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# CONCEPTUAL SEMANTICS AS GROUNDED IN PERSONAL EXPERIENCE*

*abstract*

*Semantic memory for an object encompasses multi-modal knowledge gained through personal experience over the lifetime, and coded in grounded sensory-motor brain systems, independently of the level of subjective awareness. Linguistic access to semantic memories in verbal format relies on the functional coupling between perisylvian language regions and the grounded brain systems implied by our lifetime experience with the concept's referents. Linguistic structure exerts modulatory influences on this functional coupling, as in the case of sentential negation, which reduces the interactions between perisylvian language regions and the grounded brain systems.*

*keywords*

*semantic memory; grounded cognition; language; personal experience; action-related brain system*

**1. Introduction: theories of semantic memory**

Semantic memory encompasses all the knowledge acquired over the lifetime and stored in a generalized form, independently of the actual time and space (Patterson *et al.*, 2007). The content of semantic knowledge enables a wide variety of human actions, from the ability to move, perceive and interact with the external world, to higher cognitive functions including the possibility to speak, plan and decide (Binder & Desai, 2011). The nature of conceptual representations, and in particular their relation with sensory and motor experiences, has long constituted a matter of debate, which dates back to Greek philosophers. Rationalist philosophers have traditionally been skeptical about the role of perceptual experience in shaping conceptual knowledge, asserting that veridical knowledge is only gained through reason and is based on the existence of a priori categories, independently from external sources of information. On the other hand, Empiricist philosophers have strongly rejected this assumption, stating that concepts are strictly based upon sensory experience (Markie, 2017). In the last decades, this debate has been revitalized by contrasting neuroscientific theories of semantic memory (Binder & Desai, 2011). At one extreme are disembodied or amodal theories, which propose a complete separation between perception and cognition. At the other extreme are grounded cognition and embodied theories, which assume that a common system underlies both sensory-motor and conceptual-semantic representations. As for the latter class of theories, Barsalou (1999, 2008) argued that the neural states subtending perception are stored in long-term semantic memory as modal symbols for external referents. Such perceptual symbols originate in all modalities of experience, including vision, gustation, olfaction, haptics, audition, proprioception, and introspection, and are thought to be distributed throughout the brain. As Wernicke affirmed more than a century ago (1874):

> ...the memory images of a bell... are deposited in the cortex and located according to the sensory organs. These would then include the acoustic imagery aroused by the sound of the bell, visual imagery established by means of form and color, tactile imagery acquired by cutaneous sensation, and finally, motor imagery gained by exploratory movements of the fingers and eyes (p.117).

Rather than being fixed, the subsequent re-activation of a perceptual symbol is endowed with a dynamical organization through which, for example, different contexts may bias the neural activity towards some properties more than others (Barsalou 1999, 2008). Following this proposal, the transduction of a perceptual state into an arbitrary symbol is not warranted

and the existence of amodal systems appears to be redundant, given that perceptual symbols provide both sensory and cognitive representations of external referents. A major objection moved to grounded cognition theories concerns the lack of compelling evidence able to demonstrate the causal role of the grounding mechanisms in concepts representation (Mahon & Caramazza, 2008). For instance, numerous findings reporting sensory-motor brain activity during conceptual processing offer support to the central claims of grounded cognition theories, but are nevertheless consistent with disembodied theories as well (Caramazza, 2014). Authors supporting this latter class of theories claim that it is ultimately unknown whether the activity in sensory-motor cortices follows or rather anticipates the access to symbolic representations (Mahon & Caramazza, 2008). From this perspective, sensory and motor brain activation merely accompanies and is epiphenomenal to conceptual processing, which is instead amodal and symbolic. One of the arguments in support of the amodal view emerges from neuropsychological data, in that impairments connected with objects usage (e.g., apraxia) are not necessarily paralleled by corresponding impairments in conceptual knowledge related to either the objects or their functional properties (Mahon & Caramazza, 2005; Vannuscorps & Caramazza, 2016). In contrast to both strictly embodied and disembodied theories, other models propose that modality-specific brain areas interact with one or more amodal abstract systems during semantic processing. Among these models, Damasio and colleagues proposed that multiple convergence zones exist and are differentially engaged depending on the specific conceptual domains and contextual constraints (A. Damasio, 1989; H. Damasio *et al.*, 1996). Convergence zones are defined as amodal regions, in that they do not map information in an embodied or feature-based manner (i.e. preserving sensory-motor patterns of experience), but they nonetheless strictly interact with sensory-motor cortices and prompt their co-activation through back-projections. More generally, the central function of high-level convergence zones is to unify the representations gained through different modalities, such as visual shape and action-related properties of tools. A related, yet different, proposal is the hub-and-spoke model (Rogers *et al.*, 2004; Patterson *et al.*, 2007). At least two main factors differentiate the two models: firstly, the convergence zone model suggests the existence of multiple convergence zones in semantic processing; secondly, it implies a differential activation in these areas based on differences in stimuli and tasks requests. The hub-and-spoke model assumes that concepts are mainly assembled through the contribution of multimodal experiences encoded in widespread modality-selective brain areas. Crucially, a single trans-modal hub, placed bilaterally in the anterior temporal lobes (ATLs), integrates these sources of information. In this view, the spokes, or units, generate several inputs, which all converge to the ATLs, where they are assembled into an unified semantic concept. As direct prediction of the hub-and-spoke model, damage to the ATLs hub should determine a general semantic impairment, which is neither dependent of the input or output modalities (i.e. pictures, words, sounds), nor limited to a specific semantic category (i.e. animals, tools) (Lambon Ralph & Patterson, 2008). This idea is strengthened by clinical observation that patients with semantic dementia, associated with atrophy and hypo-metabolism in anterior temporal regions (Gorno-Tempini *et al.*, 2011), show a consistent pattern of deficits across modalities, stimuli types, response modalities, and tasks. However, new evidence has prompted a slight revision of the original hub-and-spoke model, with the ventrolateral ATL assuming the role of the hub core-component (Rice *et al.*, 2015; Lambon Ralph *et al.*, 2017). For instance, cytoarchitectonic studies revealed a graded variation in function and structure within the anterior temporal lobe (Ding *et al.*, 2009) that matches differences in functional connectivity (Pascual *et al.*, 2013) and structural white matter connectivity (Binney *et al.*, 2012) patterns across ATL sub-regions. Moreover, neuroimaging studies reported that the ventrolateral ATL activates strongly in semantic tasks, irrespectively of input or output

modalities or stimuli category (Spitsyna *et al.,* 2006; Visser *et al.,* 2012). A further related model of semantic memory is the so called "embodied abstraction" (Binder & Desai, 2011; Kiefer & Pulvermüller, 2012), which asserts that multiple levels of abstraction exist in conceptual knowledge, from sensory-motor information to schematic and abstract representations. The contribution of each level varies flexibly in accordance with numerous factors, encompassing task demands, contextual constraints, and familiarity. For example, van Dam and colleagues (2012) observed that the activity in motor brain areas elicited by action-related words strongly depended on the context in which the words were presented. More specifically, BOLD response in inferior parietal region increased when participants focused on the action versus perceptual features associated with a word's referent object (e.g., *tennis ball:* play tennis versus yellow color). These results contrast the idea of a lexical entry invariably triggering a rigid semantic representation, and rather emphasize representational flexibility. Similarly, Hoenig *et al.* (2008) claimed that a variety of non-dominant object features can differentially contribute in conveying different nuances of meaning, while leaving the core meaning relatively unaffected. Familiarity is another key factor modulating the involvement of sensory-motor areas in conceptual processing, as less familiar concepts appear to be more dependent on detailed information encoded by modality-selective regions (Desai *et al.*, 2011).

**2. Concepts in semantic memory**

Category-specific semantic deficits, in which the identification of a category of items can be selectively damaged despite the relatively intact performance in other domains, have been particularly informative in unraveling the organization of conceptual knowledge in the human brain (Warrington, 1975; Capitani *et al.,* 2003; Cree & McCrae, 2003). One of the earliest recognized neuropsychological dissociations was the one distinguishing living (e.g., animals, plants) from non-living (e.g., inanimate objects) semantic categories. For instance, patients with Alzheimer's Disease generally show a spared performance with artifacts and non-living items, but a selective impairment with living entities (Silveri *et al.,* 1991; Garrard *et al.,* 1998; Chan *et al.,* 2001; Catricalà *et al.,* 2014). The opposite pattern, characterized by selectively impaired knowledge of artifacts, has been reported in cases of general brain atrophy (Moss *et al.,* 2000) and cerebrovascular accidents (Sacchett & Humphreys, 1992). However, a note of caution has been raised against the generalization of these effects, claiming for the necessity of a more controlled analysis of the different tasks and stimuli employed in existing studies (Laws *et al.,* 2005). Recent proposals suggested a continuum rather than a dichotomous distinction between living and non-living items. For example, Sha and colleagues (2015) proposed that a graded level of animacy discriminated between inanimate and animate entities, but then also between different animate exemplars, such as animals. In this view, higher animacy levels characterize those animals which more closely resemble the animate prototype of humans (e.g., monkeys), whereas the lower animacy bound encompasses the more phylogenetically distant ones (e.g., fishes). fMRI BOLD responses found in the ventral visual pathway mirrored this graded rather than dichotomous representational dimension for living and non-living entities (Sha *et al.*, 2015). A related and more general assumption states that the core of category-specific semantic deficits does not reflect a true category impairment but encompasses impairments in the modalities and features which mostly contribute to the acquisition, storing, and identification of a certain domain of concepts (Nastase & Haxby, 2017). For instance, greater importance of visual versus functional-motor information in the interaction with, respectively, animals and artifacts. In this view, categorical distinctions emerge as a complex combination of attributes.

Among non-living entities, manipulable objects have received particular attention, as several studies have been devoted to explore the constitutive dimensions that subtend their conceptual knowledge. The ability to use simple tools to extend motor skills constitutes

a shared ability between humans and certain animals (Johnson-Frey, 2004). For instance, non-human primates generally use sticks to reach distant objects. However, in humans this ability has achieved the most sophisticated level of complexity. At the beginning of the twentieth century, Liepmann and colleagues (1900) first described cases of ideomotor apraxia, manifested as the inability to use everyday objects and attributed to a loss of knowledge about tools. In most patients, ideomotor apraxia is caused by lesions in left premotor and parietal cortices or results from the disconnection of the right from the left hemisphere after damage to the corpus callosum. More recently, neuroimaging techniques have begun to precisely describe the brain underpinnings that subtend tools-related knowledge. A recent meta-analysis by Ishibashi *et al.* (2016) differentiated the neural substrates mediating the identification of tools from those subtending planning and executing actions toward tools. The former involve the bilateral fusiform gyrus and the left occipito-temporal cortex, whereas the latter involve the left dorsal and ventral premotor cortices and the left superior and inferior parietal cortices. In particular, motor-based properties, coding for object-directed actions, are crucial in the semantic representation of manipulable objects. Viewing and naming pictures of tools, but not pictures of other categories (i.e. animals, faces, houses), entails brain activations in left ventral premotor and posterior parietal cortices (Chao & Martin, 2000), despite the absence of motor task requests. Canonical neurons, located in premotor-parietal circuits, constitute an anatomical basis for the visuo-motor encoding of tools. As affirmed by Rizzolatti *et al.* (2014): "…when an object is seen, the discharge of canonical neurons encode a potential motor act congruent with the properties of the presented object, independently of whether the act will be executed or not" (p. 667).

Two aspects of motor-based manipulability properties are usually distinguished (Salmon *et al.,* 2010). The first one pertains to grasping, picking up, and lifting an object with one or both hands. This is the case with most manipulable artifacts, but can also occur with natural entities, for example small animals. The second one is the functional aspect of manipulability, which is coded independently of the object's dimension. For example, a grand piano requires both hands to fulfill its specific function, in spite of the fact that we typically not interact with it by picking it up and lifting it by the hands. Generally, semantic representation of manipulable objects conjointly involve both aspects, but partially distinct neural bases subtend each of them. In a semantic categorization task performed during fMRI scanning, Canessa *et al.* (2007) asked participants to indicate whether a pair of manipulable man-made objects shared, respectively, the same action-related pattern (i.e. grasping properties) or the same function (i.e. context of use). Direct comparison highlighted selective activation for action-related judgment in a left fronto-parietal system encompassing intraparietal sulcus, rostral part of the inferior parietal lobule, and dorsal premotor cortex. Function-specific activation was found in retrosplenial and parahippocampal regions, extending to inferotemporal cortex.

Recently, several studies have begun to explore the role of personal experience and context in modulating the access to tools' motor-based properties, both action- and function-related. Barsalou (1982) distinguished two types of properties in building conceptual representations and influencing the associations and similarities between concepts. On the one end, context-independent properties refer to those features whose memory access is unaffected by contextual constrains. For example, distinguishing properties for a given category fall into this domain (e.g., *gills* are diagnostic properties for identifying fishes). Crucially, context-independent properties include all the features that are particularly salient when people interact with the concept's referent (e.g., the property of being edible is central in interacting with an apple). On the contrary, context-dependent properties are not part of the concept's core meaning and constitute a source of variability in semantic representations, as they are only recruited in relevant contexts. For example, weight does not constitute a central

component in representing the meaning of a grand piano, but when we are required to move the grand piano, its weight becomes more salient than its functional properties and, consequently, we are more likely to perceive a stronger association between the grand piano and a couch compared to a guitar. Yee & Thomson-Schill (2016) claimed that conceptual knowledge is fluid and inextricably linked to specific contexts, which include for example long-term and recent experience, and the concurrent task demands. Although not directly referred to manipulable objects, several lines of research outlined the importance of personal long-term motor experience and acquired motor skills in modulating brain processes subtending action observation and representation. For example, in Calvo-Merino et al.'s fMRI study (2004), experts in classical ballet, experts in capoeira, and a group of inexpert controls viewed videos with actions taken from ballet and capoeira dances. The results suggested that the action observation system is tuned to the observer's acquired motor repertoire. For instance, enhanced activations in premotor and superior parietal cortices, intraparietal sulcus, and superior temporal sulcus were found when experts viewed videos of their own dance style, whereas no differences emerged in inexpert controls. In a subsequent study, Calvo-Merino et al. (2006) reported the impact of gender-specific expertise in influencing brain responses in classical ballet dancers. The authors compared brain activity when male and female participants viewed gender-specific movements (i.e. usually performed primarily by males or females dancers). Premotor, parietal, and cerebellar brain responses were selectively reported when participants viewed the movements which were specific of their own gender motor expertise. Other lines of research highlighted the structural brain changes induced by long-term motor expertise, possibly with a more direct link with tool-related knowledge. For example, Jäncke and colleagues (2009) explored the neuroanatomical reorganization in professional golfers by means of voxel-based morphometry. Playing golf requires the coordination of several movements of the upper and lower limbs, head and hips, also in relation to an instrument: precise hand postures and grips have to be adapted to the length, weight, and size of the different club types. In professional, high-proficiency golfers compared to naive participants, gray matter increases were found in a fronto-parietal network, comprising mainly dorsal premotor and posterior parietal cortices. Taken together, the aforementioned findings support the hypothesis that expertise and specific manipulation skills are capable of shaping the neural representation of a specific action type. One limitation of these studies, however, is that no direct causality can be established based on the mere association between motor skills and brain measures. To do so, one would require the possibility to monitor neural changes as they are shaped by the progressive acquisition of novel motor skills. At the structural brain level, this has been shown for instance by a longitudinal morphometry study in subjects required to learn juggling (Draganski et al., 2004), which induced gray matter volume increases in area hMT/V5 and in the posterior intraparietal sulcus. At the brain functional, semantic level, a methodological innovation has consisted in employing newly invented objects without similarities with existing tools, and thus not endowed with pre-existing memory representations, as experimental stimuli to directly assess the role of experience in building tool specific semantic knowledge. Weisberg et al. (2006), who first introduced this method, investigated whether manipulation experience acquired in a training session with novel objects induced activation increases in the fronto-parieto-temporal neural system. In the motor training, participants learned the object's function and were trained in the execution of specific actions associated with the objects (e.g., lifting a wooden block by means of the invented object). Two fMRI sessions were conducted, respectively, one before and one after training, during which the participants were presented with pictures of the trained objects and of control untrained objects in a visual perception task. Following training, enhanced brain activity was reported for trained versus untrained

objects in the middle temporal gyrus, posterior parietal cortex, and premotor cortex. Thus, tool-like experience with previously unencountered invented objects leads to the formation of a neural signature in semantic memory akin to that of real tools. A subsequent fMRI study by Bellebaum *et al.* (2013) aimed at disentangling the specific role of different types of experience in building semantic representations for novel tools. Participants were trained on different sets of novel tool objects with, respectively, a manipulation or a visual training. The former closely resembled the procedure applied by Weisberg and colleagues (2006), whereas the latter involved visually inspecting the novel objects without any direct or observed manipulation. Post-training increased activations were specifically found for manipulation versus visual experience in the left inferior/middle frontal gyrus and posterior parietal cortex, and for visual versus manipulation experience in the left middle temporal cortex. Effective connectivity analysis by means of Dynamical Causal Modelling in these brain regions revealed a fine-tuned combination of inter-regional modulatory effects, with an increase of connection strengths in regions specific to each experience type (fronto-parietal for manipulation, and temporal for visual experience), and a concomitant reciprocal decrease of experience type-specific connection strengths (temporal for manipulation, and fronto-parietal for visual experience). These results suggest that the experience-dependent neural signature formation in semantic memory is not rigidly determined by the object's physical properties, but very much depends on the type of interactions we gain with that object. In contrast to the previously mentioned studies (Weisberg *et al.,* 2006; Bellebaum *et al.*, 2013) and to other studies (Creem-Regehr *et al.,* 2007; Cross *et al.*, 2012), which involved direct manipulation of previously unencountered objects as an integral part of the training procedure, Rüther *et al.* (2014) demonstrated that even indirect manipulation experience, gained by observing another person interacting with a novel object, can promote semantic memory encoding in the sensorimotor system. Observed manipulation training, compared to visual training, specifically induced an activation increase in the left inferior frontal gyrus. These findings bear direct relevance to the observation-execution matching system implied in the evolutionary and developmental emergence of tool-related skills (Rizzolatti *et al.*, 2014; Johnson-Frey, 2004). Taken together, the results just reviewed suggest that the neural representation of tools is progressively acquired and shaped according to the type of interactions that we directly or indirectly experience with them. Accordingly, functional and motor-related properties represent a constitutive component of the conceptual knowledge about tools.

Recently, Tettamanti *et al.* (2017) demonstrated that the visual appearance of a manipulable object, even when escaping perceptual awareness, entails activations in the action representation system. The authors selected colored photographs depicting manipulable and, as a control, non-manipulable objects matched for visual complexity (Brodeur *et al.,* 2014). The authors adopted a Continuous Flash Suppression (CFS, Yang *et al.,* 2014) paradigm in order to make the stimuli subliminal. In CFS stimulation, the experimental subjects wear anaglyph glasses, with a cyan-colored lens placed over their dominant eye and a red-colored lens over the non-dominant eye. This permits the selective presentation of, respectively, rapidly flashing mask images with a cyan hue to the dominant eye, and a target stationary picture with a red hue to the non-dominant eye. Below an individually tailored perceptual threshold, the conscious perception of the target stationary picture is suppressed by the rapidly flashing masks, thus effectively implementing subliminal stimulus presentation. The subjective level of target image perception was evaluated by requiring the participants to rate their degree of perception along a 4-points perceptual awareness scale (PAS; Ramsøy & Overgaard, 2004). An objective control for the true absence of perception was provided by the inclusion of void stimuli (i.e. flashing masks but no target picture). Based on the individual perceptual

threshold, which was determined in a behavioral session prior to fMRI scanning, the authors used five incremental target picture contrast levels: two below, one equal to, and two above the individual perceptual threshold. The crucial issue was the evaluation of brain activations elicited by unaware processing of manipulable versus non-manipulable object pictures in a set of a priori selected brain regions, comprising a left-lateralized premotor-parietal network (Ishibashi *et al.,* 2016). The results provided positive evidence showing that manipulable object pictures presented below contrast threshold and escaping subjective awareness significantly activated the targeted brain regions, including the ventral premotor cortex, the inferior and superior parietal cortices, and the lateral middle temporal gyrus. This result was further supported by a searchlight Multivariate Pattern Analysis (MVPA), showing that a supporting vector machine classifier was able to distinguish above chance level manipulable and non-manipulable object pictures, presented below perceptual threshold and escaping subjective awareness. Taken together, these findings demonstrate that visuomotor coding represents a constitutive component of the conceptual knowledge about tools, one that is automatically activated by the visual perception of manipulable objects, even in the absence of awareness.

**3. Concepts in language format**

As shown by convergent evidence, the traditional language system comprises a set of core brain regions, mainly housed in inferior frontal and temporal cortices and also referred to as Broca and Wernicke areas, which contribute to a variety of linguistic functions, from comprehension to production (Friederici, 2011). In contrast, the role of additional brain regions in coding for specific semantic properties still remains controversial. According to embodied semantic theories, word meaning is coded in sensory-perceptual, motor, and emotion-related brain systems (Barsalou, 1999). For instance, words referring to entities with a strong relevance for color features (e.g., *taxi*, *grass*) elicit activations in brain regions involved in color perception, mainly located in the fusiform gyrus (Simmons *et al.*, 2007), whereas reading odor-related words (e.g., *garlic*, *cinnamon*) produces brain activation in the olfactory cortex (Gonzalez *et al.,* 2006). In addition, processing words with highly-relevant acoustic features (e.g., *telephone*) engages brain system for sound perception, encompassing the left posterior and middle temporal gyri (Kiefer *et al.,* 2008). Extended work has similarly revealed that the elaboration of words indicating both actions (e.g., action verbs such as *to grasp*) and manipulable items (e.g., nouns referring to tools such as *screwdriver*) relies on the neural system subtending action execution and observation. Vitali *et al.* (2005) investigated functional connectivity during a semantic fluency task requiring the retrieval of nouns referring to tools, in one fMRI scan, and to animals, in another fMRI scan. Tool word generation was specifically associated with increased functional connectivity in a left-hemispheric network, encompassing the inferior frontal and premotor cortices, the inferior parietal lobule, and the temporo-occipital junction. Rueschemeyer *et al.* (2010) investigated whether words indicating objects associated with different kinds of manipulability elicited distinguishable neural responses. A main distinction was made between volumetrically manipulable objects (i.e. items that could be lifted and moved, such as *clock*) and functionally manipulable objects (i.e. items that had to be picked up to use, and were closer to the common description of tools, for example *cup*). The words were presented in a go/no-go lexical decision task performed within the MRI scanner. Whole-brain analysis yielded stronger activations for functionally compared to volumetrically manipulable objects in the fronto-parietal system, encompassing pre-supplementary motor area and inferior parietal lobule. No regions were more active in the opposite contrast. These findings indicated that the specific way in which an object is manipulated constitutes an integral part of the neural semantic representation of the word denoting it. More recently, Yang and colleagues (2011) designed a fMRI passive reading task, in which participants were presented with verbs indicating an action performed with the

hand (e.g., *to touch)* or an action that required the use of a tool (e.g., *to cut).* Both conditions, compared to rest, yielded similar activations in a left lateralized system, encompassing middle and inferior frontal gyri, inferior parietal lobule, and premotor cortex. Crucially, tool-related compared to hand-related verbs elicited stronger activation as well as greater functional connectivity in these fronto-parietal regions. In yet another study, nouns referring to tools yielded activations in the hand sector of the premotor area (Carota *et al.,* 2012).

Different lines of research further emphasized the close link existing between the brain system mediating action and the comprehension of linguistic materials expressing an action-related content. Specifically, recent findings indicated the existence of interference effects exerted by the processing of words or sentences referring to both actions and manipulable entities on motor system activity. The study by Yee *et al.* (2013) suggested that the amount of interference in semantic tasks is proportional to the degree of motor practice with the object referents. Participants were engaged in a hand motion task, while they had to perform, respectively, a naming or an abstract/concrete categorization task. Each target word was also subjectively rated for the amount of manual experience generally associated with it. Crucially, the more manipulating experience with an object, the greater the interference effect between the motion task and both the concomitant semantic categorization and naming tasks. Moreover, Zarr *et al.* (2013) showed a motor system adaptation after reading sentences indicating actions carried out in the direction of the subject (e.g., *Liam kicked the stone towards you*) or in the opposite direction to it (e.g., *You kicked the stone towards Liam).* Participants were presented with a sentence, followed by a video showing an hand-object interaction, in which the object was placed in a container, respectively close to or distant from the volunteer's body and that could be either congruent or incongruent with the movement described by the sentence. The task required to indicate, as accurately and quickly as possible, the moment when the object exceeded the container's edge. Adaptation effects, with slower reaction times, were found when the sentence and the video were congruent (i.e. both referring to a movement in the same direction). Similarly, in the study of Marino *et al.* (2014), participants were presented with words indicating, respectively, graspable and non-graspable items and were instructed to press a button as soon as a change in the color of the square containing the words was detected. Slower motor responses were reported for graspable object words. The phenomenon was explained taking into account the recruitment of the motor system in accessing the conceptual-semantic representation of manipulable objects, leading to a reduced availability (i.e. interference) of the motor system itself for carrying out the behavioral response task. Other studies explored the desynchronization of the *mu* (8-13 Hz) brain wave rhythm, which is traditionally associated with the activation of the motor and premotor cortices elicited by executed or observed actions (Coudè *et al.,* 2014). Moreno *et al.* (2015) investigated whether the *mu* desynchronization is also observed in processing sentences describing actions (e.g., *You will cut the strawberry cake*). Participants were presented with action-related, abstract, or perceptual-state-related sentences, while the EEG signal was recorded. A desynchronization of the *mu* rhythm was specifically found for sentences denoting actions, and it was confined to the fronto-central electrodes corresponding to the premotor cortex. Cattaneo *et al.* (2010) used state-dependent transcranial magnetic stimulation (TMS) in order to investigate the causal role of the left ventral premotor cortex in representing tool-related words (e.g., *scissors).* Specifically, state-dependent TMS paradigms employ the interaction between the initial state of a neural population and the application of TMS pulses. The initial activation state was experimentally determined by means of a priming task. A differential TMS effect for primed versus non-primed trials could reveal neural specificity, indicating that the stimulated region is susceptible to the initial manipulation state (Silvanto *et al.,* 2008). Specifically, Cattaneo and colleagues (2010) set the initial activation state of left ventral premotor cortex through

a priming task, in which the prime was a category name (*tool* or *animal*) and the participants were required to categorize a target word presented immediately after. When the target word belonged to the tool category, TMS applied over the ventral premotor cortex facilitated reaction times for incongruent compared to congruent primes. This finding supports the causal involvement of the left ventral premotor cortex in encoding tool word meanings. Consistent evidence demonstrates that the activity produced by action-related linguistic meanings in the premotor cortex reflects a somatotopic organization, mirroring the bodily effector's homuncular motor maps. Somatotopically organized responses in the left premotor cortex were observed for isolated verbs referring to arm, face, and leg actions (e.g., *to pick*, *to lick*, *to kick*) in a fMRI passive reading task (Hauk *et al.,* 2004), and in the selective interference exerted by TMS on differential premotor cortex sectors during a lexical decision task (Pulvermüller *et al.,* 2005). Similar findings were reported by Tettamanti *et al.* (2005) during the auditory presentation of action-related sentences related to mouth (e.g., *I bite an apple*), hand (e.g., *I grasp a knife*), and leg (e.g., *I kick the ball*). More specifically, mouth-related sentences produced responses confined to the ventral-most sector, hand-related sentences in a medio-dorsal sector, and leg-related sentences in the dorsal-most sector of the premotor cortex.

In contrast to words referring to concrete entities, abstract concepts are still largely unexplored and they are often assumed to rely on a linguistic-mediated definition (Hoffman, 2015). Traditionally, concrete concepts refer to tangible items placed in the external world than can be directly experienced through the senses, a feature that cannot be applied to abstract concepts, which are not provided with physical referents. Concrete and abstract words can be differentiated along multiple psycholinguistic dimensions, including age of acquisition, familiarity, context availability, and imageability (Della Rosa *et al.,* 2010). Recently, a growing body of studies systematically explored other distinguishing aspects and features lying at the core of abstract semantic meanings, in particular various kinds of experiential information. According to grounded cognition theories, experiential information is crucial for both concrete and abstract concepts, albeit operating in different ways: concrete concepts mainly rely on sensory-motor information, whereas abstract concepts mainly rely on introspective and inner state information (Barsalou & Wiemer-Hastings, 2005). This view is supported by a limited, but growing body of neuroimaging studies. Ghio & Tettamanti (2010) explored the functional integration between perisylvian language regions and modality-specific brain regions involved in elaborating, respectively, action-related and abstract sentences. Using Dynamic Causal Modelling as a measure of functional integration, the authors found greater connection strengths for action-related versus abstract sentences in the left-hemispheric action representation system, encompassing sensorimotor areas. In turn, abstract sentences selectively modulated the effective connectivity of temporal and inferior frontal regions with the retrosplenial cingulate cortex, a region of the default mode network which has indeed been implicated in internal state monitoring (Raichle, 2010), and conjoint mapping of internal and external spaces (Alexander & Nitz, 2015).

At a more fine-grained level of distinction among different types of abstract concepts, converging findings supported the role of affective, social, and magnitude information as relevant distinctive dimensions (Ghio *et al.*, 2013; Troche *et al.,* 2014, 2017), with the first two of them associated, respectively, with the anterior cingulate cortex (Vigliocco *et al.,* 2014) and the superior anterior temporal lobe (Zahn *et al.,* 2007), i.e. brain regions involved in emotion processing and social cognition. In turn, magnitude-related concepts encompass numerical-arithmetical knowledge and linguistic terms roughly corresponding to quantity, time and space (Ghio *et al.,* 2013; Troche *et al.,* 2014, 2017). The intraparietal sulcus has been postulated as a potential neural basis supporting the processing of arithmetical concepts, given its role in representing numerical magnitude (Wilson-Mendenhall *et al.,* 2013). Recently, by applying

MVPA to fMRI data, Ghio *et al.* (2016) found that inferior frontal gyrus and insular regions selectively contributed to the discrimination of fine-grained types of abstract (mental states-, emotion-, and mathematics-related) and concrete (mouth action-, hand action-, and leg action-related) concepts. Brain hubs in which conceptual-semantic information converges and maintains fine-grained, category-specific selectivity, such as the inferior frontal and the insular cortices, most likely operate by means of combined local anatomical specialization and large scale connections. Fine-grained connectivity-based parcellation within the insula region has been clearly demonstrated, with a tripartite subdivision into cognitive, affective, and sensorimotor selective modules (Chang *et al.,* 2012).

Taken together, the aforementioned results provide compelling evidence that the neural representation subtending different semantic concepts expressed by linguistic stimuli is determined by the type of experience that we commonly have with the concepts' referents. This experience may come from either the external world, in the case of action-related and tool concepts, or from introspective, emotion-related, and inner mental states, in the case of abstract concepts.

As we have seen, in the context of grounded cognition theories, the qualities and degrees of personal experience with objects, feelings, and facts play a major role in the formation of distinctive semantic memories. Studies that challenge experimentally the role of personal experience are therefore vital to provide the theories with solid bases. Beilock and colleagues (2008) explored whether the degree of individual experience in specific actions was capable of modulating the neural resources which subtended the comprehension of language describing the same action. Ice-hockey players, fans (without direct experience but with extensive hockey viewing) and novices (without direct or indirect experience) participated in the experiment. During fMRI, participants were acoustically presented with sentences describing, respectively, ice-hockey actions (e.g., *The hockey player finished the stride*) and common everyday actions (e.g., *The individual pushed the bell*). Following each sentence, a picture was displayed and participants had to indicate whether it correctly matched the sentence by button press. As for everyday actions, all the three groups of participants responded faster to the pictures that matched the sentences, compared to those pictures that did not. In contrast, only ice-hockey players and fans showed a similar facilitatory effect for hockey-related sentences. The authors next explored whether the brain regions involved in sentence comprehension were also related to hockey experience. Specifically, activity within left dorsal premotor cortex positively correlated with hockey experience, and, in turn, bilateral dorsal primary sensory-motor cortex displayed a negative correlation. These findings provided evidence that individual sport experience influences action-specific language comprehension. Although remarkable, Beilock *et al.*'s (2008) study was characterized by a cross-sectional comparison between different populations (i.e. players, fans, novices), a feature that does not allow to draw strong conclusions as to the decisive role of motor experience, as opposed to other types of experiences (e.g., specialistic language use) or even individual predispositions leading to greater search and accumulation of motor experience. To overcome these limitations, a longitudinal study by Locatelli *et al.* (2012) was designed to train participants in performing previously unencountered manual actions, and to assess semantic language performance in pre and post training sessions. Over a period of three weeks, participants were trained in three different manual actions (e.g., origami, prestidigitation, tying sailors' knots). Before and after training they were tested on a semantic congruency task, similar to Beilock *et al.'s* (2008) study. Sentences and pictures could be congruent or incongruent and either related or unrelated to the trained actions. Reaction times of both trained and untrained congruent trials significantly decreased after compared to before training. Noteworthy, however, the post training reduction of reaction times was greater for trained compared to untrained

action-related concepts. The results suggested that manual expertise leads to an improvement in semantic processing specifically for concepts related to trained actions.

Since we rarely use abstract or concrete words in isolation, but rather use them in combination with other words in sentences and discourse, a crucial matter of investigation is how linguistic structure shapes semantic composition and the underlying neural dynamics. In the context of embodied and grounded cognition theories, a prototypical example, which we will only superficially deal with here, is that of figurative action-related expressions, as in the contrast between *I grasp the knife*, with a clear reference to motor action (i.e. *prehend*), versus *I grasp the idea*, in which a more metaphorical, abstract meaning is conveyed (i.e. *comprehend*). The complexity and diversity of figurative language constructions (e.g., metaphors, idioms, fictive motion expressions), diverging for global meaning access versus lexical decomposition, has not permitted until now to reach a general consensus with respect to the involvement of experience-dependent sensory-motor systems (for a review, see Ghio & Tettamanti, 2015).

A further quite interesting example of linguistic structural composition, which has recently fallen under increased scrutiny in the field of grounded cognition, is that of sentential negation. Sentential negation is a property embedded in syntactic structure, which is able to reverse the truth value of a declarative sentence (Horn, 1989; MacDonald & Just, 1989). The neural underpinnings subtending syntactic negation are still largely unexplored, although in previous years several psycholinguistic studies have been devoted to unravel how negation affects the processing of meanings. Several mental computations are required to understand linguistic utterances that include a negation marker such as *no* or *not*. Specifically, negation has to be linked to the mental representation of the concept or scope on which it operates. In sentence-picture matching tasks, longer reaction times have been traditionally found for negative (e.g., *The dots aren't red*) compared to affirmative (e.g., *The dots are black*) sentences (Just & Carpenter, 1971). Early proposals interpreted these effects as evidence that negated information is more difficult to process and requires additional computational resources than its affirmative counterpart. Subsequently, other approaches have also suggested that negation reduces the mental accessibility of the meanings expressed in its scope. MacDonald & Just (1989) investigated in three behavioral experiments the effects of negation during noun processing. In the first experiment, participants were presented with simple sentences containing a negation (e.g., *Almost every weekend, Elizabeth bakes no bread but only cookies for the children*) and were required to judge the truth value of a verification statement (e.g., *Elizabeth bakes cookies for the children*). Response times to negated nouns target were slower compared to non-negated ones. Similar results were obtained in the second and third experiments, where the interference effect of negation was investigated in naming tasks. The authors suggested that negating a noun exerts an influence on its semantic representation and, more specifically, reduces the strength of activation of the concept representation.

This body of behavioral observations led Tettamanti *et al.* (2008) to make predictions on the neural effects of negation on the semantic representation of action-related meanings from a grounded cognition perspective. These predictions were tested in an fMRI study involving sentential negation in a passive-listening task. The experimental stimuli were sentences characterized by the manipulation of negation polarity (i.e. negative vs. affirmative) and semantic concreteness (i.e. abstract, for example: *Now I appreciate loyalty*, vs. concrete, action-related, for example: *Now I push the button*). Independently of the level of concreteness, negative sentences compared to affirmative ones, yielded stronger inhibitory deactivations in the right middle frontal gyrus, right middle occipital gyrus, and left pallidum. As a main effect of concreteness, action-related sentences induced widespread activation in the left hemispheric fronto-parieto-temporal network underlying action representation, whereas abstract sentences yielded stronger brain responses in the left ventral inferior frontal gyrus,

in the inferior and middle temporal gyri, and in the posterior cingulate cortex. Crucially, the interaction between polarity and concreteness yielded significant modulatory effects in both networks, revealing a semantic category-specific BOLD signal reduction for negative compared to affirmative sentences. As for negative abstract sentences, an activity reduction was found in the posterior cingulate cortex, whereas for negative action-related sentences the reduced responses encompassed the left fronto-parieto-temporal network. Functional connectivity tested in the left fronto-parieto-temporal network by means of Dynamic Causal Modelling showed a significant reduction of connection strengths (i.e. of functional integration) specific for negative versus affirmative action-related sentences. These findings suggested a reduced access to the negated semantic information coded in experience-dependent, category-specific grounded representations, and led the authors to propose a "disembodiment effect" for sentential negation (Bartoli *et al.*, 2013). Subsequent experiments provided further evidence in support of this proposal. For instance, Tomasino *et al.* (2010) found that neural activity in the bilateral motor and premotor cortices was reduced when imperative verbs were presented in negative (e.g., *Don't write!*) compared to affirmative form (e.g., *Write!*). In a similar vein, Liuzza and colleagues (2011) applied paired-pulses Transcranial Magnetic Stimulation to the primary motor cortex, which at baseline exerts a facilitatory motor effect that is revealed by an increased amplitude of motor-evoked potentials (MEPs) in peripheral muscles. Simultaneously, participants were required to perform a passive reading task, including either abstract or hand-action related sentences, in both negative and affirmative forms. Crucially, reading action-related affirmative sentences suppressed MEPs, whereas this effect was absent for action-related negative sentences. The aforementioned results were recently corroborated by Bartoli *et al.* (2013), who tested the simultaneous recruitment of shared neural resources by semantic and motor tasks. The authors measured proximal (i.e. reach) and distal (i.e. grasp) upper limb movement kinematics during a motor task with simultaneous presentation of action-related sentences, including, respectively, either proximal (e.g., *I grasp*) or distal (e.g., *I pinch*) arm movements, in both affirmative and negative forms. Crucially, sentences describing actions in the negative, compared to the affirmative form exerted less interfering effects on kinematic parameters in the congruent conditions (e.g., proximal movement with proximal action-related negative sentence). These findings suggested that the comprehension of negative action-related sentences is characterized by a reduced computational load in embodied conceptual representations which, in turn, leaves more neural resources available to perform the concurrent motor task.

**4. Conclusions**

Far-reaching progress across all branches of the modern neurosciences has revealed the remarkable plasticity of the brain, as a learning organ that adaptively responds across the lifetime to stimuli, sensations, and experiences, and even insults. Evidence of brain plasticity confutes the view of the brain as an isolated, central storage and calculation machine, disconnected from the rest of the body and from the external world. In turn, it promotes a view of life as an integrated mind and body experience that is deeply rooted in the physical, social, and cultural environment. At the cognitive level, grounded cognition theories emphasize such plastic brain-body-environment integration, leading to a view of our mnemonic, linguistic, and more in general intellectual abilities as the product of our lifetime personal experiences, which ultimately shape our uniqueness as individuals.

**REFERENCES**

Barsalou, L. W. (2008). Grounded cognition. *Annu. Rev. Psychol.*, 59, 617-645;

— (1999). Perceptions of perceptual symbols. *Behavioral and brain sciences*, 22(4), 637-660;

— (1982). Context-independent and context-dependent information in concepts. *Memory & Cognition,* 10(1), 82-93;

Barsalou, L. W. & Wiemer-Hastings, K. (2005). Situating abstract concepts. Grounding cognition: The role of perception and action in memory, language, and thought, 129-163;

Bartoli, E., Tettamanti, A., Farronato, P., Caporizzo, A., Moro, A., Gatti, R., Perani, D. & Tettamanti, M. (2013). The disembodiment effect of negation: negating action-related sentences attenuates their interference on congruent upper limb movements. *Journal of neurophysiology*, 109(7), 1782-1792;

Beilock, S. L., Lyons, I. M., Mattarella-Micke, A., Nusbaum, H. C. & Small, S. L. (2008). Sports experience changes the neural processing of action language. *Proceedings of the National Academy of Sciences*, 105(36), 13269–13273, https://doi.org/10.1073/pnas.0803424105;

Bellebaum, C., Tettamanti, M., Marchetta, E., Della Rosa, P., Rizzo, G., Daum, I. & Cappa, S. F. (2013). Neural representations of unfamiliar objects are modulated by sensorimotor experience. *Cortex*, 49(4), 1110-1125;

Binder, J. R. & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in cognitive sciences*, 15(11), 527-536;

Binney, R. J., Parker, G. J. & Lambon Ralph, M. A. (2012). Convergent connectivity and graded specialization in the rostral human temporal lobe as revealed by diffusion-weighted imaging probabilistic tractography. *Journal of cognitive neuroscience*, 24(10), 1998-2014;

Brodeur, M. B., Guérard, K. & Bouras, M. (2014). Bank of standardized stimuli (BOSS) phase II: 930 new normative photos. *PLoS One*, 9(9), e106953;

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E. & Haggard, P. (2004). Action observation and acquired motor skills: an FMRI study with expert dancers. *Cerebral Cortex*, 15(8), 1243-1249;

Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E. & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology*, 16(19), 1905-1910;

Canessa, N., Borgo, F., Cappa, S. F., Perani, D., Falini, A., Buccino, G., Tettamanti, M. & Shallice, T. (2007). The different neural correlates of action and functional knowledge in semantic memory: an FMRI study. *Cerebral Cortex*, 18(4), 740-751;

Capitani, E., Laiacona, M., Mahon, B. & Caramazza, A. (2003). What are the facts of semantic category-specific deficits? A critical review of the clinical evidence. *Cognitive Neuropsychology*, 20(3-6), 213-261;

Caramazza, A., Anzellotti, S., Strnad, L. & Lingnau, A. (2014). Embodied cognition and mirror neurons: a critical assessment. *Annual review of neuroscience*, 37, 1-15;

Carota, F., Moseley, R. & Pulvermüller, F. (2012). Body-part-specific representations of semantic noun categories. *Journal of Cognitive Neuroscience*, 24(6), 1492-1509;

Catricalà, E., Della Rosa, P. A., Plebani, V., Vigliocco, G., & Cappa, S. F. (2014). Abstract and concrete categories? Evidences from neurodegenerative diseases. *Neuropsychologia*, 64, 271-281;

Cattaneo, Z., Devlin, J. T., Salvini, F., Vecchi, T. & Silvanto, J. (2010). The causal role of category-specific neuronal representations in the left ventral premotor cortex (PMv) in semantic processing. *Neuroimage,* 49(3), 2728-2734;

Chan, A. S., Salmon, D. P., & De La Pena, J. (2001). Abnormal semantic network for "Animals" but not "Tools" in patients with Alzheimer's disease. *Cortex*, 37(2), 197-217;

Chang, L. J., Yarkoni, T., Khaw, M. W. & Sanfey, A. G. (2012). Decoding the role of the insula in human cognition: functional parcellation and large-scale reverse inference. *Cerebral Cortex*, 23(3), 739-749:

Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, 12(4), 478-484;

Coudé, G., Vanderwert, R. E., Thorpe, S., Festante, F., Bimbi, M., Fox, N. A. & Ferrari, P. F. (2014). Frequency and topography in monkey electroencephalogram during action observation: possible neural correlates of the mirror neuron system. *Phil. Trans. R. Soc. B*, 369(1644), 20130415;

Cree, G. S., & McRae, K. (2003). Analyzing the factors underlying the structure and computation of the meaning of chipmunk, cherry, chisel, cheese, and cello (and many other such concrete nouns). *Journal of Experimental Psychology: General*, 132(2), 163;

Creem-Regehr, S. H., Dilda, V., Vicchrilli, A. E., Federer, F. & Lee, J. N. (2007). The influence of complex action knowledge on representations of novel graspable objects: evidence from functional magnetic resonance imaging. *Journal of the International Neuropsychological Society*, 13(6), 1009-1020;

Cross, E. S., Cohen, N. R., Hamilton, A. F. D. C., Ramsey, R., Wolford, G., & Grafton, S. T. (2012). Physical experience leads to enhanced object perception in parietal cortex: insights from knot tying. *Neuropsychologia*, 50(14), 3207-3217;

Damasio, A. R. (1989). Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition. *Cognition*, 33(1-2), 25-62;

Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D. & Damasio, A. R. (1996). A neural basis for lexical retrieval. *Nature*, 380(6574), 499;

Della Rosa, P. A., Catricalà, E., Vigliocco, G. & Cappa, S. F. (2010). Beyond the abstract—concrete dichotomy: Mode of acquisition, concreteness, imageability, familiarity, age of acquisition, context availability, and abstractness norms for a set of 417 Italian words. *Behavior research methods*, 42(4), 1042-1048;

Desai, R. H., Binder, J. R., Conant, L. L., Mano, Q. R. & Seidenberg, M. S. (2011). The neural career of sensory-motor metaphors. *Journal of cognitive neuroscience*, 23(9), 2376-2386;

Ding, S. L., Van Hoesen, G. W., Cassell, M. D. & Poremba, A. (2009). Parcellation of human temporal polar cortex: a combined analysis of multiple cytoarchitectonic, chemoarchitectonic, and pathological markers. J*ournal of Comparative Neurology*, 514(6), 595-623;

Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U. & May, A. (2004). Neuroplasticity: changes in grey matter induced by training. *Nature*, 427(6972), 311;

Friederici, A. D. (2011). The brain basis of language processing: from structure to function. *Physiological reviews*, 91(4), 1357-1392;

Garrard, P., Patterson, K., Watson, P. C. & Hodges, J. R. (1998). Category specific semantic loss in dementia of Alzheimer's type. Functional-anatomical correlations from cross-sectional analyses. *Brain: A Journal of Neurology*, 121(4), 633-646;

Ghio, M. & Tettamanti, M. (2015). Grounding Sentence Processing in the Sensory-Motor System. In *Neurobiology of Language* (pp. 647-657);

— (2010). Semantic domain-specific functional integration for action-related vs. abstract concepts. *Brain and language*, 112(3), 223-232;

Ghio, M., Vaghi, M. M. S., Perani, D & Tettamanti, M. (2016). Decoding the neural representation of fine-grained conceptual categories. *Neuroimage*, 132, 93-103;

Ghio, M., Vaghi, M. M. S. & Tettamanti, M. (2013). Fine-grained semantic categorization across the abstract and concrete domains. *PloS one*, 8(6), e67090;

Gonzalez J, Barros-Loscertales A, Pulvermüller F, Meseguer V, Sanjuan A, Belloch V, et al. (2006). Reading cinnamon activates olfactory brain regions. *NeuroImage*, 32(2): 906-912.

Gorno-Tempini, M. L., Hillis, A. E., Weintraub, S., Kertesz, A., Mendez, M., Cappa, S. F., Ogar J. M., J.D. Rohrer, J. D., Black, S., Boeve, B. F., Manes, F., Dronkers, N. F., Vandenberghe, R., Rascovsky, K., Patterson, K., Miller, B. I., Knopman, D. S., Hodges, J. R., Mesulam, M.M., &

Grossman, M. (2011). Classification of primary progressive aphasia and its variants. *Neurology*, 76(11), 1006-1014;

Hauk, O., Johnsrude, I. & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41(2), 301-307;

Hoenig, K., Sim, E. J., Bochev, V., Herrnberger, B., & Kiefer, M. (2008). Conceptual flexibility in the human brain: dynamic recruitment of semantic maps from visual, motor, and motion-related areas. *Journal of Cognitive Neuroscience*, 20(10), 1799-1814;

Hoffman, P. (2016). The meaning of 'life' and other abstract words: Insights from neuropsychology. *Journal of neuropsychology*, 10(2), 317-343;

Horn, L. (1989). *A natural history of negation*. Chicago, IL: University of Chicago Press;

Ishibashi, R., Pobric, G., Saito, S., & Lambon Ralph, M. A. (2016). The neural network for tool-related cognition: an activation likelihood estimation meta-analysis of 70 neuroimaging contrasts. *Cognitive neuropsychology*, 33(3-4), 241-256;

Jäncke, L., Koeneke, S., Hoppe, A., Rominger, C., & Hänggi, J. (2009). The architecture of the golfer's brain. *PloS one*, 4(3), e4785;

Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends in cognitive sciences*, 8(2), 71-78;

Just, M. A., & Carpenter, P. A. (1971). Comprehension of negation with quantification. *Journal of Verbal Learning and Verbal Behavior*, 10(3), 244-253;

Kiefer, M., & Pulvermüller, F. (2012). Conceptual representations in mind and brain: theoretical developments, current evidence and future directions. *Cortex*, 48(7), 805-825;

Kiefer, M., Sim, E. J., Herrnberger, B., Grothe, J., & Hoenig, K. (2008). The sound of concepts: four markers for a link between auditory and conceptual brain systems. *Journal of Neuroscience*, 28(47), 12224-12230.

Laws, K. R., Gale, T. M., Leeson, V. C. & Crawford, J. R. (2005). When is category specific in Alzheimer's disease?. *Cortex*, 41(4), 452-463;

Liepmann, H. (1900) Das Krankheitsbild der Apraxie (motorischen/ asymbolie). *Monatschrift fur Psychiatry und Neurologie* 8, 15–44.102–132, 182–197;

Liuzza, M. T., Candidi, M., & Aglioti, S. M. (2011). Do not resonate with actions: sentence polarity modulates cortico-spinal excitability during action-related sentence reading. *PloS one*, 6(2), e16855;

Locatelli, M., Gatti, R., & Tettamanti, M. (2012). Training of manual actions improves language understanding of semantically related action sentences. *Frontiers in psychology*, 3, 547;

MacDonald, M. C., & Just, M. A. (1989). Changes in activation levels with negation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 15(4), 633;

Mahon, B. Z. & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of physiology-Paris*, 102(1-3), 59-70;

— (2005). The orchestration of the sensory-motor systems: Clues from neuropsychology. *Cognitive neuropsychology*, 22(3-4), 480-494;

Marino, B. F., Sirianni, M., Volta, R. D., Magliocco, F., Silipo, F., Quattrone, A. & Buccino, G. (2014). Viewing photos and reading nouns of natural graspable objects similarly modulate motor responses. *Frontiers in human neuroscience*, 8, 968;

Markie, P., (Fall 2017). Rationalism vs. Empiricism, The Stanford Encyclopedia of Philosophy, Edward N. Zalta (ed.), Retrieved from https://plato.stanford.edu/archives/fall2017/entries/rationalism-empiricism/;

Moreno, I., De Vega, M., León, I., Bastiaansen, M., Lewis, A. G. & Magyari, L. (2015). Brain dynamics in the comprehension of action-related language. A time-frequency analysis of mu rhythms. *Neuroimage*, 109, 50-62;

Moss, H. E. & Tyler, L. K. (2000). A progressive category-specific semantic deficit for non-living things. *Neuropsychologia*, 38(1), 60-82;

Nastase, S. A. & Haxby, J. V. (2017). Structural Basis of Semantic Memory, in Learning and Memory: A Comprehensive Reference, 2nd edition, Volume 3; http://dx.doi.org/10.1016/B978-0-12-809324-5.21073-0

Pascual, B., Masdeu, J. C., Hollenbeck, M., Makris, N., Insausti, R., Ding, S. L. & Dickerson, B. C. (2013). Large-scale brain networks of the human left temporal pole: a functional connectivity MRI study. *Cerebral Cortex*, 25(3), 680-702;

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, 8(12), 976;

Pulvermüller, F., Hauk, O., Nikulin, V. V. & Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *European Journal of Neuroscience*, 21(3), 793-797;

Raichle, M. E. (2010). Two views of brain function. T*rends in cognitive sciences*, 14(4), 180-190;

Ralph, L., Matthew, A., & Patterson, K. (2008). Generalization and differentiation in semantic memory. *Annals of the New York Academy of Sciences*, 1124(1), 61-76;

Ralph, M. A. L., Jefferies, E., Patterson, K. & Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience*, 18(1), 42;

Ramsøy, T. Z. & Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenology and the Cognitive Sciences*, 3(1), 1-23;

Rice, G. E., Hoffman, P., Ralph, L., & Matthew, A. (2015). Graded specialization within and between the anterior temporal lobes. *Annals of the New York Academy of Sciences*, 1359(1), 84-97;

Rizzolatti, G., Cattaneo, L., Fabbri-Destro, M., & Rozzi, S. (2014). Cortical mechanisms underlying the organization of goal-directed actions and mirror neuron-based action understanding. *Physiological reviews*, 94(2), 655-706;

Rogers, T. T., Ralph, L., Matthew, A., Garrard, P., Bozeat, S., McClelland, J. L., Hodges J. R. & Patterson, K. (2004). Structure and deterioration of semantic memory: a neuropsychological and computational investigation. *Psychological review*, 111(1), 205;

Rueschemeyer, S. A., van Rooij, D., Lindemann, O., Willems, R. M. & Bekkering, H. (2010). The function of words: Distinct neural correlates for words denoting differently manipulable objects. *Journal of cognitive neuroscience*, 22(8), 1844-1851;

Rüther, N. N., Tettamanti, M., Cappa, S. F. & Bellebaum, C. (2014). Observed Manipulation Enhances Left Fronto-Parietal Activations in the Processing of Unfamiliar Tools. *PLoS ONE*, *9*(6), e99401;

Sacchett, C. & Humphreys, G. W. (1992). Calling a squirrel a squirrel but a canoe a wigwam: A category-specific deficit for artefactual objects and body parts. *Cognitive Neuropsychology*, 9(1), 73-86;

Salmon, J. P., McMullen, P. A. & Filliter, J. H. (2010). Norms for two types of manipulability (graspability and functional usage), familiarity, and age of acquisition for 320 photographs of objects. *Behavior research methods*, 42(1), 82-95;

Sha, L., Haxby, J. V., Abdi, H., Guntupalli, J. S., Oosterhof, N. N., Halchenko, Y. O. & Connolly, A. C. (2015). The animacy continuum in the human ventral vision pathway. *Journal of cognitive neuroscience*, 27(4), 665-678;

Silvanto, J., Muggleton, N. & Walsh, V. (2008). State-dependency in brain stimulation studies of perception and cognition. *Trends in cognitive sciences*, 12(12), 447-454;

Silveri, M. C., Daniele, A., Giustolisi, L. & Gainotti, G. (1991). Dissociation between knowledge of living and nonliving things in dementia of the Alzheimer type. *Neurology*, 41(4), 545-545;

Simmons, W. K., Ramjee, V., Beauchamp, M. S., McRae, K., Martin, A. & Barsalou, L. W. (2007). A common neural substrate for perceiving and knowing about color. *Neuropsychologia*, 45(12), 2802-2810;

Spitsyna, G., Warren, J. E., Scott, S. K., Turkheimer, F. E. & Wise, R. J. (2006). Converging language streams in the human temporal lobe. *Journal of Neuroscience*, 26(28), 7328-7336;

Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., Fazio F., Rizzolatti G., Cappa S. F. & Perani, D. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of cognitive neuroscience*, 17(2), 273-281;

Tettamanti, M., Conca, F., Falini, A. & Perani, D. (2017). Unaware processing of tools in the neural system for object-directed action representation. *Journal of Neuroscience*, 37(44), 10712-10724;

Tettamanti, M., Manenti, R., Della Rosa, P. A., Falini, A., Perani, D., Cappa, S. F. & Moro, A. (2008). Negation in the brain: Modulating action representations. *Neuroimage*, 43(2), 358-367;

Tomasino, B., Weiss, P. H. & Fink, G. R. (2010). To move or not to move: imperatives modulate action-related verb processing in the motor system. *Neuroscience*, 169(1), 246-258;

Troche, J., Crutch, S. J. & Reilly, J. (2017). Defining a Conceptual Topography of Word Concreteness: Clustering Properties of Emotion, Sensation, and Magnitude among 750 English Words. *Frontiers in psychology*, 8, 1787;

Troche, J., Crutch, S. & Reilly, J. (2014). Clustering, hierarchical organization, and the topography of abstract and concrete nouns. F*rontiers in psychology*, 5, 360;

van Dam, W. O., van Dijk, M., Bekkering, H. & Rueschemeyer, S. A. (2012). Flexibility in embodied lexical-semantic representations. *Human brain mapping*, 33(10), 2322-2333;

Vannuscorps, G. & Caramazza, A. (2016). Typical action perception and interpretation without motor simulation. *Proceedings of the National Academy of Sciences*, 113(1), 86-91;

Vigliocco, G., Kousta, S. T., Della Rosa, P. A., Vinson, D. P., Tettamanti, M., Devlin, J. T. & Cappa, S. F. (2013). The neural representation of abstract words: the role of emotion. *Cerebral Cortex*, 24(7), 1767-1777;

Visser, M., Jefferies, E., Embleton, K. V. & Lambon Ralph, M. A. (2012). Both the middle temporal gyrus and the ventral anterior temporal area are crucial for multimodal semantic processing: distortion-corrected fMRI evidence for a double gradient of information convergence in the temporal lobes. *Journal of Cognitive Neuroscience*, 24(8), 1766-1778;

Vitali, P., Abutalebi, J., Tettamanti, M., Rowe, J., Scifo, P., Fazio, F., ... & Perani, D. (2005). Generating animal and tool names: An fMRI study of effective connectivity. *Brain and language*, 93(1), 32-45.

Warrington, E. K. (1975). The selective impairment of semantic memory. T*he Quarterly journal of experimental psychology*, 27(4), 635-657;

Weisberg, J., Van Turennout, M. & Martin, A. (2006). A neural system for learning about object function. *Cerebral Cortex*, 17(3), 513-521;

Wernicke, C. (1874). Der aphasische Symptomencomplex: eine psychologische Studie auf anatomischer Basis. Cohn, 1874;

Wilson-Mendenhall, C. D., Simmons, W. K., Martin, A. & Barsalou, L. W. (2013). Contextual processing of abstract concepts reveals neural representations of nonlinguistic semantic content. *Journal of cognitive neuroscience*, 25(6), 920-935;

Yang, E., Brascamp, J., Kang, M. S. & Blake, R. (2014). On the use of continuous flash suppression for the study of visual processing outside of awareness. *Frontiers in psychology*, 5, 724;

Yang, J., Shu, H., Bi, Y., Liu, Y., & Wang, X. (2011). Dissociation and association of the embodied representation of tool-use verbs and hand verbs: An fMRI study. *Brain and language*, 119(3), 167-174;

Yee, E., Chrysikou, E. G., Hoffman, E. & Thompson-Schill, S. L. (2013). Manual experience shapes object representations. *Psychological science*, 24(6), 909-919;

Yee, E. & Thompson-Schill, S. L. (2016). Putting concepts into context. *Psychonomic bulletin & review*, 23(4), 1015-1027;

Zahn, R., Moll, J., Krueger, F., Huey, E. D., Garrido, G. & Grafman, J. (2007). Social concepts are represented in the superior anterior temporal cortex. *Proceedings of the National Academy of Sciences*, 104(15), 6430-6435;

Zarr, N., Ferguson, R. & Glenberg, A. M. (2013). Language comprehension warps the mirror neuron system. *Frontiers in human neuroscience*, 7, 870.