neighbors, a purely lexical variable, was shown to not affect large parts of left hemispheric fMRI activation patterns for proper words, thus justifying the conclusion that these activations indeed reflect genuine semantic-, rather than basal lexical processing. It can therefore be concluded that observed category specific deficits presented in Chapters 3 and 4 indeed reflect impairments of semantic nature and hence point to a causal and necessary role of the respective lesioned areas for semantics.

For similar reasons the passive reading paradigm can likewise be interpreted to be informative about semantic processing. As long as the interpretation of results rests on comparisons between semantic classes, as presented in Chapter 5, any non-semantic, basal lexical and sub-lexical orthographic feature should not influence the observed effects, as those effects should cancel each other out in analysis, given the aforementioned close matching of semantic categories. However, as for the LDT, also for the reading paradigm potential phonological or morphological confounds should be considered in addition to the orthographic variables that guided stimulus selection. While phonological matching could not be tested, for the same reasons as described above for the LDT, post hoc analysis of morphological complexity revealed significant differences between categories (see Fig. 8.2.4 in the Supplementary Material of Chapter 5). However, critical comparisons, of abstract emotion vs. abstract mental and food vs. tool nouns, revealed no significant differences in morphological complexity. Results of contrast within abstract or concrete noun categories, as presented in Chapter 5, are therefore not confounded by differences in morphological complexity.

As a further remark, differences in paradigms and stimuli should be considered when comparing results of the patient approaches in Chapters 3 and 4 to those of the fMRI approach in Chapter 5. Although both studies were designed with similar intend and show some overlap of stimuli applied, the words used in the fMRI paradigm were considerably longer and more complex. Whereas stimuli of Chapters 3 and 4 had a maximum syllable length of two syllables, stimuli of Chapter 5 were up to three syllables long. This was necessary due to the inclusion of abstract mental words in the stimulus set, which tended to be longer than the previous stimulus selections. As a consequence, also the contents of those other semantic categories had to be altered, in order to still allow for psycholinguistic matching between all categories. Thus, results of the patient approaches (Chapters 3 and 4) and the fMRI Study of Chapter 5 cannot be compared directly.

6.5 Implications on modality-preferential semantic representations of concrete and abstract words

Results of all three studies presented in detail in this dissertation are in line with the notion of modal, rather than exclusively amodal semantic representations, realized, at least in part, in modality specific sensorimotor systems of the brain.

Reports of processing accuracy for tool nouns being impaired after lesions in areas related to tool usage (dorsal hand motor areas and parts of the parietal tool network) in Chapters 3 and 4 indicate a grounding of concrete word semantics in the sensorimotor system. This position sees further support in findings of fMRI dissociations in face and hand action-related motor areas when processing food and tool nouns (Chapter 5), although here a mere single dissociation was reported whereas earlier approaches revealed a full double dissociation (see Chapter 5 and discussion below). Critically the results from the patient investigation directly point to a causal and necessary, rather than a mere epiphenomenal contribution (as argued by Mahon and Caramazza, 2008; Mahon 2015) of these modality-preferential areas to semantics.

Such an involvement of the sensorimotor system was also reported for abstract words previously thought to be entirely disembodied and detached from sensorimotor information (Mahon and Caramazza, 2008; Dove, 2016). Here, lesions in parts of the motor system, in particular in the supplementary motor area (see Chapter 3), as well as in dorsal and ventral motor systems (see Chapter 4), including face and hand motor areas, were indicated to be necessary for processing abstract emotion words. An involvement of hand and face motor systems in processing abstract emotion semantics is also in line with earlier fMRI observations on abstract emotion word processing (Moseley *et al.*, 2012). Chapter 5 replicated those observations in so far, as hand and face motor systems were shown to contribute equally to abstract emotion word processing (see Discussion of Chapter 5), but contrary to results of Chapter 3 a prominent role of the SMA was not indicated. Reasons for this difference in results may be seen in differences in the stimuli applied in the two paradigms (see discussion above). Furthermore, Chapter 5 demonstrates an involvement of motor systems to be not restricted to abstract emotion words, but motor activation topographies to be also informative about processing abstract mental words, which do not have transparent emotional semantics. Thus embodied or grounded approaches towards the neural underpinnings of semantics are therefore likely not restricted in their scope to the concrete domain, as argued previously (Mahon and Caramazza, 2008), but can be applied also to the processing and representation of abstract words.

Importantly, all of those findings do not necessarily indicate semantic processing to be entirely modality specific and correspondingly realized in modality-preferential brain areas only, but are compatible with accounts that assume neural circuits carrying word semantics to be distributed over perisylvian inferior-frontal and temporal regions in addition to extrasylvian motor areas. Such a position has recently seen criticism by Mahon (2015) as he argues that any embodied account which allows the involvement of amodal/multi modal processing (described as “weak” embodied approaches) would be indistinguishable from disembodied accounts. In his view, conceptual processing would lead to sensory/motor activation in a cascading fashion, from the actual conceptual representation to modality specific information, but this activation would not be constitutive for semantic representation. To put it differently, the representational format of a words meaning could be amodal, even if its processing leads to modality specific systems, which may become involved merely indirectly (for a further iteration of this position see Mahon and Hickok, 2016). However, this interpretation neglects a crucial difference between this grounding by interaction (Mahon & Caramazza, 2008) and action-perception cell assembly proposals: the functional role of these modality specific systems. Whereas the former cannot attribute a functional role to these areas, that is if modality specific information is indeed just a by-product but not constitutive for the actual concepts, the latter directly predicts such a causal involvement. As the focal lesions of patients in Chapter 3 and 4 indeed indicate a necessary and functional role of the motor systems for semantic processing, the current findings cannot be aligned with and thus falsify the proposals brought forward by Mahon and Caramazza (2008) and Mahon (2015).

On a related note, it should be noted that those statements of Mahon (2015) are also problematic on a theoretical level alone already (and likewise similar positions by Hickok, 2014), as pointed out by Pulvermüller (2017). Assuming that modality-preferential representations might be associated to a words meaning but not part of the actual semantics appears to be problematic, as it provokes the question what mechanisms might be left once learning by association (and disassociation) are excluded from models on the learning and usage of a words meaning. Likewise Pulvermüller (2013b, 2017) points out that it is illogical and unjustified, to attribute the locus of semantics exclusively in an amodal semantic system, once it has been acknowledged that this system interacts and exchanges genuine semantic information with modality specific systems.

6.6 Implications for grounded approaches towards abstract word semantics

The current findings on a functional role of hand and face motor areas for abstract emotion words and a grounding of abstract mental terms in face motor systems is not only of relevance for the general differentiation of embodied and disembodied approaches towards the neural underpinnings of semantics, but also for theories that targeted abstract word semantics specifically. In the following paragraphs I will briefly discuss the implications of the findings reported in my dissertation projects for theories on abstract word representation and processing.

Relation to classical approaches of dual coding and context availability

Like the previous findings on a grounding of concrete concepts summarized in Chapter 1, the current results on abstract concepts support neither classical dual coding, nor the context availability theory. While the principle idea of greater involvement of linguistic information may very well still hold true for abstract words (more on this issue in Chapter 5), critical predictions of either model are not met by the findings of my three dissertation projects. For the dual coding model, involvement of “image” based modality-preferential systems was not predicted for abstract concepts and furthermore not predicted to occur in the right, but not on the left hemisphere. Instead, the left hemisphere was assumed to take a primary role for representation in “verbal” code, for both concrete and abstract words, whereas any “imagistic” content, available predominantly for concrete words, was expected to be represented in the right hemisphere. Furthermore, the observed functional involvement of motor areas in semantic processing (of both, abstract and concrete words) was in general not predicted in the dual coding model, as its predictions were only made on the differential contributions of the left and right hemispheres, a level of granularity which appears to be insufficient in light of the current findings presented in Chapters 3-5.

With regards to the context availability hypothesis, it has to be noted that it does not make any specific predictions concerning the neural bases of abstract or concrete words semantics. Therefore, strictly speaking, the findings of Chapters 3-5 cannot be applied directly in order to discuss this hypothesis. One of the central predictions of the context availability approach is that abstract and concrete words do not differ in their representational format. If one assumes the neural bases of semantic representations to be, at least to some degree, also informative for their representational format, the overall similarity in activation patterns for concrete food and abstract mental nouns, as presented in Chapter 5, could be interpreted in favor of the context availability hypothesis. At the same time, a further critical prediction of the context availability hypothesis is that this unitary code, shared between concrete and abstract word semantics, is of “verbal” nature, independent from modality specific information. Applying the same rationale as described above, the involvement and even necessary role of modality-preferential motor systems in processing word semantics (both, abstract and concrete), as indicated by results of Chapters 3-5, appears to be conflicting with such a notion of an amodal “verbal” code. Furthermore, post hoc analysis on the context availability of the applied stimuli revealed concrete words to show a higher context availability on average than their abstract counterparts in Chapter 5 (Abstract nouns: Context availability $M = 4.24$, $S.E. = .11$; concrete nouns: Context availability $M = 6.14$, $S.E. = .06.$, $p < .001$). However, this difference in context availability scores was not reflected in results of Chapter 5, as food and abstract mental nouns showed comparable activity patterns, despite food nouns showing a higher context availability than abstract mental nouns (Context availability abstract words: $M = 3.88$, $S.E. = .12$; food nouns: $M = 6.07$, $S.E. = .08.$, $p < .001$).

Hence, neither of these two classical models appear to explain or could be aligned with the findings of Chapters 3-5 on the neural underpinnings of either abstract or concrete words.

Relation to emotion as a basis for grounding of abstract semantics

The current results do not provide evidence for the hypothesis that emotional content provides a general basis for a grounding of abstract word semantics (Kousta *et al.*, 2011; Vigliocco *et al.*, 2014). While results of Kousta and coworkers (2011) indicate an inherent emotionality of abstract words in general, this results might be based on either a sampling bias or on a general bias towards abstract emotion words in the lexicon of abstract terms. At least it appears to be problematic to assume emotion as meaning defining criterion for abstract words that do not have transparent emotional semantics. One instance of such abstract words are abstract mental nouns, as presented in Chapter 5. This does not mean that the meaning of words like ‘thought’ or ‘logic’ cannot be liked or disliked by some individuals and hence be associated to affective processing, but emotionality does not appear to be of systematic, constitutive relevance for their meaning in language usage across individuals. This becomes apparent when considering the semantic rating results on emotion relatedness for abstract mental words, which only revealed very low associations to emotions ($M < 2.3$, $SD = .8$, on a scale from 1-7; see Chapter 5, Fig. 5.1).

Vigliocco *et al.* (2014) identified the rostral anterior cingulate cortex, which has been previously associated with emotion processing, to show stronger activation for abstract than concrete words and to have its activity modulated as a function of absolute emotional valence (i.e. independent of positive-negative polarity) especially for abstract words. In contrast, fMRI results of Chapter 5, did not reveal neither abstract emotional, nor mental words to be characterized by pronounced activations in rostral anterior cingulate cortex and also limbic areas in general were not revealed to be involved in processing abstract word semantics. Instead, distinct patterns in motor activation characterized abstract emotion and non-emotional, abstract mental subclasses. It should be noted however that unlike the approach by Vigliocco *et al.* (2014), the fMRI study presented in Chapter 5 did not attempt to investigate processing *differences* between abstract and concrete stimuli, but rather focused on their possible representational commonalities. In addition Vigliocco *et al.* (2014) treated abstract (and also concrete) words as monolithic categories in stimulus selection and analysis, whereas the fMRI approach of Chapter 5 was concerned with activation dissociations between different subclasses within the abstract or concrete domain. Furthermore, emotionality was defined differently in both approaches: whereas Vigliocco *et al.* (2014) focused on absolute valence for analysis, Chapter 5 merely included high emotion relatedness as one key criterion for abstract emotion stimuli selection. Therefore, a clear comparison of the current and their previous findings (Vigliocco *et al.*, 2014) is difficult to achieve from a methods and analysis perspective. Still, according to predictions of the original proposal, neural systems involved in processing emotions would be engaged automatically when processing abstract word semantics. This prediction however is not met by results of Chapter 5. The presentation of abstract emotion words elicited activity (though on a more lenient statistical threshold), also in the insula, which has previously been shown to be involved in emotional processing (for a recent review see Gasquoine, 2014), but such a contribution of emotion systems was not observed for abstract mental words. A grounding of abstract semantics in emotional/affective experience and corresponding neural substrates therefore appears to occur not for all kinds of abstract words, contrary to predictions of Vigliocco *et al.* (2009).

Relation to Conceptual Metaphor Theory

Strictly speaking, my three dissertation projects are entirely silent on the issue whether or not conceptual metaphors are relevant for processing abstract terms, as any possibly underlying metaphorical expressions of the abstract emotion and abstract mental terms were not investigated directly in neither project. Furthermore, the conceptual metaphor theory is a cognitive rather than a neural theory on (abstract) word semantics. While this theory predicts abstract meaning to be carried by a mapping from an (abstract) target domain into concrete source domains via usage of metaphorical expressions (e.g. “boiling with anger”, see Chapter 1), no specific predictions regarding the neural underpinnings of those metaphorical mappings (and expressions) are proposed (Lakoff and Johnson, 1980).

However, it could be argued that the results on the face motor systems’ involvement in processing abstract emotion and non-emotional abstract mental semantics could be, at least in part, the result of a grounding of their meaning via metaphorical expressions. Using metaphorical pattern analysis on a sample of 1000 occurrences of the abstract emotion word ‘joy’ in the British National Corpus, Stefanowitsch (2006) revealed for example 906 instances of metaphorical expressions. From those, 709 were characterized as event structure metaphors, which (among others) include actions and related changes of locations or objects (Lakoff, 1993). How many of these metaphors indeed revolve around actions (e.g. “to give joy to someone”, “to seek out joy”; see Stefanowitsch, 2004), however was not further analyzed, so it is difficult to attribute any specific importance to metaphorical mappings into the action domain for ‘joy’, in order to align this approach with the results of my dissertation projects. Independent of the exact nature of the underlying metaphorical mappings, i.e. whether or not there are specific actions or motor effectors an abstract word meaning is being mapped to, a grounding in face motor system could also be based on the verbal format of the corresponding metaphorical expressions, independent of the exact concrete source domain of the underlying metaphorical mapping. At the same time, current results on abstract emotion words demonstrate that a verbal format of metaphorical expressions alone can likely not account for all aspects of grounding abstract semantics, as hand and face motor areas were indicated to contribute to a similar degree to abstract emotion semantics (Chapter 5), or could not be disentangled from another (Chapter 4). In order to align this observation to the content of metaphorical mappings one would need to investigate the exact domains, abstract words are being mapped to and determine how many of those indeed relate to hand actions (e.g. by a semantic ratings of metaphorical expressions revealed in metaphorical pattern analysis). This endeavor however, is beyond the scope of my thesis, but could be relevant for future research. Even if those effector specific mappings were indeed observed, criticism from a developmental perspective brought forward by Dove (2009) against the conceptual metaphor theory would still apply. Here Dove points out that in development knowledge of metaphors occurs rather late in children (Winner *et al.*, 1976; Ackerman, 1982), after the onset of first abstract word usage and thus rendering it unlikely that metaphorical expressions (and the related metaphorical mappings) are indeed necessary to represent abstract semantics (see also Borghi *et al.*, 2017). Therefore, if at all, conceptual metaphors may be seen as one complementary (and not exhaustive) mechanism to account for a grounding of abstract word semantics.

Relation to multiple representation approaches

The finding of modality-preferential motor contributions for both abstract mental and abstract emotion words in Chapters 3-5 can in principle be aligned with multiple representation approaches of (abstract) word meaning. This applies in part even to those instances which assume entirely amodal representations on the linguistic level, like the representational pluralism approach by Dove (2011), as this approach still leaves room for representations on an action-related or perceptual level even for abstract words. The observed differential contributions of representations related to hand and face actions however would not be predicted by this position. Results from Chapter 5 on the involvement of face motor systems to be specifically informative about abstract mental words (in contrast to hand motor area contributions) appear to be very well aligned with predictions by the Words-as-Tools approach (Borghi and Cimatti, 2009; Borghi and Binkofski, 2014). Here, information derived from linguistic context relevant for learning (including verbal explanations of an abstract word's meaning) and understanding the meaning of an abstract word is assumed to be reflected in face motor contributions to semantics, which would predict a role for face motor areas for the processing of abstract words. At the same time, the equal contribution of hand- and face-related motor areas would not correspond to predictions of the Words-as-Tools approach, as hand motor contributions are not predicted following an alleged stronger reliance of abstract words on linguistic representations. Again, as in the last previous paragraphs above, this approach therefore can only account for parts of the current results, but appears to be ill suited as a general mechanism for grounding abstract words in general.

Relation to grounding of abstract semantics in distributed neural cell assemblies

As mentioned already in the Discussions of Chapters 3-5, the necessity of fronto-parietal cortex, including motor areas, for processing abstract emotion words, like it is demonstrated in the patient investigations of Chapter 3 and 4, as well as the differential contributions of arm and face motor systems to subclasses of abstract emotion and abstract mental terms in the fMRI results of Chapter 5, can very well be accounted for in terms of neural cell assembly approaches. To summarize, direct, but also indirect grounding for abstract words in action could be achieved by Hebbian learning derived cell assemblies, connecting classical perisylvian language areas in inferior temporal and superior temporal cortex to extrasylvian affective and sensorimotor systems, including precentral motor areas. For abstract emotion word semantics a direct grounding in face and hand motor systems appears to be possible, given that actions with both effectors are used to express internal emotional states and infer them in others (e.g. Ekman *et al.*, 1969; Aviezer *et al.,* 2008). Correspondingly, the underlying neural cell assemblies of abstract emotion words would be predicted to cover perisylvian cortex and to reach into ventral face and dorsal hand-related motor areas in precentral and central cortex. In addition to results by Moseley *et al.* (2012), this view sees support in results of Chapter 4, where lesions including dorsal and/or ventral motor areas were reported to be related to accuracy deficits in a lexical decision task. Please note that results of Chapter 3 are silent on the issue whether abstract emotion semantics are processed specifically in hand/face motor systems, as the SMA, which was lesioned in patient CA and associated with specifically pronounced abstract emotion word processing deficits, is involved in motor processing in general but lacking a motor effector specific somatotopy (Roland *et al.*, 1980; Fried *et al.*, 1991). Instead, this finding supports a general functional involvement of the motor system in processing abstract emotion semantics, but it can still be aligned with the above notion of distributed neural cell assemblies as the neural bases for word semantics. For abstract mental words, such a direct grounding in action representations and related neural systems might be possible for some cases (see Discussion of Chapter 5), but indirect grounding, via linguistic input alone, may be of general relevance across different abstract mental words. Here, a words meaning is not learned and represented by relating it to correlated sensorimotor input directly, but indirectly via the proxy of other words and their respective sensorimotor referents, a process described as “symbolic theft” by some authors (Cangelosi *et al.*, 2000; Cangelosi and Harnad, 2001) or as “parasitic” semantic learning by others (Pulvermüller, 2002). Please note that this process is not exclusive for abstract words but can occur for concrete words as well. In cell assembly terms a handing over of sensorimotor referents between linguistic signs could be realized via correlations between abstract and previously grounded words and their entire cell assemblies, not only including their word form but also their sensorimotor components. This way a cell assembly is formed that connects the word form representation of an abstract word, realized in perisylvian regions, to those extrasylvian modality-preferential areas holding the directly grounded meanings of related words. This grounding can, at least in theory, be achieved via a whole series of indirect grounding iterations. It does not matter, whether words that provide this proxy are derived from explicit (verbal) explanations of an abstract word’s meaning or whether they are derived from implicit, distributional co-occurrence properties, as the cell assemblies could account for both mechanisms (Pulvermüller, 2002; 2017). Those indirect sensorimotor referents are not predicted to be exclusively found in the face motor domain, but in case this indirect learning occurs in social discourse and spoken language, an involvement for articulator motor systems would be predicted by this account, corresponding to the observations on abstract mental words in Chapter 5. It is important to point out though that this mechanism is not exclusive for abstract mental nouns, but would be assumed to occur for all kinds of abstract words that are characterized by meaning learning and usage in linguistic contexts. However, in any case this mechanism is assumed to be potentially complementary to other means of grounding in direct sensorimotor or introspective experience. In contrast to alternative approaches mentioned above (Borghi and Cimatti, 2009; Vigliocco *et al.*, 2009), Hebbian learning derived neural action perception cell assemblies do not predict any particular modality-preferential system to be relevant for all kinds of abstract words, like emotional (Vigliocco *et al.*, 2009) or face motor systems (Borghi and Cimatti, 2009). Instead, these cell assemblies provide a general mechanism to ground different kinds of abstract word semantics differentially into sensorimotor, affective or introspective systems. The validity for such a position that takes into account specific semantic of abstract words is reflected in the observed category specificity in motor system contributions to different abstract subclasses of Chapter 5.

6.7 Implications for other general models on the neural bases of language and semantics

In addition to the overall issue, whether semantic representation is grounded in modality specific information or entirely amodal instead, the current results can also provide implications for neurolinguistic models alternative to the cell assembly account presented here.

Relation to Hickok and Poeppel's (2007) dual-stream model of the functional anatomy of language.

One of the arguably most influential current models on the neural bases of language processing is the dual-stream model proposed by Hickok and Poeppel (2007). In a nutshell, this model proposes language processing to be split up in a ventral stream, responsible for speech recognition and comprehension of semantics and a dorsal stream involved in auditory-motor integration, speech segmentation and verbal working memory. The dorsal stream is thought to cover the parieto-temporal boundary of the sylvian fissure and the inferior frontal, as well as dorsal premotor cortex, whereas the ventral stream is assumed to spread over posterior medial and inferior portions of the temporal cortex in addition to anterior medial and inferior temporal lobe. Posterior medial and inferior temporal lobe are believed to serve as a “lexical interface” which binds (phonological) word forms to their meaning. The locations of the actual semantic representations are not specified further but just characterized as “widely distributed”. This latter assumption leaves the semantic category specific deficits after focal motor area lesions (Chapter 3) or general fronto-parietal lesion patterns (Chapter 4) and the category specific dissociations between dorsal hand and ventral face motor areas for abstract and concrete words (Chapter 5) entirely unexplained. Furthermore, the observations indicating not only a general involvement, but also a necessary role of dorsal (pre-) motor areas for semantics, whereas the dual stream model would predict these regions to be explicitly not involved in semantic processing. Furthermore, the inferior-frontal activation across categories in Chapter 5 is at least unlikely to be explained in terms of either auditory-motor integration or verbal working memory, as these observations were made in a passive reading paradigm, not encouraging specific access of verbal working memory, with the explicit instruction to avoid articulator movements. Therefore, this model can be seen to be in stark contrast to the results of all three of my dissertation projects.

Relation to Hub-and-spoke models

One model of semantic representation coming from grounded or embodied cognition background is the Hub-and-spoke model (Patterson *et al.*, 2007). Here, the neural bases of semantics are seen in modality-preferential sensory and motor areas and their interconnections, with word forms (or names) being stored in perisylvian areas. The critical claim of this model however is that the contribution of those "spokes" are not sufficient, but a single central and amodal semantic hub is necessary in order to process semantic similarity across words situated in the anterior temporal lobes. Two of those spokes, situated in motor- and anterior parietal cortex, are believed to be involved in handling action-related semantics. The proposed location of these spokes appears to align with results of Chapter 4, as fronto-parietal lesions were shown to affect processing of (hand-) action-related nouns. At the same time however, the observed dissociations between different word semantics in hand and face motor systems, as demonstrated by results of Chapters 3-5 cannot be explained by the original version of the Hub-and-spoke model (Patterson *et al.*, 2007), as the proposed action spokes are merely assumed to be involved in processing action-related word semantics in general, but any further effector specific granularity is missing. In addition, the critical role of the anterior temporal lobe could not be revealed in either of the dissertation projects. For the patient approaches in Chapters 3 and 4, it has to be noted that lesion coverage in the left anterior temporal lobe was rather weak, so that it is difficult to derive strong statements on the existence or absence of a semantic hub in this area. In Chapter 5 the anterior temporal lobe was not reported to be activated across all semantic categories, contrary to predictions of the Hub-and-spoke model. It should be noted though, that the fMRI study of Chapter 5 and its imaging parameters were not optimized for measurement of this area, potentially resulting in signal loss (Ojemann *et al.*, 1997; Devlin *et al.*, 2000). This renders it difficult to properly evaluate the role of the anterior temporal lobe for semantics.

Recent (computational) extensions of the Hub-and-spoke model (Chen *et al.*, 2017) are even more difficult to align with the current results of Chapters 3-5. While maintaining the notion of an amodal hub in the anterior temporal poles, Chen and coworkers (2017) assume action and praxis-related semantics to be represented in superior and inferior parietal areas only. This notion contrasts with results on patient HS in Chapter 3, which demonstrated a specific processing deficit for tool words following a focal lesion affecting hand motor areas. Also results of Chapter 4 contradict this position, as a tool noun processing deficit was not only associated with parietal, but also with frontal motor cortex lesions in the respective patient sample. In addition, also the fMRI dissociations reported in Chapter 5 to occur between hand and face motor areas within concrete (and abstract) categories cannot be aligned with the model by Chen and colleagues (2017).

Relation to Binder and Desai (2012)

In line with embodied or grounded proposals of semantics, and also with parallels to the Hub-and-spoke account mentioned above, Binder and Desai (2012) assume modality specific representation, but specifically emphasize also the need of supermodal representations in their neuroanatomical model of semantic processing. Modality specific nodes or components are believed to be situated in modality-preferential systems, like motor, auditory, visual and emotion processing related areas. Supramodal information in turn is assumed to be represented in modal convergence zones in inferior parietal cortex, as well as in ventral and lateral temporal lobe. The role of those convergence zones is hypothesized to provide means for binding representations from different modality specific systems, like for example the haptic, visual, auditory and motor information related to the meaning of ‘hammer’. In that respect this model appears to be quite similar to the action-perception-cell assembly model, as both models assume modality specific and modality independent components of semantics. However, critical differences can be seen in the role and location of the supramodal convergence zones, or network “hubs”. The cell assembly model assumes the modality unspecific representations in terms of the word form in perisylvian inferior frontal and superior temporal areas, whereas the model of Binder and Desai ascribe top down semantic content selection processes to the inferior frontal gyrus instead (specifically to pars orbitalis and pars triangularis). With regards to the inferior frontal gyrus this position is challenged by the observations of Chapter 5, as inferior frontal activation was observed across semantic categories in an entirely passive reading paradigm, thus rendering no need for any specific strategy of semantic access. The same results did also not reveal inferior parietal areas to be of particular relevance across categories, whereas Binder and Desai (2012) would predict this area to hold a supramodal convergence zone. In their defense it should be noted that they leave the exact nature of modalities that are combined in each convergence zone unspecified and according to their definition it would already be sufficient in case merely two modality specific types of representations would be combined with another in order to treat the respective brain area as a convergence zone. Therefore it could be, from their perspective, that the word categories applied in Chapter 5 just did not engage those modalities consistently that are merged together in the inferior parietal convergence zone.

6.8 Clinical implications and translational perspectives

An involvement of sensory and motor systems in language processing, especially if it is of causal nature (as indicated by results of Chapters 3 and 4), is not only of importance with regard to general theories of language comprehension in a purely academic context, but furthermore provide implications also for putative clinical translation. Given that neuronal cell assemblies storing form and meaning of words are widely distributed over the cortex and even involve neurons in the motor system, these widely distributed circuits would potentially be more resistant to focal lesions within the limits of the perisylvian “language cortex” compared with more local networks (Pulvermüller, 1999; Pulvermüller & Fadiga, 2010). The reason for this robustness is that the remaining neurons outside perisylvian space may still support distributed circuit function even if part of the circuit is damaged. In contrast, the classic perspective seeing language processing as confined to perisylvian regions would suggest fatal lesion of any language circuits restricted to these regions after substantial lesions therein. Furthermore, and over and above general robustness of language circuits, the wider distributions with semantic circuit parts even extending into motor areas predicts better potential for language reorganization. After perisylvian damage, the spared extrasylvian neurons of the partly damaged circuits could become the subject of synaptic strengthening if intensive language therapy is applied to encourage Hebbian strengthening of synapses. Some studies of cortical reorganization during language therapy in chronic post-stroke aphasia encourage this perspective (Pulvermüller *et al.*, 2005c; Saur *et al.*, 2006; Berthier and Pulvermüller, 2011; Barbancho *et al.*, 2015; Crinion and Leff, 2015).

There is one practical suggestion coming from the proof of motor systems being directly relevant for language processing: If neurons in motor systems indeed participate in the cortical circuits underlying language processing, the re-activation of motor programs during overt action may potentially benefit language rehabilitation. Therefore, language therapy may become especially effective in case of extra motor activity, as it is induced if words and sentences are used in the context of communicative actions. Consider the case of making a request, where the requesting person expects the addressee to hand over an object and is prepared to take the handed-over item. A communicative task such as requesting thus likely activates language and motor systems together. The current findings of differential involvement of motor regions in semantic processing, even of abstract words of different kinds, suggests and reinforce new directions for language therapies, whereby intensive therapies are administered in communicative action contexts such as request interactions. Some indication that this is indeed correct comes from experimental therapy research using randomized controlled trials (RCTs). In the domain of therapy of chronic post stroke aphasia therapy, such communicative action embedded therapy methods, including CIAT (Pulvermüller *et al.*, 2001) and ILAT (Difrancesco *et al.*, 2012), were shown to be successful, even in chronic patients several years after onset of their neurological disease. A recent RCT study could even show that, given the same high intensity of therapy is delivered, action-embedded communicative therapy yields better outcomes than classic language therapy methods focusing on verbal utterance training without communicative or action embedding (Stahl *et al.*, 2016).

The involvement of the motor system in language comprehension, as shown in the current as well as in several aforementioned pre-existing neuroimaging, behavioural, neurostimulation and lesion results, could in part provide an explanation for the superiority of action oriented language therapies and hence justify further efforts to extend and improve these therapeutic methods, also strengthening the neuroscience foundation of these methods (Berthier and Pulvermüller, 2011; Pulvermüller *et al.*, 2016). With the current finding of motor system activation being not only informative about the processing of concrete, but also abstract concepts, the potential scope of action-embedded language therapies may increase significantly.

6.9 Limitations and perspectives for future research

Whereas the current findings already offer important implications in favor of grounded approaches of semantics, they also come with certain limitations that leave room for improvement and could motivate future research on the same matter.

Chapters 3 and 4 presented evidence on the causal involvement of hand motor areas for tool noun processing with high spatial specificity of lesions in the patients investigated. However, such evidence could not be collected for the other action-related concrete category applied, i.e. food nouns, which are hypothesized to show, among others, specific contributions of face motor areas to their semantics. The reason for this lies in the lack of patients with lesion profiles of focal lesions in ventral motor or premotor areas, while having perisylvian inferior frontal and temporal areas unimpaired. Therefore, patients of this lesion profile would be of special interest for future approaches, as this would potentially allow to directly reveal a double dissociation between hand and face action affording words within the motor system in a somatotopic fashion, rather than the mere single dissociation in dorsal fronto-parietal areas, as present in the current patient results of Chapters 3 and 4. However, given the close proximity of ventral face motor and inferior frontal areas, it might need significant effort to find a sufficient number of patients with very focal lesions fulfilling these criteria.

A further approach concerning studies on clinical populations would be to investigate brain areas that hold a specific causal and necessary role in a more unconstrained and exploratory fashion, using voxel-wise lesion symptom mapping to compare semantic processing performance between patients with and without a lesion for each voxel separately (Bates *et al.*, 2003). This analysis is less restrictive in patient selection than the grouping approach presented in Chapter 4. This procedure has the advantage of a potential increase in statistical power for individual voxels (compared to the grouping approach) as fewer patients have to be excluded due to their lesion profiles, potentially resulting in a larger sample size for some voxels. Here, initial analyses using this approach on the results from the same paradigm as in Chapters 3 and 4 appear to support the general notion of causal and necessary contributions of motor systems (Dreyer and Pulvermüller, 2017) to abstract and concrete semantics. However, it should be noted that also for voxel based lesion symptom mappings the exact individual lesion patterns in analysis determine the spatial resolution of inferences that can be drawn on the causal involvement on brain areas in language (or general cognitive) processes (Kimberg *et al.*, 2007; Rorden *et al.*, 2009). Therefore also for this approach patients with focal lesions in either face or hand motor areas would be of special interest.

Alternatively it could also be fruitful to investigate the causal relation of motor systems and specific semantic processing from the reverse direction, by testing participants with a high level of training of motor function and respective facilitation of motor system performance, like professional athletes, rather than investigating patients with motor deficits or motor cortex lesions. The expected effects would be like the ones observed in Chapters 3 and 4, but reversed, i.e. specific performance improvements rather than impairments when compared to a normal control populations, which lacks such motor proficiency. This rationale has been applied previously, by investigating action language processing in professional hockey players with fMRI and comparing results to those of hockey novices (Beilock *et al.*, 2008). Here, results indicated increased involvement of dorsal premotor areas for hockey players and also improved action language comprehension on a behavioural level compared to the novice control group.

In order to extend on this issue and to make inferences on a semantic somatotopy of motor system contribution in this scenario, one would need to investigate athletes proficient in sports that require fine grained training of specific effectors, like hands or feet. In this context, comparisons in semantic category specific performance (or fMRI/EEG effects) between those athletes could potentially be most relevant, as this would warrant proper test for double dissociations in facilitation effects. In any way, this general procedure of testing athletes would allow to derive inferences on the causal involvement of motor systems for processing word semantics by investigating healthy and unimpaired brain function, whereas this is by design not possible in lesion approaches as presented in Chapters 3 and 4.

The novel contribution of Chapter 5, the grounding of also abstract mental semantics in the motor system could only be shown merely on a correlational level, i.e. motor system activity was shown to be informative about differentiating abstract mental and abstract emotion semantics, but it is not clear whether it also holds a causal role in this differentiation. This observation is therefore in line with earlier criticism towards previous neuroimaging evidence on a grounding of concrete semantics in modality-preferential sensorimotor systems (Mahon and Caramazza 2008, see Chapter 1). Given the aforementioned investigations of clinical populations with focal lesions including those sensorimotor systems, it might appear straight forward to simply include abstract mental words to the stimulus lists applied in Chapters 3 and 4. While such a procedure would be ideal in order to directly investigate a necessary role of face motor systems for abstract mental words, it again comes to high costs for patient recruitment, as described above. However, this effort might not be necessary to investigate at least a specific causal contribution of face motor systems for abstract mental nouns and likewise of the dissociations of abstract emotion and abstract mental words in the motor system. Instead, either neurostimulation or pure behavioural paradigms could be conducted on healthy participants, manipulating the state of hand and/or face motor activity, behaviorally or via neurostimulation and determining whether this causes semantic category specific changes in semantic processing. The overall design could be potentially quite similar to earlier approaches on a functional involvement of the sensorimotor system for concrete word semantics (e.g. Connell *et al.*, 2012; Shebani and Pulvermüller, 2013), not necessarily applying lexical decision paradigms as in Chapters 3 and 4. As mentioned already in Chapter 5, Borghi and Zarcone (2016) recently presented a behavioural semantic decision paradigm with responses given via the mouth or hand to be informative on the causal involvement of face motor areas for abstract word processing.

Furthermore, in order to investigate the temporal dynamics of processing of both, abstract emotion and abstract mental processing, one would need to resort to other methods than fMRI (like in Chapter 5), as it only has a very limited temporal resolution. Ideal candidates in this respect could be found in EEG or MEG paradigms. Here either passive reading tasks, or passive mismatch negativity paradigms could be applied on abstract mental or emotional words, like in previous investigations of the temporal dynamics of concrete words (e.g. Hauk and Pulvermüller, 2004; Pulvermüller *et al.*, 2005).

A further possibility would be to adapt the strategy of a recent mismatch negativity paradigm from Grisoni *et al.* (2016). In this paradigm frequent action-related and effector specific sounds were paired with effector specific, concrete action word deviants. Results indicate somatotopic priming effects in face and leg motor areas in case of effector congruency between sound and action word, thus indexing genuine semantic processing in these motor systems with high temporal resolution. The same rationale could be applied for abstract mental and abstract emotion words as deviant word stimuli while presenting hand- and face-related action sounds as primes. This procedure would allow for inferences on the temporal dynamics of motor system contributions to abstract semantics processing, which was not possible in neither of the three dissertation projects (Chapters 3-5). Such a paradigm would have the additional advantage that only few matched linguistic stimuli are needed, whereas all dissertation projects required large lists of stimuli for each semantic category. For the investigation of abstract mental words in Chapter 5, this resulted in the need to include also morphologically complex words, with a length up to three syllables (for all categories to maintain matching between semantic types), which has previously been related to attenuated modality-preferential sensorimotor fMRI signal strength in language processing (Pulvermüller *et al.*, 2012; see also Discussion of Chapter 5). In contrast, a paradigm that parallels the design of Grisoni and coworkers (2016) could potentially avoid this issue by applying only a limited set of abstract emotion and abstract mental words of lower morphological complexity.

6.10 Conclusion

In conclusion, results of all three studied conducted in the context of this dissertation support a grounding in sensorimotor experience of abstract and concrete concepts. Results are in line with models which assume word meaning to be represented in distributed cell assemblies covering both, perisylvian language and extrasylvian, modality-preferential sensorimotor systems, with their exact structure depending on specific word semantics, following shaping via Hebbian learning mechanisms. Investigations on clinical populations revealed these extrasylvian, modality-preferential systems to be of functional relevance and also necessary for semantic processing. Previously similar observations were restricted to the domain of words referring to concrete entities or actions, whereas the current results demonstrate also a necessary role of fronto-parietal sensorimotor areas for semantic processing and representation. This contrasts with alternative interpretations that ascribe merely an epiphenomenal role to modality-preferential systems for semantics. Furthermore, like for concrete words, also somatotopic activation differences within the motor system were observed to be information for processing of different abstract meaning types, providing important implications for future research on the grounding of abstract concepts.

7. References

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8. Supplementary Material

8.1 Supplementary Material Chapter 3

Post hoc control of morphological complexity between noun categories

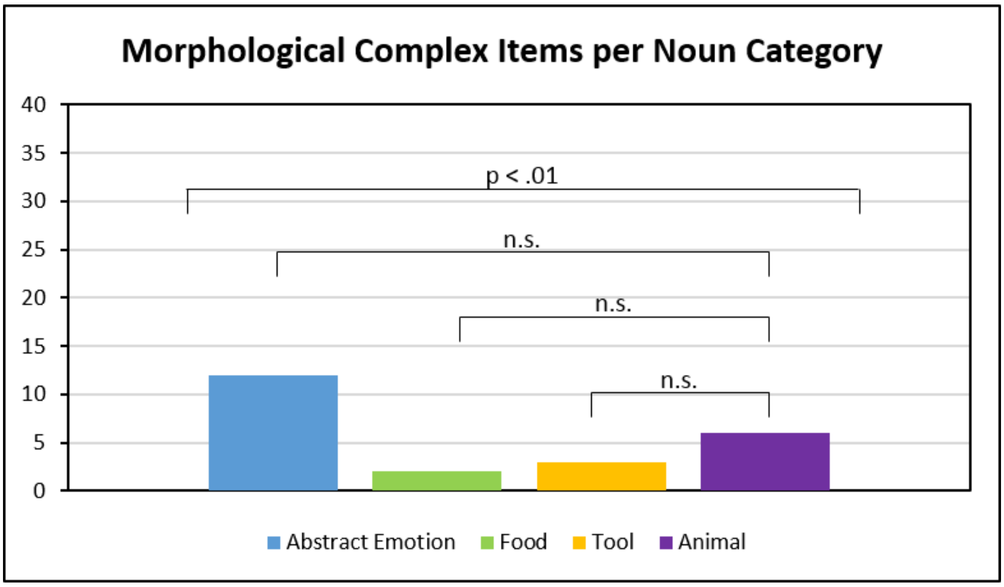

Figure 8.1.1: Post hoc comparisons of morphological complex items between LDT noun categories. Bar graphs depict numbers of morphological complex items (words containing either derivational or compound morphology) per noun category, "n.s." represents non-significant statistical comparisons.

In order to compare the amount of morphological complex (words containing either derivational or compound morphology) items between noun categories, χ^2- and, in case of insufficient cell sizes ($n < 5$), Fisher's Exact Tests were applied. Results indicate significant differences between the four word categories ($\chi^2 = 12.33$, $df = 3$, $p = .006$, Cramer's $V = .28$). Comparisons of individual categories to the non-action animal control category however, revealed no significant differences in terms of the amount of morphologically complex words. Abstract emotion nouns (high morphological complexity in 30% of items) did not differ significantly in their morphological complexity to animal nouns (high morphological complexity in 15% of items; $\chi^2 = 2.58$, $df = 1$, $p = .11$, Cramer's $V = .18$) and neither did food nouns (high morphological complexity in 5% of items; $\chi^2 = 2.22$, $df = 1$, $p = .26$, Cramer's $V = .17$), nor tool nouns (high morphological complexity in 7.5% of items; $\chi^2 = 1.04$, $df = 1$, $p = .48$, Cramer's $V = .11$). Results of comparisons of individual categories to the non-action control category of animal nouns, as presented in Chapters 3 (and 4) are therefore not significantly confounded by morphological complexity differences between categories.

List of LDT target stimuli applied in Chapter 3

Table 8.1.1: Abstract emotion noun stimuli.

Abstract Emotion Nouns

Word	*Translation*	*Word*	*Translation*
Abscheu	abhorrence	Neugier	curiousness
Ärger	anger	Ohnmacht	powerlessness
Ehrgeiz	ambition	Pech	misfortune
Eifer	zealousness	Pein	anguish
Elend	misery	Rache	revenge
Frechheit	impertinence	Respekt	respect
Friede	peace	Reue	regret
Geiz	stinginess	Ruhm	fame
Gnade	mercy	Scham	pudency
Groll	resentment	Skepsis	scepticism
Hohn	taunt	Stress	stress
Horror	horror	Trauer	sorrow
Humor	humour	Triumph	triumph
Kummer	grief	Trotz	defiance
Leid	suffering	Trübsal	tribulation
Milde	blandness	Unheil	doom
Missgunst	malevolence	Unlust	reluctance
Missmut	moroseness	Wahn	delusion
Mitleid	pity	Willkür	capriciousness
Neid	envy	Wonne	blissfulness

Table 8.1.2: Animal noun stimuli.

Animal Nouns

Word	*Translation*	*Word*	*Translation*
Affe	monkey	Kuh	cow
Biene	bee	Laubfrosch	tree-frog
Eisbär	polar bear	Löwe	lion
Ente	duck	Maulwurf	mole
Eule	owl	Maus	mouse
Falke	falcon	Möwe	seagull
Faultier	sloth	Ochse	ox
Fuchs	fox	Ratte	rat
Grille	cricket	Schaf	sheep
Habicht	hawk	Schlange	snake
Hahn	cock	Schnecke	snail
Hase	hare	Schwein	pig
Hecht	pike	Stinktier	skunk
Hirsch	stag	Taube	dove
Huhn	chicken	Tiger	tiger
Igel	hedgehog	Wespe	wasp
Karpfen	carp	Wildgans	brant
Krabbe	crab	Wolf	wolf
Krähe	crow	Wurm	worm
Krebs	crustacean	Ziege	goat

Table 8.1.3: Food noun stimuli.

Food Nouns			
Word	*Translation*	*Word*	*Translation*
Apfel	apple	Nudel	noodle
Birne	pear	Nuss	nut
Bohne	bean	Pfirsich	peach
Erbse	pea	Pflaume	plum
Fleisch	meat	Pommes	french fries
Frühstück	breakfast	Porree	leek
Gebäck	pastry	Pudding	blancmange
Gulasch	goulash	Reis	rice
Gurke	cucumber	Rettich	radish
Käse	cheese	Rübe	turnip
Keks	cookie	Sahne	cream
Kirsche	cherry	Salat	salad
Kohl	cabbage	Schinken	ham
Kompott	compote	Schnitzel	schnitzel
Kuchen	cake	Speck	bacon
Kürbis	pumpkin	Spinat	spinach
Lauch	allium	Torte	gateau
Mais	sweet corn	Traube	grape
Mandel	almond	Wurst	sausage
Möhre	carrot	Zwiebel	onion

Table 8.1.4: Tool noun stimuli.

Tool Nouns			
Word	Translation	Word	Translation
Axt	axe	Nagel	nail
Besen	broom	Paddel	paddle
Bohrer	drill	Peitsche	whip
Bürste	brush	Pinsel	paint-brush
Fächer	fan	Pumpe	pump
Feile	file	Reibe	grater
Gabel	fork	Ruder	rudder
Hacke	pick	Schalter	switch
Hammer	hammer	Schaufel	shovel
Hebel	lever	Schere	scissors
Hobel	planer	Schlüssel	key
Kamm	comb	Schwert	sword
Kelle	dipper	Speer	spear
Klingel	bell	Stempel	stamp
Knüppel	club	Stift	pen
Kuli	biro	Streichholz	match
Lenkrad	steering wheel	Taste	button
Löffel	spoon	Trommel	drum
Messer	knife	Zange	pliers
Nadel	needle	Zirkel	compass

Table 8.1.5: Abstract verb stimuli.

Abstract Verbs

Word	*Translation*	*Word*	*Translation*
achten	to respect	merken	to recognize
ahnen	to anticipate	neiden	to envy
ärgern	to annoy	plagen	to bother
danken	to thank	planen	to plan
deuten	to interpret	raten	to guess
dulden	to condone sth.	schämen	to be ashamed
ehren	to honour	schätzen	to appreciate sth.
folgern	to conclude	scheitern	to fail
fürchten	to fear	scheuen	to dread sth.
glücken	to succeed	schmachten	to yearn
grauen	to dread	schmeicheln	to flatter
grausen	to dread	siegen	to win
grübeln	to ruminate	täuschen	to decive
hassen	to hate	trauen	to trust
hoffen	to hope	träumen	to dream
irren	to be wrong	wundern	to wonder
kriseln	to trouble	wünschen	to wish
leiden	to suffer	zögern	to hesitate
lieben	to love	zürnen	to be angry with sb.
meiden	to avoid	zweifeln	to doubt

Table 8.1.6: Hand action verb stimuli.

Hand Action Verbs

Word	*Translation*	*Word*	*Translation*
biegen	to bend	malen	to paint
bohren	to drill	nähen	to sew
boxen	to box	putzen	to clean
drehen	to turn	reiben	to rub
drücken	to press	reißen	to rip
fangen	to catch	rupfen	to pluck
fechten	to fence	rütteln	to shake
greifen	to grap	schälen	to peel
hacken	to peck	schieben	to push
häkeln	to crochet	schlagen	to beat
harken	to rake	schleppen	to carry
hauen	to hit	schneiden	to cut
kämmen	to comb	schrubben	to scrup
kehren	to sweep	schütteln	to shake
klatschen	to clap	schwenken	to slew
klicken	to click	stempeln	to stamp
klopfen	to knock	streuen	to sprinkle
kneten	to knead	stricken	to knit
kratzen	to scratch	winken	to wave
lenken	to steer	zeichnen	to draw

Table 8.1.7: Face action verb stimuli.

Face Action Verbs

Word	*Translation*	*Word*	*Translation*
atmen	to breath	pfeifen	to whistle
äußern	to express	plaudern	to chat
brüllen	to scream	pusten	to blow
brummen	to hum	quieken	to squeal
fauchen	to hiss	reden	to talk
flüstern	to whisper	rufen	to yell
fressen	to devour	saufen	to swig
gähnen	to yawn	saugen	to suck
hauchen	to aspirate	schlucken	to swallow
kauen	to chew	schlürfen	to slurp
keuchen	to gasp	schmatzen	to smack
kreischen	to screech	schmecken	to taste
lallen	to slurp	schmunzeln	to smirk
lecken	to lick	schreien	to scream
lutschen	to suck	schwatzen	to gossip
murmeln	to mumble	seufzen	to sigh
nagen	to nibble	singen	to sing
nennen	to state	spucken	to spit
niesen	to sneeze	stottern	to stutter
nippen	to sip	zischen	to fizz

Table 8.1.8: Leg action verb stimuli.

Leg Action Verbs

Word	*Translation*	*Word*	*Translation*
bummeln	to stroll	schlittern	to glide
eilen	to hurry	schlurfen	to shuffle
fliehen	to flee	schreiten	to pace
flitzen	to bolt	springen	to jump
flüchten	to escape	sprinten	to sprint
folgen	to follow	spurten	to spurt
hetzen	to scamper	stampfen	to stomp
hinken	to limp	stapfen	to tromp
hocken	to squat	steigen	to ascent
humpeln	to hobble	stiefeln	to stride
hüpfen	to bounce	stolpern	to stumble
huschen	to scamper	strampeln	to pedal
joggen	to jog	streunen	to stray
kicken	to kick	stürmen	to rush
knien	to knee	tanzen	to dance
lahmen	to founder	traben	to trot
laufen	to run	treten	to kick
radeln	to cycle	trotten	to amble
schleichen	to tiptoe	wandern	to wander
schlendern	to saunter	waten	to wade

8.2 Supplementary Material Chapter 5

Left hemispheric activations for individual categories

Left hemispheric results, with small volume correction of precentral and rolandic face and hand motor areas, for contrasts of individual semantic categories against the visual hashmark baseline are depicted in Fig. 8.2.1 and Tab. 8.2.1. For this contrast, abstract emotion nouns showed activation clusters in dorsal and ventral precentral and rolandic motor areas (though only at an uncorrected p < .005), whereas abstract mental nouns activated almost the entire area of small volume correction, with strongest activation peaks being situated in ventral rolandic and precentral areas. Likewise, food items also exhibited widespread activation throughout the small volume of interest in this analysis, with activation peaks being situated in both, ventral and dorsal parts. For tools, a ventral precentral cluster was observed, in addition to a ventral rolandic cluster.

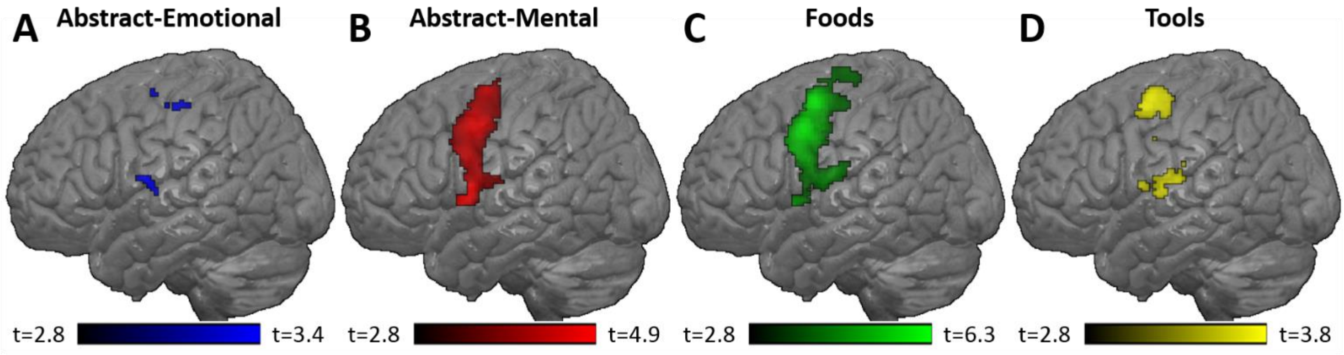

Figure 8.2.1: Left hemispheric patterns of activation in gray matter of face and hand motor systems, presented for each individual semantic noun category against a low level visual baseline: for abstract emotion (B, in blue), abstract mental words (C, in red), food-related words (D, in green) and tool-related words (E, in yellow). Contrasts are thresholded at *p* < .05 (peak-wise), FDR corrected (B-D) and *p* < .005 (peak wise), uncorrected (A).

Table 8.2.1: MNI coordinates for activation peaks of individual against a visual hashmark baseline. Coordinates are plotted at a false discovery rate corrected *p* < .05 (peak-wise), or at p < .005 (uncorrected, indicated by §), given in mm in Montreal Neurological Institute space.

Contrast	Cluster Size	MNI Coordinates			*t*	*p*
		x	*y*	*z*		
Abstract Emotion vs Baseline	22	-40	-2	14	3.44	<.001§
		-44	-8	8	3.17	<.001§
	13	-40	-20	54	3.23	<.001§
	5	-38	-8	60	2.99	<.001§
	1	-38	-14	54	2.82	<.001§
Abstract Mental vs Baseline	1374	-54	4	8	4.93	.007
		-52	2	44	4.48	.007
		-34	-6	62	3.93	.008
Foods vs Baseline	1529	-48	4	40	6.37	<.001
		-38	-2	56	6.2	<.001
		-52	2	24	4.31	.001
	1	-50	-20	22	2.06	.048
Tools vs Baseline	305	-38	-2	58	3.81	.037
		-48	0	52	3.74	.037
	91	-52	-8	10	3.41	.037
		-50	-16	14	3.38	.037
	12	-58	4	10	2.91	.04
	1	-50	-4	36	2.67	.049
	1	-50	-20	22	2.64	.050

Analysis of Semantic ROIs from Vigneau et al. (2006)

For the first set of ROI analyses, 10 semantic ROIs were defined as spheres of 5 mm radius according to semantic network nodes derived from a meta-analysis of 322 activation peaks for semantic processing (Vigneau *et al.*, 2006), excluding the most dorsal operculary semantic node due to its proximity to motor regions. Resulting ROIs and results for the contrasts of individual semantic categories against visual hashmark baseline are depicted in Figure 8.2.2.

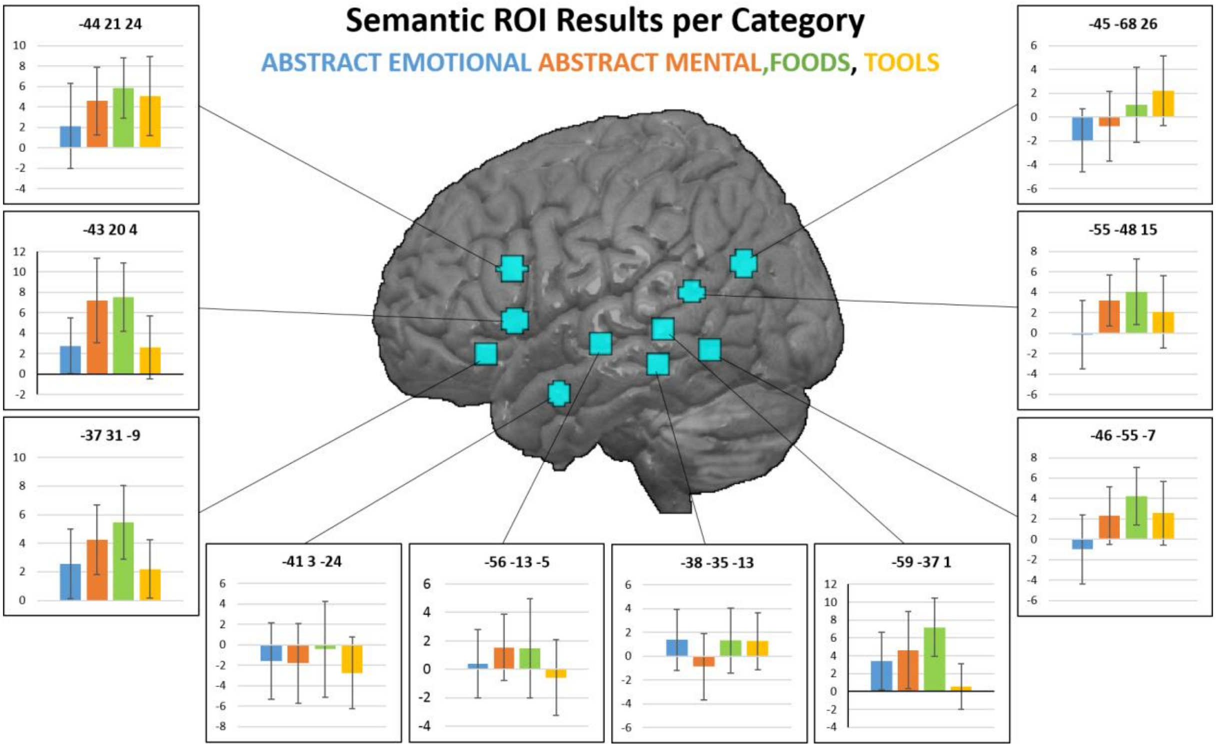

Figure 8.2.2: Overview of group level regions of interest (ROIs) on semantic network nodes (Vigneau *et al.*, 2006). Each ROI is shown with its central X,Y,Z mm coordinates in MNI space. Bar graphs represent raw parameter estimates of noun categories against hashmarks in these ROIs with error bars denoting 95% confidence intervals corrected for between participant variance (Morey, 2008). Blue bars depict results for abstract emotion nouns, red bars for abstract mental nouns, green bars for food nouns and yellow bars for tool nouns.

A 10 (ROIs) X 4 (Semantics: abstract emotion/abstract mental/foods/tools) RM ANOVA on the 10 semantic nodes from Vigneau and colleagues (2006) revealed a significant main effect for ROIs [*F*(4.9,131.3) = 2.95, *p* = .02, *partial* $\eta 2$ = .1], but only a tendency towards significance for the main effect of Semantics [*F*(3, 27) = 2.63, *p* = .055, *partial* $\eta 2$ = .09] and also the interaction between ROIs and Semantics was not significant [*F*(10.6, 284.9) = 1.4, *p*= .18, *partial* $\eta 2$ = .05]. Regarding the ROI main effect, the three inferior frontal ROIs (MNI X = -43 mm, Y = 20 mm, Z = 4 mm; X = -37 mm, Y = 31 mm, Z = -9 mm; X = -44 mm, Y = 21 mm, Z = 24 mm), as well as the middle temporal ROI (MNI X = -43 mm, Y = 20 mm, Z = 4 mm) were shown to have stronger signal across categories than other ROIs (all *t*s > 2.1).

Data-driven Group-level ROI Analysis

In a separate analysis, ROIs for the group-level analysis were all defined in a data driven manner. To this end, overlapping the contrast of all nouns vs. baseline (at an FDR-corrected $p < .05$, peak wise, with small volume correction for left hemispheric gray matter) with an inclusive anatomical mask of inferior-frontal Broca’s area, as it is classically defined, i.e. as the union of pars triangularis and pars opercularis, resulted in a ROI of 653 voxels; a posterior-temporal ROI was obtained from the 96 voxels in posterior temporal cortex, in the vicinity of a region sometimes called the visual word form area (Cohen *et al.*, 2000). The results of the motor localizer tasks showed most prominent activation in the face tasks centered in the ventral motor cortex (MNI X = -62 mm, Y =-14 mm, Z = 38 mm), whereas the hand motor task activated more dorsal motor cortex (MNI X = -34 mm, Y = -22 mm, Z = 52 mm), which each provided the center of a 5 mm radius sphere defining the motor system ROIs. All ROIs considered in this analysis and respective category specific results are summarized in Fig. 8.2.3.

A 4 (ROIs: Inferior Frontal/ Posterior Temporal/ Face Motor/ Hand Motor) X 4 (Semantics: abstract mental/ abstract emotion/ foods/ tools) RM ANOVA revealed no significant main effect of Semantics [$F(3,81) = 2.14$, $p = .1$, *partial* $\eta 2 = .074$], but a significant main effect for ROIs [$F(3,81) = 2.99$, $p = .036$, *partial* $\eta 2 = .01$] and a significant ROI*Semantics interaction [$F(9,243) = 2.17$, $p = .02$, *partial* $\eta 2 = .075$]. When investigating the main effect for semantics further, the inferior frontal ROI was revealed to have significantly stronger signal than the hand motor ROI [$t(27) = 3.84$, $p < .001$, *Cohen's d* = 1.03]. To disentangle the observed ROI*Semantic interaction, the analysis was repeated, specifically for motor and non-motor ROIs. Within the non-motor ROIs, a 2 (ROIs: inferior frontal/posterior temporal) X 4 (Semantics: abstract mental/ abstract emotion/ foods/ tools) RM ANOVA, revealed a significant main effect for semantics [$F(1,27) = 1.86$, $p = .18$, *partial* $\eta 2 = .11$] , but no significant main effect for ROIs [$F(1,27) = 1.86$, $p = .18$, *partial* $\eta 2 = .06$] and also the ROI*Semantics interaction was not significant [$F(3,81) = 1.44$, $p = .24$, *partial* $\eta 2 = .05$]. The main effect for semantics was shown to be based on stronger signals for foods over abstract emotion- and tool nouns, across inferior frontal and posterior temporal ROIs (*t*s > 2.5). The results for the motor ROIs are reported in Chapter 5 (i.e. they are the same, as the reported motor ROI results in the group-level analysis).

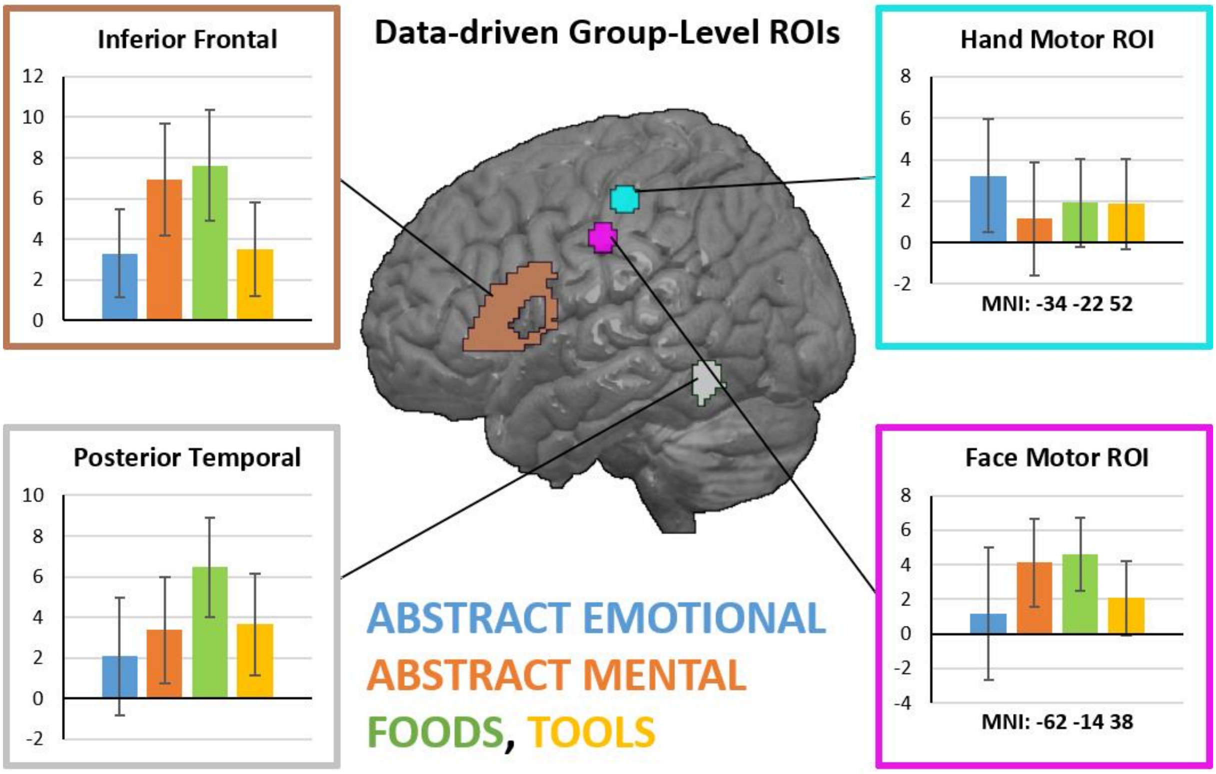

Figure 8.2.3: Overview of group level Regions of interest (ROIs). Results of the contrast of all nouns against hashmarks in Broca's region constitute the inferior-frontal ROI (shown in brown) and likewise the posterior-temporal activation cluster for this contrast the respective posterior-temporal ROI (shown in light gray). Face- (purple) and hand motor ROIs (cyan) are defined as spheres of 5 mm radius centered on corresponding activation peaks in the motor localizer paradigm. Bar graphs represent activation of noun categories against hashmarks in these ROIs with error bars denoting standard errors, blue bars representing results for abstract emotion nouns, red bars for abstract mental nouns, green bars for food nouns and yellow bars for tool nouns.

Post hoc control of morphological complexity between noun categories

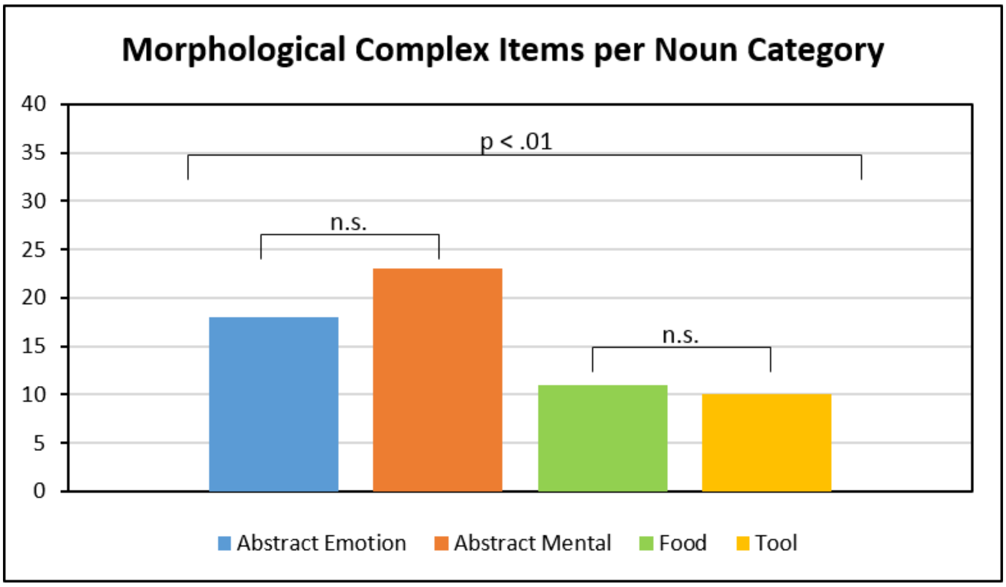

Figure 8.2.4: Post hoc comparisons of morphological complex items between critical fMRI noun categories. Bar graphs depict numbers of morphological complex items (words containing either derivational or compound morphology) per noun category, "n.s." represents non-significant statistical comparisons.

In order to compare the amount of morphological complex (words containing either derivational or compound morphology) items between noun categories, χ^2-tests were applied. Results indicate significant differences between the four word categories (χ^2 = 11.9, *df* = 3, *p* = .008, Cramer's *V* = .27). Comparisons between categories critical for analysis (within the abstract and concrete domain) however, revealed no significant differences between categories in terms of the amount of morphologically complex items. Abstract emotion nouns (high morphological complexity in 45% of items) did not differ significantly in their morphological complexity to abstract mental nouns (high morphological complexity in 57.5% of items; χ^2 = 1.25, *df* = 1, *p* = .26, Cramer's *V* = .13) and also the amount of morphological complex food nouns (high morphological complexity in 27.5% of items) did not differ significantly to that of tool nouns (high morphological complexity in 25% of items; χ^2 = .06, *df* = 1, *p* = .8 Cramer's *V* = .03). Results of comparisons within abstract and concrete nouns are therefore not significantly confounded by morphological complexity differences between noun categories.

List of stimuli critical for analysis in Chapter 5

Table 8.2.2: Abstract emotion nouns

Abstract Emotion Nouns

Word	Translation	Word	Translation
Abscheu	abhorrence	Missgunst	malevolence
Anspannung	strain	Missmut	moroseness
Ärger	anger	Mitleid	pity
Beistand	support	Neid	envy
Dramatik	drama	Neugier	curiousness
Ehrgeiz	ambition	Rache	revenge
Eifer	zealousness	Respekt	respect
Ekstase	ecstasy	Reue	regret
Elend	misery	Romanze	romance
Erbarmen	mercy	Ruhm	fame
Euphorie	euphoria	Schrecken	fright
Feindschaft	hostility	Skepsis	scepticism
Frechheit	impertinence	Trauer	sorrow
Frohsinn	cheerfulness	Triumph	triumph
Gnade	mercy	Trübsal	tribulation
Harmonie	harmony	Unheil	doom
Horror	horror	Unlust	reluctance
Humor	humour	Vorurteil	prejudice
Kummer	grief	Wonne	blissfulness
Milde	clemency	Zumutung	disgrace

Table 8.2.3: Abstract mental nouns

Abstract Mental Nouns

Word	Translation	Word	Translation
Abwägung	consideration	Irrtum	misapprehension
Ahnung	presentiment	Kalkül	calculatio
Anstand	modesty	Klugheit	prudence
Denkstil	style of thinking	Kodex	code of ethics
Deutung	interpretation	Konsens	concensus
Dummheit	stupidity	Konzept	concept
Einfall	idea	Leitbild	approach
Ethos	ethos	List	ruse
Fleiß	diligence	Logik	logic
Geduld	patience	Mutmaßung	guess
Gehorsam	obedience	Planung	planning
Genie	wiz	Ratio	rationality
Genius	genius	Scharfsinn	acumen
Gespür	intuition	Schätzung	estimation
Gewöhnung	habituation	Schlauheit	smartness
Grübeln	rumination	Schwachsinn	imbecility
Ignoranz	ignorance	Sorgfalt	painstakingness
Impuls	impulse	Taktik	tactic
Instinkt	instinct	Weisheit	wisdom
Intellekt	intellect	Weltbild	world view

Table 8.2.4: Food nouns

Food Nouns

Word	Translation	Word	Translation
Abendbrot	dinner	Nahrung	food
Apfel	apple	Paprika	pepper
Birne	pear	Pfirsich	peach
Blumenkohl	cauliflower	Pflaume	plum
Bohne	bean	Pudding	blancmange
Brot	bread	Radieschen	radish
Erbse	pea	Reis	rice
Erdbeere	strawberry	Salat	salad
Fleisch	meat	Sauerkraut	sauerkraut
Frühstück	breakfast	Schinken	ham
Gebäck	pastry	Schlagsahne	whipped cream
Gurke	cucumber	Schnittlauch	chive
Honig	honey	Speck	bacon
Käse	cheese	Tomate	tomato
Kirsche	cherry	Torte	gateau
Kohl	cabbage	Traube	grape
Kompott	compote	Verpflegung	proviant
Kuchen	cake	Wurst	sausage
Mahlzeit	meal	Zitrone	lemon
Mandel	almond	Zwiebel	onion

Table 8.2.5: Tool nouns

Tool Nouns

Word	Translation	Word	Translation
Besen	broom	Peitsche	whip
Bleistift	pencil	Pinsel	paint-brush
Bürste	brush	Postkarte	postcard
Fächer	fan	Pumpe	pump
Gabel	fork	Ruder	rudder
Hammer	hammer	Schalter	switch
Handbremse	hand brake	Schaufel	shovel
Handtuch	towel	Schere	scissors
Hebel	lever	Schlüssel	key
Instrument	instrument	Staubsauger	vacuum cleaner
Kelle	dipper	Stempel	stamp
Klammer	clip	Streichholz	match
Klingel	bell	Tablett	tray
Lappen	rag	Taste	button
Lenkrad	steeringwheel	Trommel	drum
Löffel	spoon	Wasserhahn	faucet
Messer	knife	Werkzeug	tool
Nadel	needle	Würfel	dice
Nagel	nail	Zange	pliers
Notizbuch	notebook	Zirkel	compass

9. Summary

This dissertation investigates in how far modality preferential motoric regions of the brain contribute to and are necessary for the processing of word semantics. Whereas classical models on the neural substrates of language processing attribute semantics to be handled in encapsulated modules in an entirely amodal format in perisylvian regions, recent theoretical approaches assume the meaning of words to be represented in a distributed fashion, extending over classical perisylvian areas but also involving sensory and action systems of the brain, depending on exact word semantics. While in recent years plenty of evidence could be collected in favor of the latter perspective, criticism has been raised that much of these supporting data is merely of correlative nature, leaving the possibility that modality-preferential systems' involvement in semantic processing occurs entirely in an epiphenomenal fashion. Furthermore, it has been questioned whether grounded approaches can also be applied for abstract words, which lack transparent sensory or motor referents, as the majority of previous evidence has been collected for words referring to concrete entities or actions exclusively. To tackle both issues, two studies are presented in which neurological patients with focal brain lesions were tested on recognition of words with concrete action related semantics (like 'hammer') or abstract emotion semantics (like 'love') via a speeded lexical decision task. Here, results indicate modality preferential action systems in the brain to indeed hold a causal and necessary role in processing of word semantics of concrete hand action related tool and abstract emotion nouns. Using functional magnetic imaging it was investigated in a passive reading paradigm, whether contributions of the motor system to processing of abstract semantics is found exclusively for concrete and abstract emotion words or whether they can also be observed for abstract "mental" words like 'thought' or 'logic' which do not hold emotional content. Here, results show that activation patterns of hand and face motor systems dissociate between and are informative for concrete, as well as for abstract emotional and abstract mental semantic classes.

Given the results of all three studies it can be concluded that a role of motor systems in semantic processing is not restricted to concrete words but extends to at least some abstract mental symbols previously thought to be entirely "disembodied" and divorced from semantically related sensorimotor processing. Motor systems were shown to hold a necessary role for undisturbed processing of semantics of concrete action related-, but also for abstract emotion words. Results can therefore not be reconciled with the idea that sensorimotor systems are somehow peripheral or "epiphenomenal" to meaning and concept processing. In contrast, the current observations are in line with models that assume the neural substrates of word

semantics to resemble cell assemblies distributed over multi-modal perisylvian and also extrasylvian modality preferential systems, with their exact structure being shaped by correlational, Hebbian learning mechanisms, according to specific word semantics.

10. Zusammenfassung

Die vorliegende Arbeit befasst sich mit der Frage, inwieweit modalitätspezifische motorische Regionen des Gehirns an der Verarbeitung von Wortsemantik beteiligt und notwendig sind. Klassische Modelle der neuronalen Grundlagen von Sprache nehmen an, dass die Bedeutung von Wörtern in einem komplett amodalen Format vorliegt und in separaten, abgekapselten Modulen verarbeitet wird. Im Gegensatz dazu stehen neuere Theorien, die Wortsemantik in weit verzweigten Netzwerken repräsentiert sehen, die sowohl die klassischen perisylvischen Sprachareale umfassen, aber auch, in Abhängigkeit von der genauen Wortbedeutung, motorische und sensorische Areale des Gehirns mit einbeziehen. Zahlreiche Studien konnten in den letzten Jahren Hinweise für dieses Modell sammeln, allerdings wurde von manchen Autoren kritisiert, dass die Evidenz für eine Rolle sensorischer und motorischer Areale für semantische Verarbeitung in vielen Fällen lediglich korrelativer Natur ist und die Möglichkeit offen lässt, dass diese modalitäts-spezifischen Areale lediglich epiphänomenal involviert sind, ohne tatsächlich an den eigentlichen semantischen Verarbeitungsprozessen beteiligt zu sein. Da sich ein Großteil der bisherigen Studien zumeist nur mit der Rolle von sensomotorischen Arealen für die Bedeutungsverarbeitung von Wörtern mit konkreten, physischen oder handlungsbezogenen Referenten befasste, wurde zuletzt zusätzlich in Frage gestellt, ob eine Verankerung von Wortsemantik in basale sensorische oder motorische Areale auch für abstrakte Wörter zutreffend ist, da diese über keine offensichtlichen konkreten Referenten verfügen.

Um beide Fragestellungen zu erörtern, wurden im Rahmen dieser Arbeit zwei Studien durchgeführt, in denen mittels einer beschleunigten lexikalischen Entscheidungsaufgabe die Wortverarbeitung von Wörtern mit konkreter, handlungsbezogener Bedeutung (wie zum Beispiel „Hammer“), oder abstrakt-emotionaler Semantik (wie „Liebe“) bei neurologischen Patienten mit fokalen Läsionen untersucht wurde. Die Ergebnisse beider Studien deuten darauf hin, dass modalitäts-spezifische motorische Areale sowohl für Wörter mit konkreter Semantik, als auch für abstrakte Emotionswörter notwendig sind und eine kausale Rolle in deren Verarbeitung spielen.

Mit Hilfe eines passiven Leseparadigmas unter funktioneller Magnetresonanzbildgebung wurde in einer dritten Studie untersucht, ob motorische Areale lediglich für abstrakte Emotionswörter eine Rolle spielen, oder ob sie auch in die Verarbeitung von abstrakt-mentalen Begriffen, ohne emotionale Konnotation, wie „Logik“ oder „Gedanke“, involviert sind. Die Ergebnisse dieser Studie zeigen, dass neuronale Aktivierungsmuster innerhalb von Arm- und Gesichtsmotorarealen nicht nur für konkrete, sondern auch für abstrakt-emotionale und abstrakt-mentale Wörter unterscheidbar und aussagekräftig sind.

Angesichts der Ergebnisse aller drei vorgestellten Studien lässt sich auf eine Rolle des motorischen Systems bei der Verarbeitung von Wörtern mit konkreter Semantik, aber auch zumindest einiger abstrakter Bedeutungsklassen schließen, die zuvor als komplett unabhängig von basalen sensorischen oder motorischen Informationen betrachtet wurden. Es konnte dabei gezeigt werden, dass diese motorischen Areale tatsächlich notwendig für die ungestörte Verarbeitung von Wörtern mit konkreter und abstrakt-emotionaler Bedeutung sind. Die aktuellen Ergebnisse sind daher nicht mit Modellen in Einklang zu bringen, die diesen modalitäts-spezifischen Arealen lediglich eine periphere und epiphänomenale Rolle in der Verarbeitung von Wortsemantik zuschreiben. Im Gegensatz dazu sind die aktuellen Ergebnisse im Sinne von Theorieansätzen interpretierbar, die Wortsemantik in neuronalen Netzwerken realisiert sehen, welche sich über multi-modale persisylvische, aber auch extrasylvische modalitätsspezifische Hirnareale erstrecken, wobei ihre genaue Struktur durch korrelative, der Hebbschen Lernregel folgenden Mechanismen geformt wird.

11. List of publications

Dreyer, F. R., Frey, D., Arana, S., von Saldern, S., Picht, T., Vajkoczy, P., & Pulvermüller, F. (2015). Is the motor system necessary for processing action and abstract emotion words? Evidence from focal brain lesions. *Frontiers in psychology*, *6*.

Dreyer, F. R., & Pulvermüller, F. (*in press*). Abstract semantics in the motor system? – An event-related fMRI study on passive reading of semantic word categories carrying abstract emotional and mental meaning. *Cortex.*

12. Erklärung

Hiermit versichere ich, dass ich die vorgelegte Arbeit selbständig verfasst habe und keine anderen als die angegebenen Hilfsmittel verwendet habe. Die Arbeit ist in keinem früheren Promotionsverfahren angenommen oder abgelehnt worden.

Felix R. Dreyer, Leipzig, Dezember 2017