PERSPECTIVES

OPINION

Brain mechanisms linking language and action

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Abstract | For a long time the cortical systems for language and actions were believed to be independent modules. However, as these systems are reciprocally connected with each other, information about language and actions might interact in distributed neuronal assemblies. A critical case is that of action words that are semantically related to different parts of the body (for example, 'lick', 'pick' and 'kick'): does the comprehension of these words specifically, rapidly and automatically activate the motor system in a somatotopic manner, and does their comprehension rely on activity in the action system?

The cortical systems for language and action control were traditionally thought to be paradigmatic examples of independent and autonomous functional systems or modules[1,2]. These systems have different cortical bases in circumscribed areas (motor and premotor cortex versus left perisylvian 'language regions'), are fully dissociable by neurological disease (paralysis and apraxic action deficits versus aphasic language deficits) and can themselves be subdivided into finer functional systems — for movement of different body parts and linguistic functions of different types (for example, speech production versus comprehension, or phonology versus syntax versus semantics). The specific inability of patients who have had a stroke to move one extremity while all other motor and language functions remain relatively intact, or the predominant loss of usage of one category of words have been interpreted as strong evidence for a strict modular organization of both the language and the action systems. The conceptual roots of local encapsulated modules date back to the functional centres of nineteenth century connectionist models[3], and the results of many brain imaging studies are largely consistent with the modular perspective[4].

Modern theoretical perspectives offer a different view: cortical functions might be served by distributed interactive functional systems rather than local encapsulated modules[5–10]. Evidence for this idea has been provided by neuroanatomical investigations that have shown neuronal connections both within and between the cortical systems for action and the homologues of the human language system in monkeys. For example, there are links between the dorsal and ventral premotor cortex and between the left inferior frontal (Broca's area) and superior temporal (Wernicke's area) language regions[11,12]. Importantly, many links have also been shown between the premotor and language areas where they are adjoined, in the inferior frontal cortex, and through long-distance cortico-cortical connections[11–15] (FIG. 1b). The dorsal and ventral prefrontal and premotor cortex connects with auditory areas in the belt and parabelt region of the superior temporal gyrus and sulcus, thereby providing multiple links between the superior temporal language area and the motor system. These links indicate that information flow is possible between the cortical systems for language and action.

Taking into account well-known facts about the cortical basis of learning — namely that frequently co-activated neurons strengthen their mutual connections — it is likely that the cortical systems for language and action develop specific links between each other whenever actions correlate with specific language processes. From this we can predict that whenever language and action information processing correlate with each other in the different cortical areas, distributed functional systems are being established that allow for fast, interactive processing of multimodal information across cortical areas. The existence of distributed interactive systems has been proposed by several researchers who have called them cell assemblies[5], neuronal ensembles[6,8], distributed functional networks[7], and, if they have specific cognitive functions, neurocognitive networks[9] or cognits[10].

Dissociations and distributed systems

For some time, especially in the realm of language, modular models were preferred because it was thought that they were necessary for explaining neuropsychological double dissociations. An example of a double dissociation is the predominant loss of speech that coincides with relatively intact comprehension in patients with Broca's aphasia and the reverse pattern of comprehension deficits with fluent speech output in Wernicke's aphasia. Double dissociations also occur in the processing of conceptual and lexico–semantic word categories; for example, meaningful content versus grammatical function words[16], nouns versus verbs[17,18] or animal versus tool names[19], with the complementary category being relatively spared. Therefore, local encapsulated modules for speech production, comprehension and the processing of specific lexico–semantic categories were proposed[2,19].

However, this line of argument was weakened as it became clear that double dissociations can also be explained by accounts of distributed interactive systems[2,20,21]. If they are structured according to the neuroanatomical

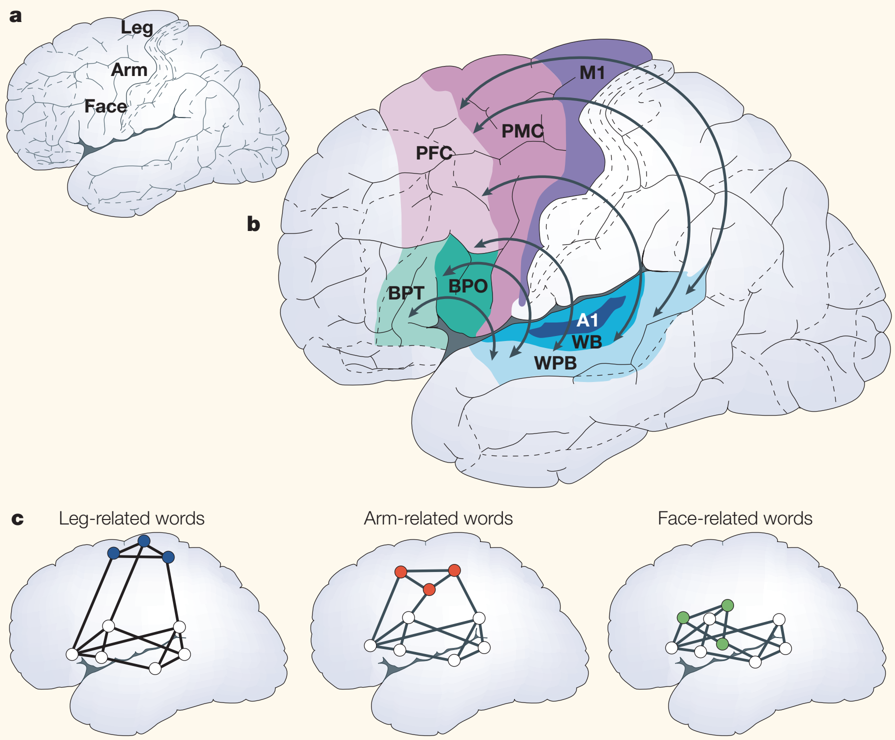

Figure 1 | **Schematic illustration of the cortical systems for language and action. a** | Somatotopy of the motor and premotor cortex: the approximate location of the face/articulators, arm/hand and foot/leg representations. **b** | Connections between the language and action systems. Inferences about cortico-cortical links in humans are based on neuroanatomical studies in monkeys. The arrows indicate long-distance cortico-cortical links. **c** | Semantic somatotopy model of action word processing: distributed neuronal assemblies bind information about word forms and the actions to which they are semantically linked. Because action words can relate to different body parts (for example, 'lick', 'pick' or 'kick'), the cortical distributions of their neurocognitive networks differ. A1, core region of the primary auditory cortex; BPO, Broca's area, pars opercularis; BPT, Broca's area, pars triangularis; M1, primary motor cortex; PFC, prefrontal cortex, posterior part adjacent to motor system; PMC, premotor cortex; WB, auditory belt region in Wernicke's area; WPB, auditory parabelt region in Wernicke's area. Data from REFS 11–15,20,36. Panel **c** modified, with permission, from REF. 83 © (2001) Elsevier Science.

connectivity of the left perisylvian language areas, such models can be used to explain the emergence of double dissociations that occur between aphasia syndromes as a result of focal cortical damage[22]. In principle, any double dissociation between categories of knowledge that can be attributed to separate local encapsulated modules can also be explained by distributed functional systems with specific topographies that involve neurons in the critical areas to different degrees[20,23,24].

Imaging studies have been used to directly address the question of whether the left hemispheric inferior frontal and superior temporal language areas are modules specialized in either speech perception or production, or whether they represent two local areas that house neural elements participating in interactive distributed cortical processes that contribute to both speech production and comprehension. Such studies have shown that while listening to syllables and words, the left inferior frontal cortex is active, as are the superior temporal areas in the vicinity of the auditory cortex[25–27] (FIG. 2). During speaking, the superior temporal cortex is active, as are areas in the inferior motor, premotor and prefrontal cortex, even when self-produced sounds are prevented from being perceived through the auditory channel[28]. This indicates that interactive neural systems that are distributed over the inferior frontal and superior temporal cortex contribute to both speech production and perception. During spoken word recognition and understanding, these systems are activated near-simultaneously and largely in parallel, with a peak activation delay in the inferior frontal cortex of ~20 ms after the activation peak in superior temporal areas[26]. These results indicate tight and rapid functional links between speech perception and speech production processes, as postulated by established psycholinguistic theories, including the motor[29,30] and direct realist[31,32] theories of speech perception.

That the links between superior temporal perceptual circuits and frontocentral speech production machinery are functionally effective has been shown using transcranial magnetic stimulation (TMS). During the perception of spoken words and language sounds (phonemes) that strongly involve the tongue, TMS applied to the inferior motor cortex elicits stronger muscular responses of the articulators compared with control conditions[33]. Interestingly, this effect is most prominent when the critical phonemes are presented in a meaningful word context, which indicates that cell assemblies for meaningful words have a role in linking articulatory gestures and auditory signals at the cortical level[22]. Converging evidence from functional connectivity studies based on positron emission tomography (PET) and functional MRI (fMRI) data indicates that the links between superior temporal and inferior frontal language areas depend on the amount of meaningful information being transmitted by words[34].

Although the documented tight functional links between action and perception circuits of the left perisylvian language array[20,35] cannot be explained in a straightforward manner within a modular approach, they meet the predictions of a distributed interaction model that has been used to postulate sensorimotor links and binding between specific acoustic speech patterns and the articulatory gestures that generate them. However, these results do not answer the question of the universality and functional specificity of the sensorimotor links: are there one or more specific cortical areas dedicated to storing and processing different neuronal ensembles that bind information about actions and language? Or is it a general property of the language and action systems, and possibly the entire cortex, to host topographically specific and dissociable distributed networks that process linguistic information together with motor programs? Such questions can be addressed experimentally by using words that are semantically related to actions.

Semantic somatotopy of action words

Model and predictions. Action words are defined by abstract semantic links between language elements and motor programs. In infancy, action words are learned in the context of action performance. A child performs an action and, in close temporal vicinity, the caretaker typically uses the action word (usually a verb). In the cortex, the motor program and the neural representation of the word are therefore activated near-simultaneously, so that synaptic connections

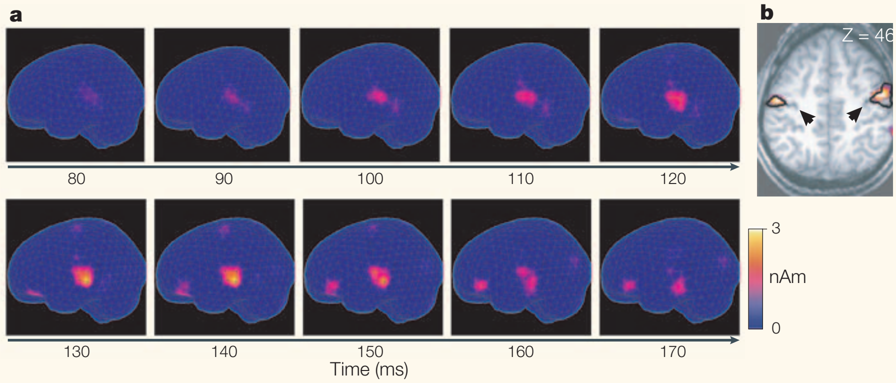

Figure 2 | **Functional links between the superior temporal speech perception and inferior frontal motor systems.** Links between speech perception and motor systems are demonstrated by functional imaging studies that show the activation of frontal areas in response to speech input.
a | Magnetoencephalography data (n = 12) showing that superior temporal activation elicited by spoken words is immediately followed by inferior frontal activation (time difference = 22 ms). Source strengths are given in nanoampère-metres (nAm). **b** | Functional MRI data from one representative participant that show premotor activation while listening to speech. The activated motor circuits might contribute to the speech perception and comprehension process, as proposed by psycholinguistic theories. Panel **a** modified, with permission, from REF. 26 © (2003) Elsevier Science. Panel **b** modified, with permission, from REF. 27 © (2004) Macmillan Magazines Ltd.

between neurons in specific motor and premotor areas and those in the language areas become stronger. This would be expected to lead to neuronal ensembles with specific cortical distributions.

The postulated specific cortical topographies are best illustrated using the case of action words that refer to different body parts. The motor cortex has a somatotopic organization (FIG. 1c), with the mouth and articulators represented close to the Sylvian fissure, the arms and hands at dorsolateral sites and the feet and legs projected to the vertex and interhemispheric sulcus[36]. There are additional somatotopic maps in the fronto-central cortex[37], a prominent one of which lies in the premotor cortex in the lateral precentral gyrus and resembles the map in the primary motor cortex[14,38]. If action words are semantically related to the movements of the face or articulators, arm or hand, or leg or foot, the distributed neuronal ensembles would include semantic neurons in perisylvian (face-related words), lateral (arm-related words) or dorsal (leg-related words) motor and premotor cortex[20]. Therefore, this semantic somatotopy model of action words implies that there are differently distributed networks for the English words 'lick', 'pick' and 'kick' (FIG. 1d). The model allows general predictions to be made about action word-related cortical activity within the limits of the well-known inter-individual variation of cortical maps, most notably as a result of practice-related reorganization[39]. This is open to further elaboration, taking into account additional mapping rules — for example, the topography of coordinated actions in a body-centred workspace that was suggested by the authors of recent work[40].

Crucial predictions about the semantic somatotopy model are as follows. First, the perception of spoken and written action words activates cortical areas involved in action control and execution in a category-specific somatotopic fashion, which depends on the semantics of the action words. Second, owing to the internal connections of the distributed neuronal ensembles through fast-conducting axons, the spread of activity is fast, so that specific sensorimotor areas are activated early in the course of spoken and written word comprehension. Third, because of the strong within-assembly connections that link language and action representations, activation of the sensorimotor cortex should not require people to attend to language stimuli, but should instead be automatic. And, finally, functional changes in the motor and premotor cortex influence the processing of action words in a category-specific manner.

Experimental evidence. In functional imaging experiments, elementary repetitive movements of single body parts activate the motor and premotor cortex. For example, Hauk *et al.* reported fMRI data showing that tongue, finger and foot movements lead to the somatotopic activation pattern illustrated in FIG. 3. When the same participants were instructed to silently read action words that related to the face, arm and leg that were otherwise matched for important psycholinguistic variables (such as word frequency, length and imageability), a similar pattern of activation emerged along the motor strip[41]. Consistent

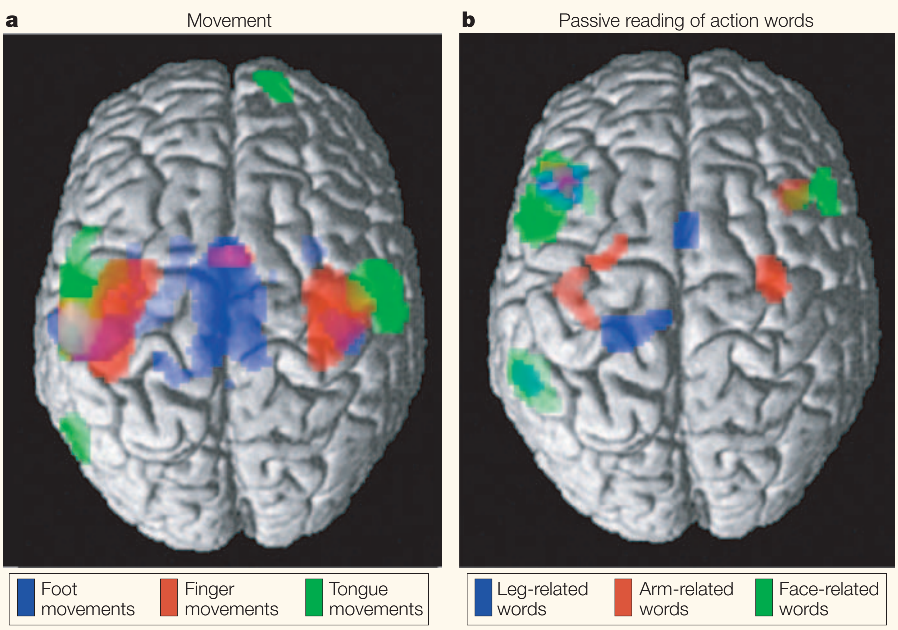

Figure 3 | **Cortical activation during movement and during passive reading of action words.** Functional MRI data (n = 14) showing that a degree of overlap in activation is elicited by corresponding actions (**a**) and action words (**b**). Leg-related words activate areas overlapping and adjacent to areas involved in foot movements, and there are similar relationships between arm-related words and finger movements and face-related words and tongue movements. This indicates that a common neural substrate is involved in the processing of actions and the meaning of action words. Modified, with permission, from REF 41 © (2004) Elsevier Science.

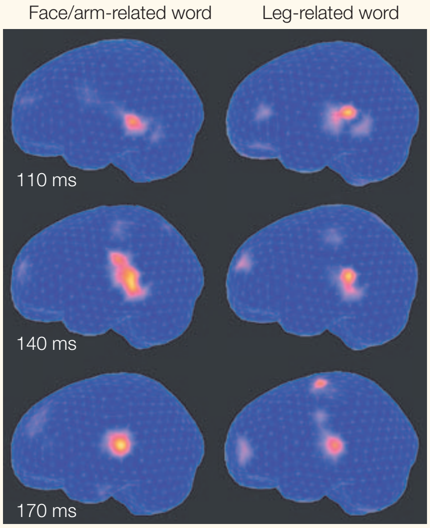

Figure 4 | **Cortical activation dynamics elicited by face/arm- and leg-related words.** Magnetoencephalography (n = 16) was used to measure the activation elicited at different times after spoken action words could be uniquely recognized. Note the slight upward movement of the inferior central source for the face/arm-related word and the delayed appearance of the superior central source for the leg-related word. These activation time courses might reflect the movement of neuronal activity in distributed neuronal assemblies that represent and process words with different action-related meanings. Modified, with permission, from REF. 49 © (2005) MIT Press.

with earlier findings, all words equally activated areas in the temporal cortex and also the inferior frontal cortex[25–27]. The additional category-specific somatotopic activation that was seen in the motor system in response to face-, arm- and leg-related words was close to and overlapped with the motor and premotor representations of the tongue, fingers and feet, respectively. These results indicate that specific action representations are activated during action word understanding.

A similar experiment was carried out with action words embedded in sentences. In this case, participants heard action descriptions such as 'the boy kicked the ball' or 'the man wrote the letter' while their brain metabolism was monitored[42]. Specific premotor areas reflecting the differential involvement of body part information in the semantic analysis of the language input were again found to be active. Taken together, these fMRI results indicate that somatotopic activation of motor circuits reflects aspects of word and sentence meaning.

Although these studies showed language-related somatotopic cortical activation, the low temporal resolution of haemodynamic imaging makes it impossible to decide between two interpretations of this finding. Action word recognition could either automatically and immediately trigger the activation of specific action-related networks, as predicted by the semantic somatotopy model, or motor activation could be the consequence of a late, postlexical strategy to imagine or plan an action. Earlier fMRI research showed that the observation of action-related pictures, and also mere mental imagery of actions, activates the premotor cortex in a somatotopic fashion[43]. Neurophysiological experiments were conducted to reveal the time course of cortical activation in action word recognition, and to investigate whether specific motor areas are activated immediately or after some delay. Late postlexical meaning-related processes are reflected by late components of the event-related potential (ERP) and field, which are maximal ~400 ms after word onset[44]. However, neurophysiological differences between word categories that reflect lexico–semantic processes have been found as early as 100–200 ms[45].

ERP experiments that focused on silent reading of the face-, arm- and leg-related words used in the fMRI study by Hauk *et al.* showed that category-specific differential activation was present ~200 ms after word onset[46,47]. Consistent with the fMRI results, distributed source localization performed on stimulus-triggered ERPs revealed an inferior frontal source that was strongest for face-related words, and a superior central source that was maximal for leg-related items[47]. This dissociation in brain activity patterns supports the idea of stimulus-triggered early lexico–semantic processes. To investigate whether motor preparation processes co-determined this effect, experiments were carried out in which the same response — a button press with the left index finger — was required for all words. The early activation difference between face- and leg-related words persisted, which indicates that lexico–semantic processes, rather than postlexical motor preparation, were reflected[46].

The earliness of word category-specific semantic activation in the sensorimotor cortex in passive reading tasks indicates that this feature might be automatic. To further investigate this possibility, participants were actively distracted while action words were being presented, and their brain responses were measured[48,49]. Participants were instructed to watch a silent video film and ignore the language input while spoken face/arm- and leg-related action words were presented. Care was taken to exactly control for physical and psycholinguistic features of the word material. For example, the Finnish words 'hotki' (eat) and 'potki' (kick) — which included the same recording of the syllable [kI] spliced to the end of each word's first syllable — were compared. In this way, any differential activation elicited by the final syllable [kI] in the context of [hot] or [pot] could be uniquely attributed to its lexico–semantic context. Magnetoencephalography (MEG) results showed that an early brain response, the mismatch negativity[50], was elicited by face/arm- and leg-related word contexts (FIG. 4). Relatively stronger activation was present in the left inferior frontal cortex for the face/arm-related word, but significantly stronger activation was seen in superior central areas, close to the cortical leg representation, for the leg-related word[49].

These MEG results were confirmed with a different method, electroencephalography (EEG), using words from different languages, including, for example, the English word pair 'pick' versus 'kick'[48]. It is remarkable that the activation peak of the superior central source followed that of the inferior frontal source with an average delay of only 30 ms, which is consistent with the spread of activation being mediated by fast-conducting cortico-cortical fibres between the perisylvian and dorsal sensorimotor cortex.

Even if action word processing activates the motor system in a specific somatotopic fashion, this does not necessarily imply that the motor and premotor cortex influence the processing of action words. In another study, different parts of the motor system were stimulated with weak magnetic pulses while participants processed action words in a lexical decision task[51]. To minimize interference between word-related activation of the motor system and response execution processes, lip movements were required while arm- and leg-related words were presented. When subthreshold TMS was applied to the arm representation in the left hemisphere, causing strong magnetic pulses to elicit muscle contractions in the right hand, faster processing of arm-related words occurred relative to leg-related words. When TMS was applied to the cortical leg area, the opposite pattern of faster leg-related than arm-related word responses emerged[51]. Processing speed did not differ between stimulus word groups in control conditions in which ineffective 'sham' stimulation or TMS to the right hemisphere was applied. This shows a specific influence of activity in the motor system in response to the processing of action-related words (FIG. 5).

Further evidence for specific functional links between the cortical language and action systems comes from TMS-induced

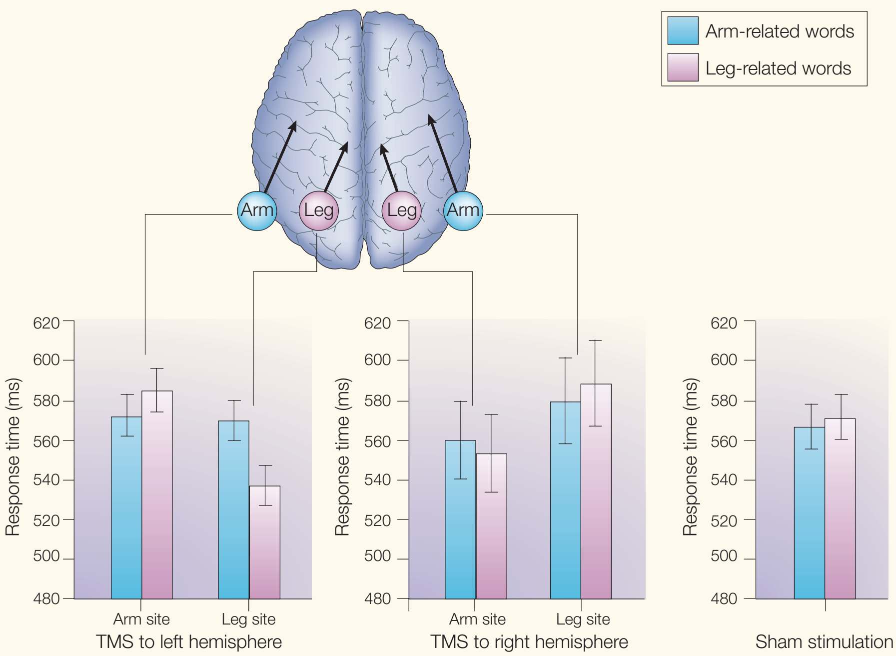

Figure 5 | **Effects of transcranial magnetic stimulation of cortical motor areas on action word processing.** Transcranial magnetic stimulation (TMS; *n* = 11) was applied to arm and leg loci over the left and right hemispheres and compared with sham control stimulation during the processing of arm- and leg-related words. Response times to arm- versus leg-related words were differentially affected only during the application of TMS to the left hemisphere. Those parts of the motor systems that reflect aspects of the semantic meaning of action words might, therefore, make a crucial contribution to the processing of these words. Reproduced, with permission, from REF. 51 © (2005) Blackwell Publishing.

motor responses[33]. Listening to Italian sentences describing actions performed with the arm or leg differentially modulates the motor responses brought about by magnetic stimulation of the hand and leg motor cortex[52]. It seems that effective specific connections of language and action systems can be documented for spoken or written language, at the word and sentence levels, and for various languages (for example, English, Italian, German and Finnish) using various neuroscientific methods (fMRI, MEG, EEG and TMS).

Implications for semantics in the brain

These results show that action words activate the cortical system for action processing in a somatotopic fashion and that this somatotopy reflects referential word meaning. However, they do not imply that all aspects of the meaning of a word are necessarily reflected in the brain activation pattern that it elicits. It seems that such cortical–semantic correspondence can be postulated for words that refer to concrete entities related to action or perception patterns. It remains to be determined whether it might be possible to read aspects of the meaning of other words, such as abstract items, from the cortex in a similar manner. The cortical systems that process information about the referential meaning of a word seem to determine the cortical distribution of the neuronal network that the word activates. During action word processing, the language regions and motor cortex are activated in parallel, following finely-tuned spatio–temporal patterns, and activity patterns in motor and language systems seem to interact, as shown by TMS experiments. So, these results support a distributed interactive systems account in general and, more particularly, a distributed model of semantic somatotopy of action word processing, and might have further implications for our understanding of cognitive brain functions (BOX 1).

The results with action words show that semantic processing can engage many cortical areas. They contradict the view that meaning processing is localized in a unitary cortical locus — for example an area that is anterior, inferior or posterior to Wernicke's area in the left temporal lobe[4,53,54] or in the inferior frontal cortex[55]. Category-specific semantic systems in a range of cortical areas that normally process sensory or action information have previously been postulated on the basis of neuropsychological[18,19,24] and neurophysiological double dissociations[56,57] between words and concepts that relate to actions and objects. However, this idea has been challenged by the observation that some of the classic dissociations — for example, between nouns and verbs or tool and animal names — are open to alternative explanations in terms of psycholinguistic variables (such as word frequency and imageability)[58] or conceptual–perceptual structure (high/low similarity between members of semantic categories)[59–61]. In light of this discussion, the action word experiments are of great theoretical relevance. In these cases, confounding psycholinguistic factors could be excluded owing to meticulous stimulus matching, and the supported *a priori* prediction of semantic somatotopy of motor and premotor areas leaves little room for explanations that deny the link between activated areas and motor function. Somatotopic semantic activation cannot be explained by a unitary semantic–conceptual system that processes all word meanings in the same cortical locus.

One semantic–conceptual binding site?

Although the results discussed here cannot be explained if all semantic processes are restricted to one cortical area, they might be compatible with the idea of a central semantic system, if this system is thought to manage dynamic functional links between various cortical areas that process word forms and conceptual–semantic information. Apart from the motor system, action words have also been shown to activate inferior temporal areas (FIG. 3), which makes these data compatible with a semantic role for this region[4,53]. In the study by Hauk *et al.*, the most pronounced activation elicited by all action words was in the inferior frontal cortex, close to the human homologue of monkey area F5, where mirror neurons are most common[35]. This is in line with the idea that this inferior frontal area has a key role in the semantic binding of action, perception and language-related information[35]. The debate about one or many cortical systems controlling semantic processing must, therefore, continue, although the data reviewed here on action words show topographically-specific activation in different areas that both reflect and influence lexico–semantic processes.

The bilateral nature of neural degeneration that is usually seen in patients with semantic dementia might indicate that one focal lesion is insufficient to cause general semantic deficits[53]. The existence of many semantic binding sites is also supported by the specific semantic deficit in action word processing that is seen in patients with motor neuron disease[62], and by double dissociations between semantic word categories that arise from lesions in right-hemispheric fronto-parietal versus

Box 1 | Action in language comprehension

The results of investigations into the brain connections between language and action systems reviewed in the main text might change the way we think about language and meaning. Hearing a word seems to be associated with activation of its articulatory motor program, and understanding an action word seems to lead to the immediate and automatic thought of the action to which it refers. A tight functional link between speech production and perception mechanisms has been proposed through psycholinguistic theories — for example, the motor[30,65] and the direct realist[31,32] theories of speech perception. A neurobiological account relates specific strengthening of neuronal links between inferior frontal speech motor circuits and the superior temporal speech perception machinery to correlations between perceptual and motor information that give rise to distributed cell assemblies that contribute to both production and comprehension of speech[22,66]. The articulatory perception–action loops might also be important as a cortical basis of short-term verbal memory[67]. In the same way that the mirror neuron theory implies that action understanding arises from an association between the perceived actions of others and one's own action control system[67–72], the comprehension of action-related language seems to require that words are mapped onto actions that one can perform oneself[57,73–76]. This grounding of language in action is essential, as comprehension of action-related language and concepts is impaired after lesions of the motor system[62,63].

Action meaning seems to be not only necessary, but also highly relevant for language. Verbs form the grammatical backbone of sentences, and the majority explicitly refer to actions. Furthermore, there are several classes of words without action reference that are, nevertheless, semantically linked to actions. Tool words, for example, relate to actions for which the tools are made[56,77], and words that denote internal states, such as 'pain' or 'disgust', can be understood only because both speaker and listener can relate them to similar motor programs that are, by genetic endowment, associated with the expression of pain or disgust[78]. Understanding language means relating language to one's own actions, possibly because the automatic and extremely rapid linkage of sensory and motor information in our brains benefits comprehension and learning processes[29,79]. These insights, which are supported by neuroscience research, have important implications for constructing life-like perception–action systems and robots with brain-like control systems[72,80–82].

temporo-occipital areas[63]. Some such lesions are so focal that they affect only the motor and premotor cortex, but, nevertheless, specifically degrade the processing of action words in psychological experiments. These dissociations indicate that there is more than one semantic integration system in both cerebral hemispheres[64].

Outlook

Investigations of words and sentences that are semantically related to actions involving the face, arm or leg show somatotopic activation of the sensorimotor cortex. Activation is rapid and largely independent of attention. Action-related word meaning is not only reflected in the cortical activity pattern, but stimulation of the motor system also produces differential effects on the recognition of action words of different semantic type. These results are best explained by distributed interactive neuronal assemblies, the cortical topographies of which reflect the loci where relevant semantic and form-related information is being processed. These differentially distributed cell assemblies might bind multimodal lexico–semantic information.

From here, various questions emerge. Does the semantic brain topography of action words persist if they are embedded in sentences with idiomatic or metaphoric expressions in which any action relationship is lost ('pull my arm versus leg')? Would the semantic topography be influenced by the grammatical status of words as either nouns or verbs? Can the time course of semantic and lexical activation be correlated with specific features of meaning processing, so that aspects of the comprehension process could be read from the spatio–temporal pattern of brain activation? What are the reliability limits of investigations of lexico–semantic brain processes in individual participants? Is there a perspective on monitoring these processes in particular neurological populations, such as elderly patients with degenerative brain disease? Finally, can the learning of word meaning be traced with large-scale neurophysiological techniques? The brain connections between language and action systems might provide a fruitful model for cognitive neuroscience, not least because these systems are ideally placed for monitoring with multimodal neuroimaging techniques.

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Competing interests statement

The author declares no competing financial interests.

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