

Cortical motor contributions to language understanding*

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ABSTRACT

Here we review evidence from cognitive neuroscience for a tight relation between language and action in the brain. We focus on two types of relation between language and action. First, we investigate whether the perception of speech and speech sounds leads to activation of parts of the cortical motor system also involved in speech production. Second, we evaluate whether understanding action-related language involves the activation of parts of the motor system. We conclude that whereas there is considerable evidence that understanding language can involve parts of our motor cortex, this relation is best thought of as inherently flexible. As we explain, the exact nature of the input as well as the intention with which language is perceived influences whether and how motor cortex plays a role in language processing.

INTRODUCTION

Do we use the motor parts of our brain in understanding language? Given our everyday experience, a relation between these two domains of behavior may seem far-fetched at best. We typically do not have the impression that our motoric capabilities contribute to our understanding of the content of, say, a chapter in a scientific book (apart from that we need to move our eyes to be able to read these words). In this contribution we investigate evidence for a more profound relationship between language and action; one in which understanding language partially relies on using the cortical structures that we also use in ‘doing’, in action. In the remainder of this section we first introduce some theoretical background which underlies this idea. In sections 2 and 3 we turn to experimental evidence for two specific action-language relationships. In section 4 we discuss the relationship between language and action and provide some directions for future research. Section 5 summarizes the chapter.

Embodied cognition

The divide between cognition on the one hand and bodily action on the other has been central within cognitive science. Although several theorists have underlined the importance of action for cognition [1, 2], action and cognition have been studied mostly as separate domains. This can be regarded as a reflection of traditional ‘Cartesian’ or ‘orthodox’ cognitive science. Mind and body are fundamentally different entities in this framework although they closely interact with each other. This strong metaphysical divide has led to the common notion that cognition is separated from action [3-7]. Consequently, language—as a sub-domain of cognition—and action have also been traditionally studied as distinct faculties of the mind [8].

From an embodied cognition viewpoint however, contrary to the classical Cartesian view, the importance of bodily processes for cognition is central. Cognition is thought of as ‘grounded’ in and therefore inseparable of bodily action [4, 5, 7, 9-13]. The representation of a concept is for instance proposed to be crucially dependent upon perceptual-motor processes that relate to that concept [14]. This stands in contrast to a more traditional, ‘cognitivist’ stance in which a concept’s meaning is considered to be an amodal symbolic representation [15].

Embodied cognition comes in very different degrees, from only slightly modifying the traditional Cartesian view to more radical claims about, for instance, the extension of the human mind into the environment [16]. These more and less radical proposals have in common that they stress the importance of connections between bodily actions and cognition or more specifically, action and language. This interrelatedness should ultimately be reflected in overlap of brain

processes supporting language and action. In the following sections we describe experimental evidence for two kinds of action-language relations.

Structure of the chapter

We have structured this review according to two different combinations of language and action that have been studied by cognitive neuroscience. First, we look at studies investigating the neural representations of speech sounds during comprehension. Some proposals argue that the neural representation of a speech sound during comprehension may involve structures in the motor cortex used in pronouncing a speech sound. This is a clear example in which researchers have looked for a neural link between language (speech sound) and action (motor cortex representation of the speech sound). Second, we review studies on the neural representation of action-related language. Here, the assertion is that the meaning of for instance an action verb is at least partially represented in the cortical motor system. In other words, to understand action-related language, activations in the motor system are crucial. The idea of a linguistic entity (e.g. action word) as being represented in the neural motor system is comparable to that for speech sounds, however now at a semantic level. A neural link between language and action would be shown in this case if indeed the perception of action verbs leads to activation of parts of the action network in the brain.

Some notes on methods

In this chapter we take a cognitive neuroscience perspective on the question of how action and language may be related. We discuss findings from measurements in the healthy human brain. The measurements that we describe are done using several neuroimaging methods. One set employs indirect measures of neural activity, such as increased blood oxygenation levels, to investigate which brain regions are activated in a given task. Examples are functional magnetic resonance imaging (fMRI) and positron emission tomography (PET). Another set of methods measure electrical or magnetic fields generated by large groups of neurons. These signals are measured at the scalp using Electroencephalography (EEG) or Magnetoencephalography (MEG). By time-locking and averaging the EEG/MEG signal to a number of stimuli representing a given cognitive event (e.g. reading of a word), event related potentials / fields (ERPs from EEG, ERFs from MEG) are generated. Another technique that we will refer to is transcranial magnetic stimulation (TMS), in which a magnetic field is exerted onto a relatively focal part of the cortex. This technique is most well-known as a ‘virtual lesioning’ technique, in which part of the cortex is temporarily (and reversibly) ‘knocked out’. This technique is mainly used to establish whether

the stimulated area is causally involved in the process under study. Another way of employing TMS is to measure the motor evoked potential (MEP) in a muscle, while stimulating the motor cortex by a TMS pulse. The pulse will evoke an MEP when the subject is at rest. The rationale of this approach is that if motor cortex is involved in reaction to a given stimulus, an increased excitability of the motor cortex will lead to an increased MEP as compared to reaction of a stimulus which does not excite the motor cortex.

Examples of studies employing these techniques will clarify their potential for the questions under study. For now it suffices to say that fMRI and PET are techniques with a moderately good spatial resolution (measuring from 'voxels', small cubes of brain tissue, of typically 3x3x3 mm), but with poor temporal resolution (in the order of several seconds). On the contrary, EEG/MEG has superior temporal resolution (in the order of milliseconds), but less accurate spatial resolution. The strongest point of TMS is that it has the potential to determine whether a cortical area is causally involved in a given process, whereas fMRI and PET are correlational techniques.

MOTOR REPRESENTATIONS OF SPEECH SOUNDS

Motor theory of speech

A first area in which the connection between language and action has been made is that of speech perception. Especially the motor theory of speech perception [17] has made strong claims about this connection. This theory posits that perceived speech sounds are directly mapped onto the motor representations of the articulatory gestures that would be necessary to produce these speech sounds. For example, upon hearing the word 'ball' the incoming sounds are mapped onto the stored motor representations that are recruited when pronouncing the word 'ball'. Crucially, in this theory, speech perception takes place by directly mapping the speech input onto a motor representation. In this way, the activation of motor representations is what constitutes speech perception. In the light of the recent findings of mirror neurons in motor areas [18, 19] this theory has gained renewed popularity. The prediction that has been tested mostly is that perceiving a speech sound should activate the same motor representation in the brain as producing that speech sound. Note that this is a far less radical claim than proposed by the motor theory of speech perception. After all, activation of similar motor areas does not implicate that these are crucial for speech perception. We will get back to this after reviewing the studies on this topic.

Experimental evidence

Several neuroimaging studies have provided evidence for the hypothesis that perceiving a speech sound activates similar brain regions as producing that speech sound. In an fMRI experiment [20] subjects listen to meaningless syllables (e.g. /pa/) and subsequently pronounce the same syllables. They report overlapping activations during perception and production in bilateral precentral gyri and central sulci (premotor and primary motor cortex). Activation in these areas was significantly higher to the perception of the syllables than to non-speech sounds (e.g. the sound of a bell). In a related experiment, it was found that producing syllables which start with phonemes that involve movement of the lips or of the tongue ([p] and [t], respectively) activated the same portions of precentral cortex as listening to these syllables [21]. Moreover, these regions overlapped with those activated when subjects simply moved their tongue or lips, that is, without speech production. Note that the cortical motor system at this level has a somatotopic organization, such that distinct parts command different effectors in a structured manner. Pulvermuller et al. showed that when listening to or pronouncing syllables related to lip or tongue movements, the same organization is preserved. In other words, parts of premotor cortex that become activated when moving the lips or tongue also become activated when listening to speech sounds that involve movement of the lips or tongue. In an interesting variant of this line of research, English speaking subjects were presented with native (English) and non-native phonemes [22]. The non-native phonemes were rated to be hard to pronounce by native speakers of English. The assumption of this study was that no motor representations would exist for the non-native phonemes, since they are not produced by speakers of English. Activity in superior temporal areas was negatively correlated with the producibility of a phoneme. That is, the harder a phoneme was to produce for the English speakers, the more superior temporal areas were activated. Premotor cortex also distinguished between native and non-native phonemes, in the sense that activation was higher for nonnative than for native phonemes. The authors argued that since a match between stored and perceived speech sounds is impossible, hearing a non-native speech sound led to an activation increase. These data neither support an exclusively sensory (reflected in superior temporal activation) nor motor (reflected in premotor activation) account of speech perception. Overall, these fMRI studies suggest that merely listening to speech sounds activates parts of the neural motor system. Moreover, this activation seems to be rather specific in the sense that listening to speech sounds which involve movement of the lips also leads to activation of part of the motor cortex involved in actually moving the lips.

Another way of assessing whether motor cortex is activated during speech perception is to use TMS to measure the excitability of the motor cortex while subjects perceive speech.

Fadiga and colleagues measured MEPs of tongue muscles while stimulating the part of the motor cortex that leads to movement of the tongue [23]. Subjects listened to Italian words containing phonemes that in production lead to strong movement of the tongue (e.g. 'birra') or to words that induce less tongue movement (e.g. 'baffo'). If listening to words evokes specific activation of the motor system, greater tongue muscle activation is expected to 'tongue words' than to 'non-tongue words'. Indeed, stronger MEPs were found when subjects listened to the 'tongue words' compared to when subjects listened to the 'non-tongue words'. Interestingly, this effect was also present with non-words with similar acoustic characteristics as the real words. However, in the non-words the MEP levels were smaller overall, which suggests a lexical influence on the motor representation of speech sounds.

Instead of looking at tongue muscles, in a related experiment the activity of lip muscles was measured [24]. Increased MEPs of lip muscles were found in response to stimulation of the mouth representation in motor cortex while subjects listened to continuous prose. Hand muscles were recorded as a control condition while the cortical hand area was stimulated. No modulation of hand muscles was found. In contrast to this latter finding, [25] found facilitation of hand muscles to stimulation of hand motor cortex during speech perception. No such facilitation was found during a nonlinguistic memory task. This finding was explained in the context of an evolutionary scenario in which language is thought to have evolved out of manual communication. It is unclear why these authors do find modulation of hand muscles, and others [24] did not. In [26] activation across the whole brain using PET as well as MEPs of mouth muscles were measured after stimulation with TMS. Activity in an area in the left inferior frontal cortex ('Broca's area') was correlated with the facilitation of the mouth muscle. The authors argue for Broca's area as 'priming' the motor system in response to speech perception. Most TMS studies complement evidence from fMRI studies that found activation of parts of the motor cortex in listening to speech sounds [but see 27]. Facilitatory effects are reported for tongue, lip as well as hand muscles, depending upon the specifics of the experiment. The activation of motor cortex is reasonably fast, such that a TMS pulse given 100 ms after onset of a critical speech sound leads to a facilitation of the muscle involved in its production [23].

In another line of work, TMS was used to temporarily interfere with processing in motor-related areas. Transcranial magnetic stimulation (TMS) allows one to briefly and temporarily interfere with processing in a relatively focal part of cortex. This technique was used to assess whether motor resonance in reaction to listening to speech sounds is effector-specific. Participants listened to 'lip-related' and 'tongue-related' phonemes (e.g. [b] and [p]) and performed a categorization task while parts of primary motor cortex involved in moving the

tongue, or part of primary motor cortex involved in moving the lips, was stimulated. Stimulation occurred briefly (50 ms) before onset of the phoneme and led to a speeded response in the case of a ‘matching’ phoneme and to a slower response in the case of a discordant phoneme [28]. That is, if the lip-related area of M1 was stimulated before hearing the ‘lip-related’ phoneme ‘[b]’, participants were faster to categorize the phoneme, whereas they were slower to categorize the ‘tongue-related’ phoneme ‘[d]’ (and vice versa). The authors concluded that motor cortex seems to be causally (and not ‘just’ correlationally) related to perception of speech sounds.

A similar line of argument was used in a study in which slow repetitive TMS was used to temporarily ‘lesion’ parts of premotor cortex [29]. It was shown that participants were selectively impaired on phoneme discrimination after such stimulation over left premotor cortex, but not after stimulation over superior temporal areas. Interestingly, the reversed pattern was observed for tone detection (impaired after superior temporal stimulation, but not after premotor cortex stimulation).

Section summary

In sum, fMRI and TMS studies indicate that representations of speech sounds in (pre)motor cortex that are activated during speaking, are also activated while listening to speech sounds. Although it might be tempting to interpret this in terms of the motor theory of speech perception, note that the studies reviewed here do not provide unequivocal evidence that motor activation is necessary in understanding language, as was argued by the motor theory of speech perception [30]. The finding of a lexical modulation of MEPs to words versus non-words with the same acoustic properties [23] for instance shows that speech sounds are not invariantly mapped onto motor representations, but are modulated by higher level processes [see also 22]. Moreover, temporal ‘lesioning’ with TMS impairs phoneme categorization / discrimination, but does not render it impossible [28, 29]. Although these studies cannot prove the motor theory of speech perception [31], they do provide evidence for a link between language and action in the brain. After all, it is consistently reported that merely listening to speech or speech sounds activates part of the motor system involved in producing speech sounds.

ACTION SEMANTICS

So far, we have discussed a connection between language and action that is restricted to a form level without the requirement of access to the semantics of words. This is different for action-related language. The question here is: Do words describing actions activate parts of the brain involved in sensorimotor processes, such as premotor cortex? If so, this would provide evidence

for a link between language and action in the brain because the assertion would be that parts of the brain that are activated when performing or observing an action are also activated when comprehending language describing that action. We will first look at studies presenting single action verbs. Later we look at studies presenting participants with sentences describing actions, either in literal or in a metaphorical sense.

Reading verbs

Hauk and colleagues [32] took advantage of the somatotopic organization of the motor cortex to investigate the representation of action verbs. Subjects read verbs describing actions performed with the feet, hands or face (e.g. ‘kick’, ‘pick’, ‘lick’). Subsequently, they performed simple actions with foot, finger or tongue, which activated primary and premotor cortex in a somatotopic fashion, as expected. Interestingly, reading action verbs led to a similar somatotopic pattern of activation. Overlap between parts of (pre)motor cortex activated by action verbs and by action production was clearly observed for two of the three effectors. Converging evidence for the involvement of motor areas in processing action words comes from a recent PET study, which reports increased activation in left precentral and central sulcus (i.e. premotor and primary motor cortex) when comparing motor words (both nouns and verbs) to sensory words (also both nouns and verbs) [33]. Kemmerer and colleagues replicated the somatotopic activation in premotor cortex and additionally showed that different verb types which share the semantic feature ‘ACTION’ all activate premotor structures [34]. On the contrary, the semantic feature ‘MOTION’ consistently activated more posterior areas known to be involved in movement processing [see 35 for discussion].

Willems, Hagoort and Casasanto investigated whether the premotor cortex activation in response to action verbs is body-specific, meaning that it could be different for individuals with a different preference to perform hand actions. They measured brain activation (with fMRI) in healthy left- and right-handed participants who engaged in a simple lexical decision task [36]. Participants read words strongly related to hand actions and action verbs less strongly related to hand actions. A different lateralization pattern in reaction to the reading of hand action verbs was observed in left- and right-handers: left-handers activated their right premotor cortex more strongly and right-handers activated left premotor cortex more strongly. This is to be expected if semantic activation in reaction to the reading of action verbs involves creating a body-specific representation. After all, the left hand is mainly controlled by the right motor cortex and vice versa. Since left-handers prefer to act out the action that the verbs referred to with their left hand, they activated right premotor cortex more strongly, and the reverse was true for right-handers.

Together, these studies provide evidence for the activation of premotor cortex in response to action words. Moreover, it shows that this activation is rather specific in the sense that action verbs performed with a certain effector elicit activation in the area that is also activated when using that effector. A possible criticism is, however, that the activations in motor cortex may be the by-product of imagery of an action. This would mean that the premotor activations are not part of the representation of the action verb, but rather emerge only after the action concept is identified. In our own work, we tried to account for this by asking participants to actually imagine performing the actions described by the action verbs. That is, the same participants were scanned twice: the first time they performed lexical decision task on visually presented action verbs, the second time they imagined themselves performing these actions [36, 37]. Our results show that both reading for lexical decision as well as explicit motor imagery evoked effector-specific activations in premotor cortex. However, these activations were not overlapping, which argues against an interpretation of the activations observed during reading as reflecting motor imagery. We will get back to this finding in the discussion section.

Studies using TMS and EEG/MEG have additionally been used to argue against an imagery-related interpretation of motor cortex involvement during reading of verbs. For instance, Some have argued against an explanation of their results in terms of mental imagery [38]. In a TMS study hand/arm and leg words were presented while stimulating the ‘hand/arm’ and ‘leg area’ of the motor cortex [38]. Subjects’ task was to make a lexical decision to the visually presented words. Faster reaction times were observed to hand/arm words after stimulation of the ‘hand/arm area’ as well as to leg words after stimulation of the ‘leg area’. This was taken as evidence that the (pre)motor activation is a crucial part of the action verb’s semantic representation, because stimulating the motor cortex speeded up lexical decision. In related MEG and EEG studies it was found that differences between leg, arm or face words emerge around 200 ms [39, 40]. Again, the localizations of these effects showed a dissociation between leg words in dorsal premotor cortex and arm and face words in more ventral premotor regions. The authors argue that the latency of this effect is too fast to be explainable in terms of general strategic effects such as imagery.

A related but partly different result than that of premotor cortex activation to action words was obtained in two fMRI studies [41, 42]. Neural activity in these studies was compared while subjects performed a semantic matching task on triads of pictures or words describing actions or objects. Subjects’ task was to indicate which two objects or actions were semantically related to each other. In one of these studies increased activity to action words was observed in the motor cortex just as in the studies described above [41]. However, additionally, increased

activation was found in the vicinity of human motion area MT/MST [41, 42], when subjects had to judge actions compared to when they had to judge objects. That is, the judging of actions evoked activity in areas implicated in the processing of motion which is implicated by actions but not by the observation of objects.

Two other studies in part confirmed the findings of activation of (pre)motor cortex to action words. Noppeney and colleagues [43] report increased activation of left posterior temporal and anterior intraparietal areas in reaction to action words compared to abstract words. Only at a lower, uncorrected statistical threshold did they observe ventral premotor cortex activation. Ruschemeyer and colleagues compared activations to action verbs with ‘complex verbs’ that had the action verb as its stem, but did not have an action-related meaning [44]. For example the German verb ‘greifen’ (to grasp) was compared to ‘begreifen’ (to understand). The rationale was that if action verbs automatically activate parts of the motor cortex, this should also be the case in complex verbs that include an action verb, such as ‘begreifen’. Action verbs did activate premotor areas compared to abstract verbs. No such activation was however found in response to the complex verbs (i.e. verbs with an action stem but a non-action meaning). The conclusions to be drawn from this study however crucially depend on whether one believes that complex verbs such as ‘begreifen’ are stored with ‘greifen’ (‘to grasp’) as their stem.

Comprehending sentences

An approach related to the study of action words has been taken by a few studies comparing sentences describing actions to sentences describing abstract events. One fMRI study presented subjects with spoken sentences like ‘I bite an apple’ and ‘I appreciate sincerity’ [45]. The action sentences could be of three types: describing mouth actions (‘I bite an apple’), hand actions (‘I grasp the knife’) or leg actions (‘I kick the ball’). All action sentences activated left inferior frontal cortex more strongly than abstract sentences did. Moreover, sentences describing actions with different effectors activated the premotor cortex in a somatotopic manner. This result is comparable to that of action verbs which lead to premotor cortex activation in a somatotopic manner [32].

A TMS study measured MEPs from hand and foot muscles while subjects listened to hand and foot related action sentences or to abstract sentences [46]. Stimulation of hand and foot areas in motor cortex led to decreased MEP amplitudes during perception of sentences related to the same effector; that is, for instance, stimulation of the hand area led to a decreased MEP in the hand muscle when subjects listened to a sentence implying an action done with the hand compared to a sentence describing an action done with the foot. Note that this is an opposite

finding from other TMS studies with a similar design that generally report increases in MEP amplitudes, which is then interpreted as reflecting increased facilitation of the motor cortex. Buccino and colleagues related their opposite findings to the non-specificity of spoken language as compared to the observation of real, visual action. However, this does not explain the reversal of the effect compared to other studies using action words.

The results of study by Boulenger and colleagues [47] might shed light on the conflicting findings of Buccino et al [46]. That is, Boulenger and colleagues measured arm movement kinematics of a grasping action that could either start slightly before the presentation of an action verb or after the presentation of an action verb. This manipulation resulted in a complete reversal of findings: when the word was processed before the onset of the action, grasping was facilitated. That is, the action was performed faster when preceded by an action verb than when preceded by a concrete noun (the control condition). However, when the action verb was read when the action had already started, the action was performed more slowly compared to the presentation of a concrete noun, indicating interference. As the authors note, this may explain why some TMS studies find an increase in MEPs (indicating facilitation), whereas others find a decrease in MEPs (indicating interference). Indeed, TMS pulses in Buccino et al. were delivered during the reading of an action verb, whereas they were applied shortly after the verb in other TMS studies [e.g. 38]. Future studies should systematically investigate the order of information flow in these different cases.

A TMS study showed that also abstract sentences invoke motor cortex activation [48]. Participants were presented with spoken sentences that described transfer (movement) of a concrete object, as in ‘Andrea carries the pizza to you’ or sentences describing the transfer of an abstract object, such as ‘Arthur presents the argument to you’. It was hypothesized that the abstract sentences would be understood by activating the same transfer schema that is also used to comprehend literal transfer. Control sentences described events without the involvement of transfer (e.g. ‘You smell the pizza with Andrea’). The main finding was an increase of MEPs to transfer sentences compared to non-transfer sentences. Moreover, there was no difference between concrete transfer sentences and abstract transfer sentences. This study suggests that not only concrete language describing an action activates part of the motor cortex, but that this also holds for abstract ‘transfer sentences’.

It has been found that action sentences activated premotor areas in a specific manner corresponding to whether sentences described an action done with the foot, hand or mouth [49]. Moreover, the activation to a sentence type (i.e. foot, hand or mouth) was strongest in the area that was activated when the subject watched videos of that same type of action (actions

performed with the foot, hand or mouth). Interestingly, this effect was not present when stimuli consisted of metaphors in which action verbs were used, such as ‘He was chewing on the problem’. If one envisions (pre)motor cortex activation upon reading of an action verb to be automatic [14, 50], it may be predicted that even when the action verb is used metaphorically, it will activate parts of premotor cortex. Few studies have looked into this and the evidence is mixed. Aziz-Zadeh et al. [51] and Raposo et al. [52] did not find sensitivity of premotor areas to metaphorically used action sentences, whereas Boulenger and colleagues claimed to find a somatotopic activation pattern in premotor cortex upon reading of sentences such as “He kicked the habit” [53]. The discrepancy between these studies could be due to subtle differences in sentence materials and probably also task factors (see below). A definite answer awaits future research, but these findings suggest that reading of metaphorical action-language does not necessarily or automatically evoke motor cortex activations [cf. 14, 50].

Some recent findings similarly question the robustness of motor involvement in reading of concrete action verbs. For instance, Postle and colleagues did not observe effector-specific action execution and action verb reading overlap in premotor cortex [54]. In addition, Sato and colleagues showed that interference due to repeated presentation of hand action verbs is highly task-dependent. That is, they only observed motor interference of button presses to hand action verbs when participants performed an explicit semantic judgment task in response to the action verbs, but not when they engaged in lexical decision [55].

Section summary

In short, there is a considerable amount of evidence for the claim that listening to action-related language can activate cortical motor areas. However, differences in materials and task setting influence whether motor cortex is activated in response to reading action-related language [54, 55]. Hence it is unclear whether motor cortex activation is a necessary part of the semantic representation of an action verb. What the studies reviewed here show is that motor areas can be activated upon hearing or reading an action word. To find out if the motor cortex is necessary in action word understanding, it needs to be shown that ‘knocking out’ the motor cortex (e.g. by repetitive TMS) specifically hampers the understanding of action words. Another concern in most of these studies is the role of imagining what is being heard. Many results could reflect the contribution of motor imagery, since this is often not explicitly controlled for [but see 36, 37]. In addition, it is not always easy to evaluate the weight of the conclusions, since most studies in this field are conducted without an explicit theory of semantic representation in mind. As a consequence, the precise implications of (pre)motor cortex activation are often unclear. Despite

these concerns, it is fair to conclude that the studies reviewed above provide ample evidence for a link between language and action, insofar as that parts of motor cortex can be activated in response to action-related language.

DISCUSSION

This chapter is concerned with the involvement of cortical motor areas in understanding language. We have seen that studies in cognitive neuroscience provide evidence for links between language and action in the brain. First, motor areas activated in speech production are also activated when listening to speech sounds. Second, there is evidence for the involvement of the motor system in understanding action-related language. In sum this can be taken as evidence in favor of an (embodied) approach to cognition in which language is thought to be grounded in bodily action. In the remainder of this section we set out to place these findings in a broader perspective of language understanding and to raise some issues we feel will be crucial for future research.

Embodied language understanding?

We started out our chapter with a description of embodied cognition, which forms the theoretical basis for the idea that language understanding may involve cortical motor contributions. The reviewed studies can be easily taken as evidence in favor of this position. However, as Mahon and Caramazza point out, the large majority of findings in this literature can also be explained from a *disembodied* perspective [56]. The argument goes like this: it is possible that cortical motor activation during for instance reading of action-related language arises because of spreading activation from abstract conceptual representations to sensory-motor representation. In their own words: “In the context of a disembodied theory of concept representation, those facts would indicate that activation cascades from disembodied concepts to the sensory and motor systems that interface with the conceptual system.” [56 , p. 60]. These remarks remind us that the embodied perspective is often underspecified. We do not see much sense in splitting hairs on what should be called ‘embodied’ or ‘disembodied’. The data that we reviewed provide a case for some involvement of the motor system in language processing. The remaining question is how this role can be best characterized. To put it more bluntly: what are sensory-motor parts of the brain doing during language understanding? We believe that a key answer lies in treating language understanding and semantic representations as flexible. We will elaborate on this in the next section.

The flexibility of language understanding

So far we have treated ‘language’ as a relatively unitary and stable phenomenon. For instance, we discussed reading action-related language as a single cognitive process. Here we want to argue that motor cortex activation to action semantics is flexible and depends upon the nature of the input as well as on the task at hand for the comprehender [see also 56, 57]. One could on the contrary argue that activation in the motor system to reading of the verb ‘throw’ is not influenced by the linguistic context in which it is encountered. Gallese and Lakoff describe this position in the context of literal versus idiomatic language: “A further prediction of our theory of concepts is that such results should be obtained in fMRI studies, not only with literal sentences, but also with the corresponding metaphorical sentences. Thus, the sentence ‘He grasped the idea’ should activate the sensory-motor grasping-related regions of the brain. Similarly, a metaphorical sentence like ‘They kicked him out of class’ should activate the sensory-motor kicking-related regions of the brain.” [14, p. 472].

As we have seen, there is some literature to indicate that this is not the case [49, 52], although others have claimed to find motor cortex activation to idiomatic sentences [53]. It may be that language comprehension is more flexible than Gallese and Lakoff describe, in the sense that reading of the verb ‘throw’ leads to motor cortex activation only when its meaning is to be understood as literal throwing. That is, motor cortex activation can be ‘overruled’ by the context the verb occurs in. This finding illustrates that the brain acts in a flexible manner. This flexibility predicts that if the context renders the action interpretation of the verb (which is probably its default meaning) as incorrect, the motor cortex part of the verb’s representation will wash out or will not be activated at all [see also 58]. This is in contrast to a notion in which motor cortex is a necessary part of an action verb’s semantics. For instance, Glenberg and colleagues write about “. . . an action schema in anterior portions of premotor cortex [. . .] which *becomes the meaning* of the verb ‘to give’” [48, p. 908, our emphasis]. We would rather argue that these anterior premotor structures can be part of the meaning of ‘to give’, but that they are not necessarily so. Depending upon the task at hand as well as on the input, motor cortex activation may or may not be observed.

Level of detail

Another issue relates to the level of detail of motor cortex activation during language understanding. We have seen evidence that upon reading the word ‘throw’, parts of the motor cortex involved in executing hand movements is activated. This activation is typically interpreted as some kind of covert simulation. However, what kind of ‘throwing’ is being simulated when we

read ‘to throw’? We can throw in a wide variety of ways: underhand, overhand, with two hands, upward, downward etc. Moreover, we can throw many different objects, which influences the way we throw. Throwing a bowling ball is rather different from throwing a basketball. Hence the question arises whether similar processes are going on upon reading of the verb ‘to throw’ or reading of the sentence ‘The bowler picks up the ball, concentrates for a moment, and throws a strike’. We conjecture that in the latter case the motor cortex activation is more specified, more precise, whereas it remains underspecified upon simple reading of the word ‘throw’. This could lead to qualitatively different effects, that is, different and/or more specific action plans being activated in the case of the sentence as compared to the single verb.

We similarly argue that the motor cortex activation observed during reading / listening to action-related language is different than when we explicitly imagine doing these actions. Imagining doing an action and reading of language describing that action has been hypothesized to be equal by some [14]. Here we predict that this crucially depends upon the language context and the intention with which the linguistic input is processed. For instance, motor cortex activation during reading ‘throw’ could be different than during imagining ‘throwing’, because in the latter case one has to imagine a *specific kind of* throwing. Some first evidence comes from recent finding in which we report non-overlapping effector-specific activations in premotor cortex for reading of actions verbs versus imagining performing these actions [36, 37]. However, future research is needed to get a better handle on this issue, for instance on the issue whether reading more detailed action language would change this pattern of results.

Our proposal is related to what Zwaan and colleagues have termed the ‘linguistic focus hypothesis’ [57, 59-62]. Their assertion is that the content of language which is covered by the attention of the reader or listener (which is within her ‘linguistic focus’) will lead to sensory-motor resonance if that content refers to sensory-motor properties. They presented participants with sentences like ‘During the film, the light bulb burned out. He found a new light bulb which he screwed in rapidly’. The sentences were presented in parts and participants ‘scrolled’ to the next part of the sentence by rotating a knob clockwise or counter-clockwise. Through this manipulation, the actual movement of the participants could match or mismatch with the motion described in the sentence. It was found that a mismatch between actual movement direction and direction of movement implied by the sentence lead to longer reading times, both when participants encountered the actual verb (‘screwed’) and when participants encountered the adverb (‘rapidly’) [60]. Interestingly, the effect was only present for the verb (and not for the adverb) in sentences such as ‘During the film, the light bulb burned out. He found a new light bulb which he screwed in carefully’ [60]. The authors argue that ‘carefully’ does not put focus on

the action component of the action and hence that motor resonance ceases quickly [see also 62]. This is a nice example of how motor activation during language comprehension depends upon the specific content in which action semantics occurs.

As a final note, we want to point out that although this chapter was focused on relation between language and *action*, it should be noted that an embodied or grounded semantics also entails grounding of concepts, in for instance, perceptual and emotional systems [e.g. 63]. This is a clear prediction from distributed semantics, of which the relation between action semantics and motor cortex should be regarded a specific instance. The focus of present literature as well as of this chapter could give rise to the impression that the language-action relationship is special, which we believe to be incorrect [see also 64].

CONCLUSION

In conclusion, the data reviewed in this chapter show that parts of the cortical motor system are activated during language understanding. One body of evidence suggests that perceived speech sounds activate specific parts of motor cortex also involved in speech production. The second line of work that we discussed shows that action-related language activates parts of the motor system involved in motor execution. Neuroscientific evidence in healthy volunteers shows that there is a strong and intimate link between language and action in the brain. However, it is unclear how far this relationship can be taken and whether motor cortex activation is crucial for understanding every instance of an action word, or whether for instance the broader language context can overrule this. Moreover, the level of detail at which motor representations are activated when reading action language is unclear. Future work should be devoted to investigating these issues.

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