

Review

A neuropsychological perspective on the link between language and praxis in modern humans

Agnes Roby-Brami^{1,2,*}, Joachim Hermsdörfer³, Alice C. Roy^{4,6}
and Stéphane Jacobs^{5,6}

¹Laboratory of Neurophysics and Physiology, University Paris Descartes, CNRS UMR 8119,
45 rue des Saints Pères, 75006 Paris, France

²Department of Physical Medicine and Rehabilitation, AP-HP, Raymond Poincaré Hospital,
92380 Garches, France

³Department of Sport and Health Science, Technische Universität München, Georg-Brauchle-Ring 60-62,
80992 München, Germany

⁴CNRS FRE 3406, Laboratory on Language, Brain and Cognition, Institute for Cognitive Sciences,
67 Boulevard Pinel, 69675 Bron, France

⁵INSERM U1028, CNRS UMR5292, Lyon Neuroscience Research Center, ImpAct team,
16 Avenue Lépine, 69676 Bron, France

⁶University Claude Bernard Lyon 1, 43 boulevard du 11 novembre 1918, 69622 Villeurbanne, France

Hypotheses about the emergence of human cognitive abilities postulate strong evolutionary links between language and praxis, including the possibility that language was originally gestural. The present review considers functional and neuroanatomical links between language and praxis in brain-damaged patients with aphasia and/or apraxia. The neural systems supporting these functions are predominantly located in the left hemisphere. There are many parallels between action and language for recognition, imitation and gestural communication suggesting that they rely partially on large, common networks, differentially recruited depending on the nature of the task. However, this relationship is not unequivocal and the production and understanding of gestural communication are dependent on the context in apraxic patients and remains to be clarified in aphasic patients. The phonological, semantic and syntactic levels of language seem to share some common cognitive resources with the praxic system. In conclusion, neuropsychological observations do not allow support or rejection of the hypothesis that gestural communication may have constituted an evolutionary link between tool use and language. Rather they suggest that the complexity of human behaviour is based on large interconnected networks and on the evolution of specific properties within strategic areas of the left cerebral hemisphere.

Keywords: action; language; brain damage; gesture; pantomime; tool use

1. INTRODUCTION

Language and complex actions or praxis, including tool use, are cognitive functions that, although present to some degree in many animal species, are uniquely developed in humans. In addition to being distinctive human traits, these two behaviours are mainly controlled by the left cerebral hemisphere in the vast majority of individuals, as demonstrated by neuropsychological observations. This lateralization is reminiscent of the very strong population-level bias for dextrality in the human species, whereby approximately 90 per cent of individuals favour their right

hand for fine motor skills [1]. These converging cerebral asymmetries have led researchers to consider the left hemisphere as dominant for language as well as for motor functions [2], and have triggered interest in the potential evolutionary and functional links between manual preference, tool use and language.

The origin of the left hemisphere specialization for language and praxis, including tool use, and its relation to manual preference, is still disputed. For example, some argue that dextrality might have emerged first [3], while others propose that it appeared under selective pressure for common handedness as an advantage for learning tool use through imitation [4]. Other authors suggest that human dextrality is simply a mere consequence of the ancient left lateralization of the cerebral control of vocalization, as seen in many species from birds to mammals. According to this hypothesis, the progressive incorporation of vocalization into an

* Author for correspondence (agnes.robby-brami@parisdescartes.fr).

One contribution of 12 to a Theme Issue 'From action to language: comparative perspectives on primate tool use, gesture, and the evolution of human language'.

originally gestural language would have led to a left hemispheric specialization for language and motor control [5].

Regardless of its relationship with manual preference, the study of the link between language and tool use is highly relevant to the understanding of the development of these two unique human abilities and the origins of our species. According to archaeological records, tool use emerged about 2.5 Ma, starting with simple behaviours such as modifying rocks for pounding [6] and then progressing towards the construction of more and more refined and complex compound tools through cumulative evolution [7]. In parallel, language is thought to have emerged owing to the social interactions required by the development of human technology, in particular by learning tool-related behaviours through imitation [8]. An increasingly hierarchical organization of language would then have appeared thanks to a pre-existing left hemispheric specialization for hierarchically and sequentially ordered behaviours, initially developed for the manufacture and use of tools [4]. Developmental studies investigating language and object combination behaviours in young children, as well as work carried out in primates and apes, suggest that language and tool use do indeed share some common functional and neural foundations both phylogenetically and ontogenetically during the first years of development [9].

The cerebral basis of tool use in monkeys as well as in humans has been extensively investigated over the past two decades. Iriki *et al.* [10] first demonstrated that simple tool use, i.e. using a rake to retrieve food placed out of reach, is accompanied in macaques by plastic changes of sensory responses of neurons in the parietal cortex. This seminal work, together with subsequent studies done in monkeys (e.g. [11]), led Frey [12] to propose that simple tool-use behaviours, in which the tool merely constitutes a functional extension of the limb [13,14], rely on experience-dependent changes in areas within the dorsal stream of visual processing [15,16], known to be essentially involved in sensory-motor transformations for the control of actions [17]. Recent studies in humans [18] and in monkeys [19] support this hypothesis. In contrast with simple tool use, complex tool use, like most everyday familiar actions, is a uniquely human skill whereby the use of a tool 'converts the movements of the hands into qualitatively different mechanical actions' [20]. This ability depends not only on sensory-motor transformations for the control of action, but also on access to acquired semantic knowledge about the tool and its common uses [21]. So, complex tool use draws upon the collaboration between the aforementioned dorsal stream and the ventral visual pathway [12] thought to be responsible for object recognition and the building and storage of semantic knowledge [16]. Accordingly, data obtained from brain imaging studies of various complex tool-use tasks in able-bodied subjects show that these behaviours recruit a large distributed network within the temporal, parietal and frontal areas, primarily lateralized to the left hemisphere [22,23]. Further evidence for this integration of semantics into sensory-motor control of action can be found in the fact that conceptual knowledge influences the way people

spontaneously grasp familiar tools [24]. Importantly, this effect can be disrupted in patients with left but not right side brain damage [25]. Based on these findings, it has been proposed that the unique human abilities of designing and using complex tools originate from adaptations of sensory-motor networks and their integration with cognitive processes pertaining to semantic knowledge about tools, the agent's intentions and contextual information about the task, most of these being also supported by the left hemisphere [26].

The emergence of language, on the other hand, is often conceived of as depending critically on the receiver's ability to decode the sender's message or intentions, subserved by some common representations between the two [27]. The discovery of mirror neurons in the monkey [28] might have provided the link between action execution and recognition that is necessary for communication in general. Mirror neurons fire not only when the monkey executes specific grasping actions, but also when it perceives the same action being performed by another individual. These neurons have been observed in area F5 of the ventral premotor cortex of macaques as well as in the inferior parietal lobule, where some of these neurons also show sensitivity to the goal of the action, independently from the motor details of its execution [29]. These two brain regions are known to be reciprocally connected, and are part of the dorsal visual stream subserving the sensory transformations involved in the control of reaching and grasping actions. Interestingly, in the context of the emergence of language, the putative human homologue of area F5 is the caudal part of the inferior frontal gyrus, which corresponds, on the left side, to Broca's area, known for its involvement in many aspects of language, from phonology to syntax and from production to comprehension [30,31]. In addition, evidence for the existence of a mirror system in humans has been reported [32], providing a possible neural basis for action understanding [33]. This human analogue of the monkey mirror neuron system may in addition support a variety of complex socio-cognitive phenomena, including language [34], although this view is challenged by recent work [35,36]. Regarding the evolution of language, and following Liberman's proposal mentioned earlier [27], the mirror neuron system would thus have allowed the mapping of the sender's message and intentions onto the receiver's own representations, laying the bases for a primitive gestural form of language [5,37]. If this is the case, then Broca's area as we know it now would have developed 'atop a mirror neuron system for grasping' through increasingly complex stages of gesture recognition and imitation [38].

Independently from the potential involvement of a mirror neuron system, the relationship between praxis, gesture and language has to be further examined on the basis of recent neuropsychological data [39]. The lateralization to the left hemisphere seems to be the key phenomenon for evolution of both language and complex action systems in humans. Indeed, clinical observations gathered for more than a century have demonstrated that a lesion of the left hemisphere may induce a disruption of language (aphasia) [40] and of complex action systems (apraxia) [41]. These disorders

are very often associated in brain-damaged patients [42]. Classical neuropsychological analyses rely on the clinical dissociation of the elementary impairments constituting the aphasic and apraxic syndromes and their confrontation with post-mortem neuroanatomy in order to describe brain-behaviour relationships. This classical approach has led to the elaboration of cognitive models of language and action. Nowadays, neuropsychology has largely benefited from progress in brain imaging, which allows precise investigations of the neural bases of higher brain functions and the mechanisms of their dysfunction.

Here, we will first outline the clinical picture and the first interpretations of aphasia and apraxia. In §3, we will present the more contemporary theoretical accounts of these disorders, contrasting the early localizationist approaches with current views that these behaviours are supported by widespread, dynamic neural networks. Then, we will examine the link between praxis and language by reviewing the effects of brain lesions on several relevant behaviours such as action recognition, repetition and imitation, and gestural communication. We will attempt to compare these alterations despite the fact that most clinical studies in the literature focus on either aphasia or apraxia, and use generally different clinical approaches and different theoretical backgrounds. Finally, we will examine the possibility that both action and language share common cognitive resources.

2. CLINICAL DESCRIPTION AND ORIGINAL ACCOUNTS OF APHASIA AND APRAXIA

(a) *Early interpretations of aphasia and the concept of brain localization*

Language refers to a system of signs (indices, icons, symbols) used to encode and decode information so that the pairing of a specific sign with an intended meaning is established through social conventions. Language presents several aspects: phonological, semantic, syntactic, prosodic and pragmatic, which can be differentially impaired after brain lesions [43]. The phonological level refers to the sounds used in the language. Each language thus has a different phonology, as certain sounds will be present in one language but not in another. Semantics refers to the meaning of language, and syntax represents the principles and rules for constructing sentences. The phonological, semantic and syntactic aspects of language are to a vast extent specific to humans. Prosody refers to the voice modulation that accompanies different emotional content or intention, and is classically attributed to the right hemisphere [44,45]. Finally, the pragmatic aspect of language refers to the complex combinations of symbols used to transmit complex ideas and includes many other cognitive functions, supported by both hemispheres [46].

Aphasia corresponds to impairment, following a brain lesion, of phonological, syntactic and/or semantic processing, either in isolation or in association, and may concern either language production or comprehension, or both. These three aspects of language usually being essentially supported by the left hemisphere in right-handers [47], aphasia follows left brain damage in the vast majority of patients [48].

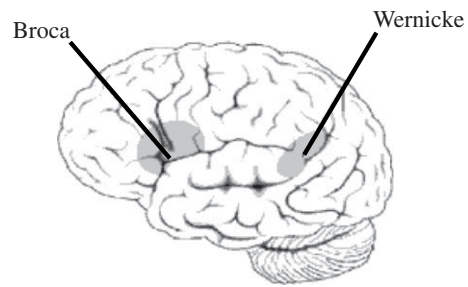


Figure 1. Localization of Broca's and Wernicke's areas.

This is an acquired disorder: the term excludes developmental language disorders in children.

(i) *The concept of localization*

Historically, the topic of aphasia was at the centre of the debate between localized versus holistic explanations of psychological functions of the brain. Franz Joseph Gall was the first to propose separate brain localizations for different behaviours. Broca [40] presented the first clinical case in which focal brain damage was associated with altered language production (figure 1). Later, Carl Wernicke described the defect of language comprehension after a lesion of the posterior section of the superior temporal gyrus. The localization of language functions was then challenged by the holistic theory, which posited a single language function performed by the left hemisphere (review in [49]). Geschwind [50,51] reconsidered localization and proposed that the impairments were the result of disconnection between brain areas (review in [52]).

(ii) *Types of aphasia*

Since the work of Broca & Wernicke in the nineteenth century, the definition and different types of aphasia [53] have been refined. Broca's aphasia (also referred to as non-fluent or agrammatic aphasia) is caused by damage to anterior regions of the brain, in particular to Broca's area, corresponding to the caudal part of the left inferior frontal gyrus (Brodmann areas 44 and 45). It is characterized by reduced, non-fluent agrammatical spontaneous speech with relatively spared comprehension. Fluency impairments include reduced phrase length, altered melody and articulation, reduced word flow or agrammatical sentences. Some over-learned social phrases may paradoxically be preserved and fluent. Comprehension is usually preserved as long as simple, semantically non-reversible sentences are used; however, patients' performance may drastically drop when tested with syntactically complex sentences [54–57]. The severity of Broca's aphasia varies greatly. When the vascular damage includes the anterior insula, the linguistic deficit is accompanied by a motor deficit (the so-called apraxia of speech) characterized by disrupted articulation and prosody [58–61]. Wernicke's aphasia (also called fluent aphasia), on the other hand, is caused by neurological damage to the posterior part of the superior temporal gyrus (Brodmann area 22). It is characterized by paragrammatic, fluent but relatively meaningless spontaneous speech expressed with the appropriate melody or intonation. Spoken language may be limited to jargon with many neologisms, paraphasias or non-words. The comprehension

within the left posterior parietal lobe. The 'innervatory patterns' are preserved, but their activation by the formula is impossible or impaired. It is characterized by adequate movements, performed in response to a command or self-generated, but their performance is degraded. *Melokinetic apraxia* corresponds to a generalized clumsiness owing to a lesion of kinaesthetic 'memories' stored in the sensorimotor cortex.

(ii) *Other neuropsychological models of apraxia*

Geschwind [50,51] reconsidered the question of localization and confirmed that in right-handed persons, the left hemisphere is dominant for complex gestures. However, he focused more on the importance of white matter lesions, than on stored representation of gestures. For him, the inability to pantomime the use of an object upon verbal command is rather the consequence of the disconnection of frontal premotor areas from Wernicke's area owing to a lesion of the left arcuate fasciculus. Geschwind [50] proposed the same interpretation and anatomical correlates to account for conduction aphasia, a syndrome that bears many functional and anatomical resemblances with ideomotor apraxia.

More recently and in line with Liepmann's original proposal, Roy & Square [69] proposed a two-system action model: a *conceptual* system, including semantic knowledge of tools, objects and actions, and a *production* system representing the sensorimotor knowledge of action as well as perceptuo-motor processes that allow its organization and implementation. The conceptual system defines the action plan according to the knowledge of objects and tools, the context-independent knowledge of action and the knowledge of the arrangement of simple actions in a sequence. The production system includes motor programmes independent of the effectors, which permit the action to be carried out according to the context and needs. Praxic disturbances can thus be interpreted in terms of impairment of the conceptual system (ideational apraxia) and/or the production system of action (ideomotor apraxia). In ideomotor apraxia, knowledge pertaining to objects and tools is preserved and patients can therefore describe and identify actions associated with tools and appreciate their adequacy, while being unable to perform them adequately.

Heilman & Rothi (review in [70,71]) proposed a cognitive model inspired by models of the language system, in order to account for all the dissociations observed in patients depending on which modality is used to elicit gestures (verbal command, presentation of objects, imitation, etc.). This model is constituted of several modules, which process specific information and are centred on an action semantic system. They propose that sensory information accesses the system via an action input lexicon that contains information about the physical attributes of perceived actions (mainly visual representations). The semantic action system then integrates information transferred from the action input lexicon and is at least partially independent from other forms of semantic knowledge. The action output lexicon subsequently includes information pertaining to the physical attributes of an action to be performed (mainly kinaesthetic representations). Apart from this indirect lexical route, a direct, non-lexical route, based

mainly on visual processing of perceived gestures, controls the imitation of meaningless or unfamiliar gestures, with a possible dissociation between those routes. Based on the observation that visual recognition of action and movement can be impaired in some apraxic patients with posterior lesions, Heilman *et al.* [72] proposed that two forms of ideomotor apraxia exist: one owing to posterior lesions, destroying the areas containing visuokinaesthetic engrams (and thus also impairing gesture recognition) and the other owing to more frontal lesions, potentially disconnecting motor areas from visuokinaesthetic engrams, therefore preserving gesture recognition.

De Renzi & Luchelli [73] investigated ideational apraxia with specific tests: multiple-step tasks, and tasks requiring the understanding of tool and/or object properties (tool selection, alternative tool selection, gesture recognition). They found that the scores for multiple and single tool-use tasks were correlated with each other but not with the results of a test assessing ideomotor apraxia. They concluded that 'ideational apraxia is an autonomous syndrome, linked to left hemisphere damage and pertaining to the area of semantic memory disorders rather than to that of defective motor control'.

An important characteristic of apraxia is the well-known 'automatic/voluntary' dissociation whereby patients fail to perform adequate gestures on command while their performance on similar self-initiated actions in daily life is preserved, showing that the full context of action is particularly important for the retrieval and execution of adequate gestures. This dissociation has been confirmed by experimental methods [74]. This observation is reminiscent of the relative sparing of over-learned social phrases described in non-fluent aphasic patients [53].

Early theories of the cerebral bases of praxis and language have thus focused on localizing different aspects of these faculties to specific areas, interpreting apraxic and aphasic disorders in terms of either damage to one of these areas or disconnection between them. However, these conceptions have failed to account for many disorders exhibited by brain-damaged patients, leading to the emergence of more complex and integrated conceptions of the brain bases of these complex cognitive faculties.

3. CONTEMPORARY THEORIES FOR THE CEREBRAL ORGANIZATION OF LANGUAGE AND PRAXIS

Beyond the neuropsychological approach, more recent work has attempted to explain the different manifestations of apraxia as dysfunctions of the sensorimotor systems for action and object manipulation, as recently identified by electrophysiological studies in monkeys [75]. In particular, Buxbaum [76] proposed a model of gesture production aimed at reconciling the classical neuropsychological interpretations of apraxic disorders with this more recent neurophysiological framework (review in [77]). In line with classical neuropsychological models [41,78], this model assumes the existence of gesture engrams, which are conceived of as memory-stored sensorimotor (i.e. non-verbal) representations of familiar gestures, involved in both gesture production and

recognition [72]. These engrams are thought to be stored in the left inferior parietal lobule [79] at the interface between the ventral and dorsal streams of visual processing. The evocation of a familiar gesture, for example by verbal command or presentation of the associated tool, would thus activate the appropriate gestural engrams via the lexical semantic system, located primarily in ventral regions. Gesture execution would then be controlled by a dynamic system constituted of the parieto-frontal networks of the dorsal stream. In accordance with this view, patients with damage to the inferior parietal lobule may be able to normally grasp objects based solely on their physical properties (i.e. affordances), while being impaired when asked to grasp the same objects in order to use them, which requires integration of conceptual knowledge of tools and their function [80,81]. More recently, Frey [26] proposed a more dynamic conception of the role of the left inferior parietal cortex. Rather than storing gesture engrams, this region would assemble praxis representations in order to fit all the constraints imposed by conceptual knowledge about tools and their function, the task context, the agent's intentions, etc.

Recent conceptions on the functional anatomy of language have also largely departed from the classical localizationist views exposed in §2, now favouring the idea that language might be organized in networks rather than specialized brain areas. Indeed, the classical concept according to which the frontal lobe is responsible for speech production and temporal areas for language comprehension could not account for the cases of patients presenting, for example, a syndrome of Broca's aphasia with no lesions to Broca's area, or deficits of speech comprehension associated with a lesion in Broca's region [54,55,57]. Furthermore, recent studies have confirmed, for example, the involvement of Broca's area in language comprehension in healthy individuals, at the phonological [31,82,83], lexical [31,84] and syntactical levels [85–87]. These observations, together with the development of neuroimaging techniques, have led researchers to consider that different, partially overlapping networks of superior temporal, posterior parietal and ventral prefrontal areas underpin the phonological, semantic and syntactic levels of language [47].

Current theoretical accounts of language and praxis thus favour the conception that these complex cognitive faculties are subserved by neural networks widely distributed in the left hemisphere. The recruitment of different neural systems would then depend on the exact nature, constraints and context of the task [26,88]. The multiple aspects of aphasia and apraxia would therefore result from disruption of, or the imbalance in, the interactions between parts of these networks, rather than from localized damage to a brain area supporting a specific function. Regardless of this evolution of the theoretical framework for the functional neuroanatomy subserving language and praxis and their disorders, it appears clearly that both cognitive abilities rely on largely overlapping networks, with critical nodes located in the superior temporal, rostral inferior parietal and ventral premotor cortices.

We now turn to examine the implications of language and praxis disorders for action recognition,

imitation and gestural communication, which, as we highlighted in §1, might have constituted critical abilities for the propagation of human technology and language evolution.

4. ACTION RECOGNITION, IMITATION AND GESTURAL COMMUNICATION IN APHASIA AND APRAXIA

(a) *Action recognition*

As mentioned above, Heilman *et al.* [72] showed that the recognition of transitive tool-use gestures was impaired in some patients with ideomotor apraxia, who were therefore also impaired for the execution of these gestures. These findings were later confirmed [89,90]. Neuroimaging experiments also showed a similar interaction between action observation and production (and imagination) in healthy humans [91]. The observation of meaningful actions activates the left hemisphere in the frontal and temporal regions while the observation of meaningless actions involves mainly the right occipito-parietal pathway [92].

The link between observation and imitation of object-related actions in apraxic patients has been recently re-examined by Buxbaum *et al.* [93] and Pazzaglia *et al.* [94] with advanced lesion reconstruction techniques. Buxbaum *et al.* observed a close relationship between performance in pantomime recognition tasks and imitation of object-related actions. Further, in line with Heilman *et al.* [72], the neuroanatomical analysis showed that lesions located in the inferior parietal lobe and in the intraparietal sulcus were significantly associated with deficits in the recognition of transitive gestures. Pazzaglia *et al.* also observed a close correlation between action execution and recognition in a subgroup of apraxic patients. However, the impairment of recognition in their sample of patients was correlated with lesions at the level of the left inferior frontal gyrus, not of the inferior parietal lobe. The authors of these studies have argued that the discrepancies in their main findings were probably due to different task structures. Pazzaglia *et al.* thus proposed that their recognition task required judgement of the ultimate goal of transitive gestures (or the symbolic meaning of intransitive gestures), while Buxbaum *et al.*'s experiment relied more on identifying kinematic cues. In addition, Buxbaum & Kalenine [77] suggested that the response in Pazzaglia *et al.*'s action-recognition task might have been based on structural rather than functional cues. While this question remains open, these two studies confirm the involvement of the left inferior parietal and ventral premotor cortices in action recognition, possibly at different levels, as well as a tight, although not absolute, functional relationship between action recognition and imitation.

Aphasia has also been known for a long time to induce deficits in the recognition of symbolic gestures and pantomimes in some patients [95]. The question of the comprehension of non-verbal signals by aphasic patients raises an important theoretical issue: is aphasia an impairment specific to the linguistic domain, or is it due to a more general cognitive disorder affecting the use of symbols and signs (asymbolia)? The asymbolia hypothesis has been supported by the experimental work of Duffy & Duffy [96], which showed strong

correlations between scores on pantomime execution and recognition, and language tasks. However, another study concluded that the deficit in pantomiming observed in some aphasic patients might be due to associated apraxia rather than to asymbolia [97]. Aphasic patients are indeed impaired in the comprehension of pantomime in comparison to healthy subjects, but with some dissociation (review in [98]). The left, predominantly frontal, localization of lesions impairing action recognition was confirmed by Tranel *et al.* [99]. A recent controlled study by Saygin *et al.* [100] compared the recognition of actions described by either linguistic (written sentences) or non-linguistic (pictures) cues. Aphasic patients tended to show deficits in both domains, but they were more impaired with linguistic cues, and were also more sensitive to semantic distracters. The authors thus rejected the interpretation of aphasia as fully caused by asymbolia, but nonetheless acknowledged the existence of strong but variable links between linguistic and non-linguistic processes involved in action recognition. Furthermore, the impairment of action recognition in these patients was associated with lesions involving the left inferior frontal areas, in line with Tranel *et al.*'s conclusion. The involvement of the left inferior frontal gyrus in action recognition has also been shown in other tasks. For example, Fazio *et al.* [101] reported that Broca's aphasic patients, though not apraxic, had specific impairment in action and tool naming with respect to object naming, thus supporting the idea that frontal regions might be crucial for action and tool recognition [102]. This specific deficit underlines the double competence of Broca's region, which is not only a language area relating to various aspects and levels of language, but is also a part of the premotor cortex, and as such, is involved in action representation [103]. This consideration has to be regarded in the actual context of embodied language comprehension. Indeed, the processing of action verbs describing leg, mouth or hand movements has been reported to activate motor and premotor areas in a somatotopic manner [104], and may interfere with or facilitate movement execution [105]. These findings suggest that cortical motor regions are involved in action word representation.

(b) *Gesture imitation and speech repetition*

Defective imitation of meaningful or meaningless gestures has often been considered a distinctive sign of apraxia [71,73], and has thus been studied quite extensively. The observation that apraxic patients may be impaired for the imitation of meaningless gestures while being able to reproduce meaningful ones flawlessly [106] has prompted researchers to investigate the processes underlying the imitation of both types of gestures. It has thus been proposed that gesture imitation may be subserved by two distinct routes: a first semantic and indirect route, and a second direct and non-semantic route [106,107]. The former is thought to support imitation of meaningful gestures, while the latter would allow imitation of meaningless gestures by matching the perceived action to the appropriate motor plans. The direct route, however, might subserve the imitation of meaningful gestures in case of damage

to the indirect route. In his seminal work on the topic, Goldenberg and co-workers [106,108] showed that apraxic patients impaired in the imitation of meaningless gestures also showed a deficit in matching the experimenter's posture on a manikin. According to Goldenberg, this demonstrated that the transposition by the direct route of an observed posture into a motor scheme requires the movement to be coded on the basis of a general knowledge of the human body structure. A deficit in imitation of meaningless gestures would thus result from the disturbance of this structural body knowledge, a conceptual body representation that would be independent of the body involved in reproducing a movement (i.e. the subject's, the examiner's or a manikin). This representation is probably supported by the left inferior parietal lobule, which was selectively damaged in Goldenberg and Hagmann's patients [106].

Recently, Schwoebel *et al.* [109] sought to further investigate the involvement of different types of body representation in meaningful and meaningless gesture imitation. Scores on tasks evaluating semantic body knowledge and the body schema (i.e. a dynamic representation of the current relative position of body parts for guiding actions) strongly predicted left brain-damaged patients' performance on imitation and production of meaningful gestures. In contrast, imitation of meaningless gestures depended only on the body schema. These findings confirmed the preferential use of a semantic route for the imitation of meaningful gestures, and the existence of a direct route bypassing semantic knowledge for the imitation of meaningless gestures. Taken together, these observations suggest that imitation of meaningless gestures is more complex than a direct matching between bodies, and is likely to involve both dynamic and more abstract representations of the body.

Gesture imitation is not often evaluated in aphasic patients. However, in the linguistic domain, speech repetition may be conceived of as an equivalent to imitation for manual gestures. According to this idea, speech repetition would be an auditory rather than a visuomotor form of imitation. As mentioned earlier, the idea that language perception relies on audio-motor decoding is not recent and has been defended by Liberman & Mattingly [27] in their motor theory of speech perception. Recent experimental data seem to confirm the existence of a motor resonance of the phonemic percept [110,111]. Speech repetition is often impaired in aphasia, in particular in the case of conduction aphasia. Interestingly, for the purpose of comparing the processes involved in the control of gestures and language, conduction aphasia seems to be associated with lesions of the supramarginal gyrus and the neighbouring planum temporale [65,66], a region also thought to be critically involved in gesture imitation. In addition to impaired repetition, patients with conduction aphasia often exhibit a particular behaviour known as '*conduite d'approche*', characterized by repeated attempts to get closer and closer to the correct utterance. The errors made by these patients are mostly phonemic paraphasias (sound-based speech errors) in which articulators are erroneously selected (e.g. 'basecall' for 'baseball', the /c/ being posterior with respect to the anterior /b/ in terms of

the articulators involved). This is similar to the difficulties seen in patients with ideomotor apraxia when trying to match the position of their hand with respect to other body parts to that demonstrated by the experimenter [106]. This parallel between imitation and repetition fits very well with the case described by Ochipa *et al.* [107], of a patient with a lesion restricted to the inferior parietal lobule and the posterior superior temporal cortex, who exhibited conduction aphasia and apraxia with a particular deficit for imitating tool-use pantomimes. Based on the fact that gesture recognition was preserved in this patient, as speech comprehension usually is in patients with conduction aphasia, the authors even proposed to term this deficit 'conduction apraxia'. Recently, strong support in favour of common functional and anatomical bases for repetition and imitation came from an investigation in patients suffering from primary progressive aphasia who often show various degrees of impairment in different aspects of language and praxis. In their study, Nelissen *et al.* [112] showed that their patients' deficit in speech repetition correlated strongly with their impairment of gesture imitation and discrimination. Lesions in the left rostral inferior parietal lobe, extending to the posterior superior temporal cortex, were significantly associated with these combined impairments. Further, tractography analyses showed that the region most often involved in the lesion was the relay for indirect connections between the superior temporal cortex and the inferior frontal gyrus, offering convincing evidence for a shared neural substrate for gesture imitation and speech repetition and a central role of the left inferior parietal cortex in these abilities.

(c) *Pantomime and gestural communication*

In apraxic patients, meaningful intransitive gestures have been much less studied than transitive gestures involving object or tool use. This may appear paradoxical given that intransitive gestures, as they are commonly tested, are in fact symbolic gestures (e.g. waving goodbye) strongly related to gestural expression and thus potentially linked to language. However, as argued by Goldenberg *et al.* [113], pantomimes of transitive gestures are also of interest for the present purpose, as they also constitute a link between tool use and communicative manual actions. Indeed, these gestures symbolize the tool and the associated action, and may be used to communicate or to demonstrate proper use of the tool. Pantomimes may thus have been essential in the development of human technology and of a gestural language.

In the context of examining the links between the cerebral control of gestures and language, it is interesting to note that the concepts of transitivity and intransitivity also apply in language to verb argument structure. Indeed, verbs can be differentiated as a function of the number of arguments they require. Intransitive verbs only need an agent, while transitive verbs need an agent and an object. Verbs can even be ditransitive, and require an agent, an object and a recipient. Broca's aphasic patients, whose linguistic production is agrammatic, tend to produce simple rather than

complex verb argument structure [114], thus favouring intransitive rather than transitive verbs, as apraxic patients do with gestures (see below). Brain imaging investigations of the neural network underlying the processing of verb argument structure have highlighted not only the role of anterior language areas (i.e. the inferior frontal gyrus), but have also put forward the decisive role played by the parietal cortex, and especially the angular gyrus [115,116].

In line with classical reports of studies in apraxic patients, Mozaz *et al.* [117] showed that apraxic patients are less impaired when performing intransitive than transitive gestures. This was later confirmed by Buxbaum *et al.* [118], who found, in addition, a much weaker relation between imitation and recognition of intransitive gestures. In agreement with this, Heath *et al.* [119] found that a similar percentage of patients with right or left hemispheric damage were impaired for performing meaningful intransitive gestures, suggesting that these gestures are neither unequivocally linked to apraxia nor strongly lateralized. Impairment of tool-use pantomimes would thus be more specific of apraxia than that of intransitive gestures. However, recent studies have challenged the classical view of distinct anatomo-functional bases for the production of transitive and intransitive gestures. Instead, these reports [117–119] suggest that both categories of gestures might rely on the same mechanisms, with transitive gestures being simply more difficult to perform than intransitive ones. Tool-use pantomime is a particularly complicated task since it requires motor imagery and cognitive analysis of the gesture before producing it in detail. In contrast, actual tool use may be guided by the structure of the object itself (affordances) as well as sensory information during hand–object interaction. Accordingly, as pointed out by Carmo & Rumiati [120], no double dissociation has been found between the performance of transitive and intransitive gestures in left-brain-damaged patients: while some patients have been described with impaired transitive and preserved intransitive gestural performance, the reverse profile has, to our knowledge, never been reported (see Stamenova *et al.* [121] for cases in right-brain-damaged patients). Carmo & Rumiati thus analysed the performance of healthy individuals on an imitation task involving transitive and intransitive gestures, and found that they were better at imitating intransitive than transitive movements, in accordance with apraxic patients' difficulties with transitive gestures. In keeping with this idea, Frey [26] and Krolczak & Frey [122] observed that, in healthy individuals, transitive and intransitive gestures activate the same, hand-independent network in the left hemisphere, suggesting indeed that the same mechanisms might be at play in both conditions. Regarding the neural substrate for the ability to pantomime tool-use actions, recent findings challenged the long-standing notion that pantomimes were primarily supported by the left inferior parietal cortex, thought to store praxic representations [41,72,93]. Indeed, a recent study in apraxic patients showed, using current lesion reconstruction and mapping techniques, that the critical region for the ability to pantomime tool-use actions is rather the posterior part of the left inferior frontal gyrus [113].

In sum, the ability to pantomime, which constitutes a link between manual tool use and communication, is very often disrupted in apraxia, and seems to rely mainly on the integrity of the left inferior frontal gyrus. The impact of brain damage and apraxia on intransitive communicative gestures, however, requires further investigation. While neuroimaging studies in healthy individuals suggest that they are supported by the same neural substrate, recent neuropsychological reports suggest that intransitive, symbolic gestures might be less tied to left hemisphere function than transitive gestures [119,121]. In particular, their relation to genuine gestural communication, language in general, and tool-use gestures, still needs to be explored.

Gestural communication, and the link between language and gestures, has been more largely studied in aphasic patients. These studies have considered several classes of communicative gestures, in contrast to the specific case of pantomime illustrated above and extensively examined in apraxic patients. McNeill [123] proposed a classification of these communicative gestures, organized along a continuum. He distinguishes co-speech gestures, spontaneously used during communication, 'language-like gestures' (grammatically integrated into the utterance), pantomimes (where speech is not necessary), emblems (which have a standard of well-formedness, like the sign 'ok') and finally sign languages used by the deaf. Along this continuum, idiosyncratic gestures are progressively replaced by socially regulated signs, the obligatory presence of speech declines (i.e. co-speech gestures accompany spoken language but are not sufficient to convey meaning by themselves, in contrast to sign languages), while language properties embedded in gestures increase. On the contrary to co-speech gestures, sign languages have genuine linguistic properties, with distinctive semantics and syntactic rules, like spoken languages do.

Co-speech gestures are frequent in human communication and have diverse functional roles with large cultural variations [124], but cannot be considered as linguistic gestures by themselves [123]. They are idiosyncratic and individual, and convey meaning by different ways (iconic, metaphoric, deictic, beats, cohesive, etc.) that are radically different from language. First, co-speech gestures are global and synthetic (i.e. neither combinatorial nor hierarchical). Second, they have no standard of form. Third, they lack duality of patterning (in contrast to words where sounds and meanings are both separately structured and arbitrarily linked). However co-speech gestures are intimately linked to language since gestures and speech are synchronous and 'semantically and pragmatically co-expressive'. According to McNeill's hypothesis [123] 'speech and gesture are elements of a single integrated process of utterance formation in which there is a synthesis of opposite modes of thought. Utterances and thought realized in them are both imagery and language'. Regarding the impact of aphasia on co-speech gestures, while it is recognized that aphasic patients may spontaneously use them, there is still no agreement on their level of gestural impairment relative to the level of verbal impairment. For some authors, gestural and verbal expressions are both impaired, owing to a common deficit in

communication [125,126]. Other studies claim that gestural expression is less impaired than language, or even that it is more developed than in healthy individuals, perhaps as a result of compensation [46,127]. The neural bases of expressive gestures in healthy individuals have attracted much attention in recent years [128]. However, little is known about the control of expressive gestures in aphasic patients. Several clinical trials have analysed the use of gestures for the rehabilitation of aphasic patients but the results are still unclear [129–133].

At the opposite end of McNeill's continuum, other studies have investigated the impact of brain lesions on the ability to sign. Poizner *et al.* [134,135] observed deaf signers who became aphasic for sign language. Importantly, the impairment was specific to the linguistic components of sign language and dissociated from the production or recognition of non-linguistic gestures and the general ability to use symbols. Studies using functional neuroimaging in neurologically intact deaf signers demonstrated that the neural systems supporting signed language were lateralized to the left hemisphere and very similar to the systems supporting spoken languages, with the additional involvement of the left parietal lobe [136].

In sum, a direct comparison between the impact of apraxia and aphasia on gestural communication is difficult based on the existing literature. Indeed, genuine co-speech gestures are usually examined only in relation to aphasia, without a clear analysis of the impact of potentially associated apraxia. In addition, the impact of apraxia on intransitive gestures, which are mostly emblems as classically assessed in the clinical examination, needs further investigation. Conflicting data in the literature on the impact of aphasia on communicative gestures may also be due to confusion between different categories of motor behaviours along McNeill's continuum, bearing very different relationships with speech and language. In addition, little is known about the spontaneous use of different kinds of communicative gestures in aphasic and apraxic patients. Despite these limitations, however, some links between gestures and language have been demonstrated. In particular, spoken and signed languages are supported by largely overlapping networks [136] (although they both can be dissociated from the production and recognition of non-linguistic gestures [134]). In addition, pantomime of tool use relies mainly on the brain region encompassing Broca's area [113]. Together, the findings reviewed in this section clearly show that if the networks subserving the various aspects of language and praxis are not identical, they largely overlap, with key nodes in the left inferior frontal, inferior parietal and superior temporal cortices.

Further, several studies suggested functional links between language and praxis, raising the possibility of shared processes between both cognitive abilities. In §5, we will try to provide clues as to whether language and praxis may indeed share some common resources.

5. COMMON RESOURCES FOR PRAXIS AND LANGUAGE

The left cerebral hemisphere is considered to play a dominant role for many aspects of praxic and linguistic

behaviours. It is certainly true that some functions related to praxis (e.g. naturalistic multi-step actions [137]) or language (e.g. pragmatic communication [46]) seem to be supported by both hemispheres, or even to be lateralized to the right hemisphere (e.g. matching of finger postures [138] or prosodic processing [44]). However, most praxic and linguistic processes appear consistently lateralized to the left hemisphere. As reviewed earlier, this is true for phonological, semantic and syntactic processing for speech comprehension and production [47]. As for praxis, the following functions depend on the left hemisphere: pantomime [93], actual tool use [68], gesture imitation and recognition [93,107,112] and conceptual knowledge about action and tools [73]. In sum, while cases of atypical cerebral dominance for praxis and language have been described in the neuropsychological literature [138,139], it remains that aphasia and apraxia are both caused by left hemispheric lesions in the vast majority of patients [48,71]. With respect to the evolutionary hypotheses outlined in the introduction, it is interesting that the cerebral lateralization for praxis is more strongly linked to the dominance for language than to manual preference [138,140,141]. This might be due to the necessary interactions between praxic representations and other linguistic-related processes, such as semantics and conceptual knowledge [26,76].

Beyond the observation that these symptoms usually arise after lesions to the same hemisphere, it is striking that apraxia and aphasia are very often associated in right-handed patients with left brain damage [71]. However, the frequent co-occurrence and common hemispheric lateralization are not sufficient to conclude that aphasia and apraxia reflect the same impairment. For example, apraxic patients may exhibit deficits that are linked to non-linguistic processes, such as mechanical reasoning. Indeed, they often have difficulties in solving mechanical puzzles, which require inferring the function of a tool or of an object solely from its structure [142], or in technical reasoning [143]. Thus, praxis implies some left lateralized cognitive ability important for actual tool use but independent from linguistic capacity.

The frequent association of aphasia and apraxia is often seen as the mere consequence of the fact that the cortical regions mediating language and praxis overlap and are vascularized by a common arterial blood supply; thus, there is a high probability that they will both be damaged in the case of stroke. The fact that the co-occurrence of aphasia and apraxia is almost systematic [144] has brought some support to this conception. A clinical study specifically aimed at evaluating the frequency of the co-occurrence of apraxia and aphasia in a large sample of left-brain-damaged right-handed patients indeed reported the existence of a double dissociation between these two disorders in a minority of cases: of 699 patients, 10 had apraxia without aphasia, and 149 were aphasic but not apraxic [42]. In neuropsychology, the existence of a double dissociation between two disorders is usually considered as evidence for a functional independence of the two corresponding cognitive functions (e.g. [145]). However, as argued by Iacoboni & Wilson [146], it is well known that cerebral organization

shows large inter-individual variability at many levels. It is thus possible that the minority of patients showing this double dissociation between aphasia and apraxia, especially in such low proportions as for apraxia without aphasia, may rather represent the two tails of the probabilistic distribution of inter-individual variability for the anatomo-functional organization of language and praxis systems. According to this view, a large majority of individuals would actually have shared neural networks for both abilities. Other interpretations of the frequent association of aphasia and apraxia have thus proposed that both disorders reflect the disturbance of common mechanisms, which may be conceived, for example, as a global communicative or semantic competence [96], or as a left hemisphere specialization for the control of complex sequences [2,124,147]. While it seems unlikely, in light of the literature reviewed here, that apraxia and aphasia strictly reflect a common disorder, many findings coming from neuropsychology and other fields suggest that language and praxis networks may actually intersect and share some common processes.

In particular, the motor aspects of speech and praxis, especially their requirements for sequentially selecting and combining successively different effectors, have long been considered to be potentially underpinned by a common specialization of the left hemisphere for such behaviours [147]. Furthermore, as we have discussed previously, speech repetition and gesture imitation, in addition to bearing similarities as gestural or linguistic imitative behaviours, seem to share common anatomo-functional bases. Indeed, the left inferior parietal cortex, and in particular the supramarginal gyrus, is critical for gesture imitation [79,107,112,148] as well as for repetition [65,66,112]. In addition, functional magnetic resonance imaging studies have allowed a network subserving audio-motor transformations and phonological processing, which are necessary for speech production and repetition, to be delineated [47,149]. This network links the anterior part of Broca's region (see also Kotz *et al.* [31] for the involvement of Broca's area in phonology perception) to the posterior part of the planum temporale and the supramarginal gyrus. A similar network has also been implicated in gesture imitation [113]. In line with these observations, a common underlying mechanism for repetition and imitation has recently been proposed by Iacoboni & Wilson [146]. In their model, the left inferior parietal cortex is thought to have the critical role of reinforcing associations between the appropriate forward and inverse models for language and gestures perception and production. Inverse modelling, allowing the translation of perceived speech or actions into motor plans, is implemented by connections (via inferior parietal areas) between the superior temporal cortex (which encompasses Wernicke's area), involved in the perception of speech and actions, and ventral premotor areas (including Broca's region), which support motor planning and programming for speech and gesture production. Forward modelling, on the other hand, allows the sensory consequences of the intended motor acts, critical for online motor control, to be predicted. These forward models are thought to be implemented by projections, again via the inferior parietal cortex, from the ventral premotor cortex to superior temporal

areas. In this framework, damage to the inferior parietal lobule would thus cause difficulties in updating the inverse model based on the forward model, resulting in impaired repetition and imitation.

Furthermore, language and praxis also seem to interact strongly at the semantic level. Recent studies have shown that the semantic system is much more distributed than originally thought. Binder *et al.* [150] carried out a meta-analysis of functional neuroimaging studies on semantic processing in healthy individuals. They concluded that the semantic system clearly depends on large networks distributed in the temporal, frontal and parietal cortices, predominantly, but not exclusively, in the left hemisphere. This network is constituted of heteromodal association areas, similar to the 'default network'¹, but with little overlap with the distributed network activated by sensorimotor activity. Valuable insight into the cerebral bases of semantic processing has also been provided by neuropsychological investigations in brain-damaged patients. These studies have shown that some patients with very focal brain lesions may present with selective impairment of naming objects of specific semantic categories (e.g. living things versus inanimate objects), thus allowing inferences about the precise semantic function supported by the damaged area. In particular, a double dissociation has been shown between the capacity to name verbs or nouns ([151], review in [152]). Interestingly, while naming nouns involves cortical areas closer to the regions activated by object recognition tasks, naming verbs is supported by areas closer to the frontal motor regions [153]. This suggests that the motor system may be involved in action representation, which could serve action recognition with the aim of pantomiming or imitating, or with the aim of denominating [34]. In this context, a recent study in healthy subjects showed that symbolic gestures and spoken language activated the same left lateralized network, corresponding to Broca's & Wernicke's areas. According to the authors, this suggests that this system 'is not committed to language processing but may function as a modality-independent semiotic system that plays a broader role in human communication, linking meaning to symbols' [154]. In line with this, MacSweeney *et al.* [136] also identified this network, with the addition of the left inferior parietal cortex, as the neural substrate for signed language in deaf individuals.

Finally, as suggested earlier, another potential functional relation between praxis and language lies in the hierarchical organization of those behaviours. Is syntax exclusive to the linguistic domain, or are complex actions and music endowed with hierarchical rules akin to linguistic syntax [155,156]? In the domain of language, Broca's aphasia is classically qualified as 'agrammatic' owing to impairment in producing grammatical sentences and in processing syntactic markers. Accordingly, a wealth of brain imaging studies has reported the activation of the caudal part of Broca's area (Brodmann area 44) in tasks involving syntactic processing [85–87]. In accordance with these observations, Grodzinsky & Santi [157] proposed that abstract linguistic abilities are neurologically coded, and that Broca's area might play a specific role in syntax processing. However, other authors have

proposed that Broca's aphasics' impairment in syntactic processing might rather be due to a lessening of available resources [56], and that the role of Broca's area might instead be to bind together the semantic, syntactic and phonological levels of language [158]. In the praxic domain, on the other hand, complex actions can be conceived of as structured according to three levels of organization: hierarchical (goals and subgoals), temporal (action sequences) and spatial (embodiment of tools). This structure could be paralleled with the organization of language [34,38]. Interestingly, the hierarchical control of action appears to involve Broca's region and its right homologue [159,160]. This is consistent with the fact that planning deficits, characteristic of dysexecutive syndromes, are attributed to lesions of the frontal lobes [161] and that both complex sequential actions (e.g. preparing a cup of coffee) [137] and pragmatic communication in a social context [46] seem to depend on both hemispheres. In addition, there is evidence for a convergence between language and praxis at the syntactic level as well. For example, Fazio *et al.* [101] have recently provided support for the existence of a link, potentially supported by Broca's area, between language syntax and sequential organization of observed actions. These authors have demonstrated that agrammatic patients with lesions involving Broca's area are also impaired in a non-linguistic test consisting of ordering action sequences. This functional relation between action recognition and language perception has recently been confirmed and further characterized by Sitnikova *et al.* [162], who examined event-related potentials in an action structural violation paradigm. In this study, healthy participants were presented with movies depicting everyday familiar tasks involving the use of tools. The authors found that the introduction of a tool irrelevant to the action context (e.g. an iron in the context of cutting bread) elicited a neurophysiological response usually linked to syntactic processes and violation detection. Interestingly, the stimuli used in this paradigm are highly reminiscent of the errors made by some patients with conceptual apraxia. These patients may indeed be unable to judge the appropriateness of the gesture demonstrated by an experimenter in association with a given tool or object [78], or they may also make similar errors when asked to demonstrate the gestures themselves, either choosing the wrong tool in a given context or executing the wrong action in response to a visually presented object [73].

6. CONCLUSION

Several hypotheses on the emergence of human culture and cognitive capacities have proposed a close evolutionary link between praxis, including tool use, and language, which are uniquely developed in the human species. Some of them have in addition proposed that gestural communication, involving action recognition and imitation, might have constituted an intermediary stage between the development of tool manufacture and use, and the emergence of spoken language. These hypotheses predict a strong relationship between the neural substrates and cognitive processes involved in language and praxis. Here we have addressed this

question by reviewing the neuropsychological literature pertaining to the impairments of language and praxis after brain lesions, respectively termed aphasia and apraxia. In particular, we examined their impact on action recognition, imitation and communicative gestures, as well as the possible anatomo-functional links between the two neural systems supporting the two uniquely human cognitive abilities.

Research in brain-damaged patients as well as healthy individuals has shown that the functional anatomy of language and praxis is complex and organized in several networks, mainly lateralized to the left hemisphere. These praxic and linguistic networks partly overlap, with critical nodes located in the superior temporal, rostral inferior parietal and ventral premotor cortices. In contrast to what has often been argued, the frequent co-occurrence of aphasia and apraxia in left-brain-damaged patients may not be only the mere consequence of the proximity of the cortical areas involved. Rather, this phenomenon might reflect the fact that praxis and language networks actually intersect and share some common functional processes. This view is compatible with the existence of joint linguistic and praxic impairments, reflecting common deficient mechanisms, as well as with the dissociation between other manifestations of aphasia and apraxia. One demonstrative example of dissociation is the case of aphasic patients who previously used sign language and have selective impairment of the linguistic aspects of their gestures [134–136].

Accordingly, several recent studies in left-brain-damaged patients have suggested strong links between speech repetition and gesture imitation, which may involve common neural substrates and mechanisms, with a critical role played by the left inferior parietal cortex. Both aphasia and apraxia may induce impairments of action recognition, but some evidence suggests that the mechanisms involved are at least partially dissociable. Regardless, investigations in aphasic and apraxic patients suggest involvement of the left inferior frontal gyrus, including Broca's area, as well as the left inferior parietal lobe. As for gestural communication, the available literature does not allow comparison of the consequences of the aphasia and apraxia, since different categories of gestures have been studied in relation to each syndrome. This question will thus need further and more specific investigation. The available literature leads to the conclusion that the hypothesis of asymbolia is too general to explain the complex relations between gesture communication, aphasia and apraxia [100,163,164]. However, evidence from neuropsychological and neuroimaging studies converges to suggest that tool-use pantomimes, which may have been critical for the transmission and propagation of human tool manufacture and use, depend at least partly on the same neural network as actual tool use and symbolic, intransitive gestures. In particular, lesions involving the left inferior frontal gyrus, known to be strongly involved in speech production and comprehension, seem to be especially associated with impairment of tool-use pantomimes. In sum, neuropsychological studies of linguistic and praxic disorders show that both systems interact more or less depending on the context and on which aspects these complex cognitive behaviours are considered. Mounting evidence suggests that the phonological,

semantic and syntactic levels of language share some common cognitive resources with the praxis system. This is consistent with the hypothesis of common phylogenetic and ontogenetic origins for language and praxis [9]. However, neuropsychological data do not allow confirmation or rejection of the hypothesis of an intermediary stage of gestural communication between the development of tool use and the emergence of language.

In addition to the development of long-range interconnected networks, evolution within some strategic areas in the left hemisphere might have conditioned the appearance and lateralization of complex human behaviour. The left lateralization might be attributed to an asymmetry of the columnar micro-architecture of the cortex inducing an asymmetry of some general processes then leading to a differential development of functions [165]. Along this line of reasoning, Goldenberg [67] proposes that the specific role of the left parietal lobe is based on categorical apprehension of spatial relationships, consistently with the left hemisphere preference for categorical coding (by opposition to coordinate coding). Similarly, the hemispheric lateralization for speech could result from an asymmetry of cortical temporal tuning, itself inducing an asymmetry of audio-motor processes [166]. According to this hypothesis, the left hemisphere might be specialized for the perception and production of sounds in the 28–40 Hz frequency domain (i.e. perception of phonemes and tongue movements) while the right hemisphere might be specialized in the 3–6 Hz frequency domain (i.e. syllabic rate and jaw movements). The role of Broca's area (or more generally speaking, the left inferior frontal gyrus) is now being revisited and ardently disputed [157]. In addition to its contribution to the human mirror system [167], it could have a generic function for hierarchical processing and nesting of chunks and sequences [160], unification of the different aspects of language [158] or binding meaning and symbol [154]. This kind of generic function might be a common resource for action and language, grounded in the left hemisphere and acting like a node in a complex and bilateral distributed network. These processes probably condition the richness and complexity of human activity.

This text is dedicated to the memory of Catherine Bergego. The research was supported by a grant from the European Communities: NEST project Hand-to-Mouth contract no. 029065. A.R.-B. is supported by INSERM. The authors thank Georg Goldenberg, Katharina Hogrefe, Wolfram Ziegler and Etienne Koechlin for useful comments and two anonymous reviewers for their suggestions. Françoise Marchand from the Federative Institute on Research on the Handicap (IFR25) and Johanna Robertson helped in the editing of the text.

ENDNOTE

¹The default network is activated in resting states for specific tasks 'interrupting the stream of consciousness'.

REFERENCES

- 1 Annett, M. 2006 The distribution of handedness in chimpanzees: estimating right shift in Hopkins' sample. *Laterality* 11, 101–109.

- 2 Kimura, D. & Archibald, Y. 1974 Motor functions of the left hemisphere. *Brain* **97**, 337–350. (doi:10.1093/brain/97.1.337)
- 3 Corbetta, D. 2003 Right-handedness may have come first: evidence from studies in human infants and non-human primates. *Behav. Brain Sci.* **26**, 217–218. (doi:10.1017/S0140525X03320060)
- 4 Bradshaw, J. L. & Nettleton, N. C. 1982 Language lateralization to the dominant hemisphere: tool use, gesture and language in hominid evolution. *Curr. Psychol. Rev.* **2**, 171–192. (doi:10.1007/BF02684498)
- 5 Corballis, M. C. 2003 From mouth to hand: gesture, speech, and the evolution of right-handedness. *Behav. Brain Sci.* **26**, 199–208. (doi:10.1017/S0140525X03000062)
- 6 Ambrose, S. H. Paleolithic technology and human evolution. *Science* **291**, 1748–1753. (doi:10.1126/science.1059487)
- 7 Tomasello, M. 1999 The human adaptation for culture. *Annu. Rev. Anthropol.* **28**, 509–529. (doi:10.1146/annurev.anthro.28.1.509)
- 8 Steele, J. & Uomini, N. 2009 Can the archaeology of manual specialization tell us anything about language evolution? A survey of the state of play. *Steps to a (neuro-) archaeology of mind* (eds L. Malafouris & C. Renfrew). *Camb. Archaeol. J.* **19**, 97–110.
- 9 Greenfield, P. M. 1991 Language, tools and brain: the ontogeny and phylogeny of hierarchically organized sequential behavior. *Behav. Brain Sci.* **14**, 531–551. (doi:10.1017/S0140525X00071235)
- 10 Iriki, A., Tanaka, M. & Iwamura, Y. 1996 Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport* **7**, 2325–2330. (doi:10.1097/00001756-199610020-00010)
- 11 Obayashi, S., Suhara, T., Kawabe, K., Okauchi, T., Maeda, J., Akine, Y., Onoe, H. & Iriki, A. 2001 Functional brain mapping of monkey tool use. *Neuroimage* **14**, 853–861. (doi:10.1006/nimg.2001.0878)
- 12 Frey, S. H. 2007 What puts the how in where? Tool use and the divided visual streams hypothesis. *Cortex* **43**, 368–375. (doi:10.1016/S0010-9452(08)70462-3)
- 13 Arbib, M. A., Bonaiuto, J. B., Jacobs, S. & Frey, S. H. 2009 Tool use and the distalization of the end-effector. *Psychol. Res.* **73**, 441–462. (doi:10.1007/s00426-009-0242-2)
- 14 Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A. C. & Farne, A. 2009 Tool-use induces morphological updating of the body schema. *Curr. Biol.* **19**, R478–R479. (doi:10.1016/j.cub.2009.05.009)
- 15 Ungerleider, L. G. & Mishkin, M. 1982 Two cortical visual system. In *Analysis of visual behaviour* (eds D. L. Ingle, M. A. Goodale & R. J. W. Mansfield), pp. 549–586. Cambridge, MA: MIT Press.
- 16 Goodale, M. A. & Milner, A. D. 1992 Separate visual pathways for perception and action. *Trends Neurosci.* **15**, 20–25. (doi:10.1016/0166-2236(92)90344-8)
- 17 Rizzolatti, G. & Luppino, G. 2001 The cortical motor system. *Neuron* **31**, 889–901. (doi:10.1016/S0896-6273(01)00423-8)
- 18 Jacobs, S., Danielmeier, C. & Frey, S. H. 2010 Human anterior intraparietal and ventral premotor cortices support representations of grasping with the hand or a novel tool. *J. Cogn. Neurosci.* **22**, 2594–2608. (doi:10.1162/jocn.2009.21372)
- 19 Umilta, M. A., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., Jezzini, A., Gallese, V. & Rizzolatti, G. 2008 When pliers become fingers in the monkey motor system. *Proc. Natl Acad. Sci. USA.* **105**, 2209–2213. (doi:10.1073/pnas.0705985105)
- 20 Johnson-Frey, S. H. 2003 What's so special about human tool use? *Neuron* **39**, 201–204. (doi:10.1016/S0896-6273(03)00424-0)
- 21 Hodges, J. R., Bozeat, S., Lambon Ralph, M. A., Patterson, K. & Spatt, J. 2000 The role of conceptual knowledge in object use evidence from semantic dementia. *Brain* **123**, 1913–1925. (doi:10.1093/brain/123.9.1913)
- 22 Johnson-Frey, S. H. 2004 The neural bases of complex tool use in humans. *Trends Cogn. Sci.* **8**, 71–78. (doi:10.1016/j.tics.2003.12.002)
- 23 Lewis, J. W. 2006 Cortical networks related to human use of tools. *Neuroscientist* **12**, 211–231. (doi:10.1177/1073858406288327)
- 24 Creem, S. H. & Proffitt, D. R. 2001 Grasping objects by their handles: a necessary interaction between cognition and action. *J. Exp. Psychol. Hum. Percept. Perform.* **27**, 218–228. (doi:10.1037/0096-1523.27.1.218)
- 25 Randerath, J., Li, Y., Goldenberg, G. & Hermsdorfer, J. 2009 Grasping tools: effects of task and apraxia. *Neuropsychologia* **47**, 497–505. (doi:10.1016/j.neuropsychologia.2008.10.005)
- 26 Frey, S. H. 2008 Tool use, communicative gesture and cerebral asymmetries in the modern human brain. *Phil. Trans. R. Soc. B* **363**, 1951–1957. (doi:10.1098/rstb.2008.0008)
- 27 Liberman, A. M. & Mattingly, I. G. 1985 The motor theory of speech perception revised. *Cognition* **21**, 1–36. (doi:10.1016/0010-0277(85)90021-6)
- 28 Rizzolatti, G. & Craighero, L. 2004 The mirror-neuron system. *Annu. Rev. Neurosci.* **27**, 169–192. (doi:10.1146/annurev.neuro.27.070203.144230)
- 29 Fogassi, L. & Luppino, G. 2005 Motor functions of the parietal lobe. *Curr. Opin. Neurobiol.* **15**, 626–631. (doi:10.1016/j.conb.2005.10.015)
- 30 Fadiga, L., Craighero, L. & D'Ausilio, A. 2009 Broca's area in language, action, and music. *Ann. N Y Acad. Sci.* **1169**, 448–458. (doi:10.1111/j.1749-6632.2009.04582.x)
- 31 Kotz, S. A., D'Ausilio, A., Raettig, T., Begliomini, C., Craighero, L., Fabbri-Destro, M., Zingales, C., Haggard, P. & Fadiga, L. 2010 Lexicality drives audio-motor transformations in Broca's area. *Brain Lang.* **112**, 3–11. (doi:10.1016/j.bandl.2009.07.008)
- 32 Fadiga, L., Fogassi, L., Pavesi, G. & Rizzolatti, G. 1995 Motor facilitation during action observation: a magnetic stimulation study. *J. Neurophysiol.* **73**, 2608–2611.
- 33 Rizzolatti, G., Fogassi, L. & Gallese, V. 2001 Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* **2**, 661–670. (doi:10.1038/35090060)
- 34 Pulvermuller, F. & Fadiga, L. 2010 Active perception: sensorimotor circuits as a cortical basis for language. *Nat. Rev. Neurosci.* **11**, 351–360. (doi:10.1038/nrn2811)
- 35 Hickok, G. 2009 Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *J. Cogn. Neurosci.* **21**, 1229–1243. (doi:10.1162/jocn.2009.21189)
- 36 Toni, I., de Lange, F. P., Noordzij, M. L. & Hagoort, P. 2008 Language beyond action. *J. Physiol. Paris* **102**, 71–79. (doi:10.1016/j.jphysparis.2008.03.005)
- 37 Rizzolatti, G. & Arbib, M. A. 1998 Language within our grasp. *Trends Neurosci.* **21**, 188–194. (doi:10.1016/S0166-2236(98)01260-0)
- 38 Arbib, M. A. 2010 Mirror system activity for action and language is embedded in the integration of dorsal and ventral pathways. *Brain Lang.* **112**, 12–24. (doi:10.1016/j.bandl.2009.10.001)
- 39 Arbib, M. A. 2006 Aphasia, apraxia and the evolution of the language-ready brain. *Aphasiology* **20**, 1125–1155. (doi:10.1080/02687030600741683)

- 40 Broca, P. 1861 Remarques sur le siège de la faculté du langage articulé suivi d'une observation d'aphémie (perte de la parole). *Bull. Soc. Anat.* **6**, 330–357.
- 41 Liepmann, H. 1908 *Drei aufsatze aus dem apraxiegebiet*. Berlin, Germany: Karger.
- 42 Papagno, C., Della Sala, S. & Basso, A. 1993 Ideomotor apraxia without aphasia and aphasia without apraxia: the anatomical support for a double dissociation. *J. Neurol. Neurosurg. Psychiat.* **56**, 286–289. (doi:10.1136/jnnp.56.3.286)
- 43 Benson, F. & Ardila, A. 1996 *Aphasia: a clinical perspective*. New York, NY: Oxford University Press.
- 44 Ross, E. D. & Monnot, M. 2008 Neurology of affective prosody and its functional-anatomic organization in right hemisphere. *Brain Lang.* **104**, 51–74. (doi:10.1016/j.bandl.2007.04.007)
- 45 Sammler, D., Kotz, S. A., Eckstein, K., Ott, D. V. & Friederici, A. D. 2010 Prosody meets syntax: the role of the corpus callosum. *Brain* **133**, 2643–2655. (doi:10.1093/brain/awq231)
- 46 Rousseaux, M., Daveluy, W. & Kozlowski, O. 2010 Communication in conversation in stroke patients. *J. Neurol.* **257**, 1099–1107. (doi:10.1007/s00415-010-5469-8)
- 47 Vigneau, M., Beaucoisin, V., Herve, P. Y., Duffau, H., Crivello, F., Houde, O., Mazoyer, B. & Tzourio-Mazoyer, N. 2006 Meta-analyzing left hemisphere language areas: phonology, semantics, and sentence processing. *Neuroimage* **30**, 1414–1432. (doi:10.1016/j.neuroimage.2005.11.002)
- 48 Caplan, D. 2003 Aphasic syndromes. In *Clinical neuropsychology* (eds K. M. Heilman & E. E. Valenstein), pp. 14–34, 4th edn. Oxford, UK: Oxford University Press.
- 49 Noppeney, U. & Wallech, C. W. 2000 Language and cognition: Kurt Goldstein's theory of semantics. *Brain Cogn.* **44**, 367–386. (doi:10.1006/brcg.1999.1199)
- 50 Geschwind, N. 1965 Disconnexion syndromes in animals and man. I. *Brain* **88**, 237–294. (doi:10.1093/brain/88.2.237)
- 51 Geschwind, N. 1965 Disconnexion syndromes in animals and man. II. *Brain* **88**, 585–644. (doi:10.1093/brain/88.3.585)
- 52 Catani, M. & ffytche, D. H. 2005 The rises and falls of disconnection syndromes. *Brain* **128**, 2224–2239. (doi:10.1093/brain/awh622)
- 53 Hillis, A. E. 2007 Aphasia: progress in the last quarter of a century. *Neurology* **69**, 200–213. (doi:10.1212/01.wnl.0000265600.69385.6f)
- 54 Caramazza, A. & Zurif, E. B. 1976 Dissociation of algorithmic and heuristic processes in language comprehension: evidence from aphasia. *Brain Lang.* **3**, 572–582. (doi:10.1016/0093-934X(76)90048-1)
- 55 O'Grady, W. & Lee, M. 2001 The isomorphic mapping hypothesis: evidence from Korea. *Brain Cogn.* **46**, 226–230. (doi:10.1016/S0278-2626(01)80072-5)
- 56 Caplan, D. 2006 Aphasic deficits in syntactic processing. *Cortex* **42**, 797–804. (doi:10.1016/S0010-9452(08)70420-9)
- 57 Caplan, D., Baker, C. & Dehaut, F. 1985 Syntactic determinants of sentence comprehension in aphasia. *Cognition* **21**, 117–175. (doi:10.1016/0010-0277(85)90048-4)
- 58 Ogar, J., Slama, H., Dronkers, N., Amici, S. & Gorno-Tempini, M. L. 2005 Apraxia of speech: an overview. *Neurocase* **11**, 427–432. (doi:10.1080/13554790500263529)
- 59 Ogar, J., Willock, S., Baldo, J., Wilkins, D., Ludy, C. & Dronkers, N. 2006 Clinical and anatomical correlates of apraxia of speech. *Brain Lang.* **97**, 343–350. (doi:10.1016/j.bandl.2006.01.008)
- 60 Dronkers, N. F. 1996 A new brain region for coordinating speech articulation. *Nature* **384**, 159–161. (doi:10.1038/384159a0)
- 61 Hillis, A. E., Work, M., Barker, P. B., Jacobs, M. A., Breese, E. L. & Maurer, K. 2004 Re-examining the brain regions crucial for orchestrating speech articulation. *Brain* **127**, 1479–1487. (doi:10.1093/brain/awh172)
- 62 Ardila, A. 2010 A review of conduction aphasia. *Curr. Neurol. Neurosci. Rep.* **10**, 499–503. (doi:10.1007/s11910-010-0142-2)
- 63 Luria, A. R. 1976 *Basic problems of neurolinguistics* (trans. B. Haigh). The Hague, The Netherlands: Mouton.
- 64 Benson, D. F., Sheremata, W. A., Bouchard, R., Segarra, J. M., Price, D. & Geschwind, N. 1973 Conduction aphasia. A clinicopathological study. *Arch. Neurol.* **28**, 339–346.
- 65 Buchsbaum, B. R., Baldo, J., Okada, K., Berman, K. F., Dronkers, N., D'Esposito, M. & Hickok, G. In press. Conduction aphasia, sensory-motor integration, and phonological short-term memory: an aggregate analysis of lesion and fMRI data. *Brain Lang.* (doi:10.1016/j.bandl.2010.12.001)
- 66 Fridriksson, J., Kjartansson, O., Morgan, P. S., Hjaltason, H., Magnusdottir, S., Bonilha, L. & Rorden, C. 2010 Impaired speech repetition and left parietal lobe damage. *J. Neurosci.* **30**, 11 057–11 061. (doi:10.1523/JNEUROSCI.1120-10.2010)
- 67 Goldenberg, G. 2009 Apraxia and the parietal lobes. *Neuropsychologia* **47**, 1449–1459. (doi:10.1016/j.neuropsychologia.2008.07.014)
- 68 Goldenberg, G. & Spatt, J. 2009 The neural basis of tool use. *Brain* **132**, 1645–1655. (doi:10.1093/brain/awp080)
- 69 Roy, E. A. & Square, P. 1985 Common considerations in the studies on limb, verbal and oral apraxia. In *Neuropsychological studies of apraxia and related disorders* (ed. E. Roy), pp. 111–162. Amsterdam, The Netherlands: North Holland.
- 70 Heilman, K. M. & Rothi, L. J. 1997 Limb apraxia: a look back. In *Apraxia: the neuropsychology of action* (eds L. J. Rothi & K. M. Heilman), pp. 7–18. Hove, UK: Psychology Press.
- 71 Heilman, K. M. & Rothi, L. J. 2003 Apraxia. In *Clinical neuropsychology* (eds K. M. Heilman & E. E. Valenstein), pp. 215–236, 4th edn. New York, NY: Oxford University Press.
- 72 Heilman, K. M., Rothi, L. J. & Valenstein, E. 1982 Two forms of ideomotor apraxia. *Neurology* **32**, 342–346.
- 73 De Renzi, E. & Lucchelli, F. 1988 Ideational apraxia. *Brain* **3**, 1173–1185. (doi:10.1093/brain/111.5.1173)
- 74 Trojano, L., Labruna, L. & Grossi, D. 2007 An experimental investigation of the automatic/voluntary dissociation in limb apraxia. *Brain Cogn.* **65**, 169–176. (doi:10.1016/j.bandc.2007.07.010)
- 75 Leiguarda, R. & Marsden, C. 2000 Limb apraxias: higher-order disorders of sensorimotor integration. *Brain* **123**, 860–879. (doi:10.1093/brain/123.5.860)
- 76 Buxbaum, L. J. 2001 Ideomotor apraxia: a call to action. *Neurocase* **7**, 445–458. (doi:10.1093/neucas/7.6.445)
- 77 Buxbaum, L. J. & Kalenine, S. 2010 Action knowledge, visuomotor activation, and embodiment in the two action systems. *Ann. NY Acad. Sci.* **1191**, 201–218. (doi:10.1111/j.1749-6632.2010.05447.x)
- 78 Rothi, L. J. & Heilman, K. M. 1997 Introduction to limb apraxia. In *Apraxia: the neuropsychology of action* (eds L. J. Rothi & K. M. Heilman), pp. 1–6. Hove, UK: Psychology Press.
- 79 Haaland, K. Y., Harrington, D. L. & Knight, R. T. 2000 Neural representations of skilled movement. *Brain* **123**, 2306–2313. (doi:10.1093/brain/123.11.2306)

- 80 Sirigu, A., Cohen, L., Duhamel, J. R., Pillon, B., Dubois, B. & Agid, Y. 1995 A selective impairment of hand posture for object utilization in apraxia. *Cortex* **31**, 41–55.
- 81 Buxbaum, L. J., Sirigu, A., Schwartz, M. F. & Klatzky, R. 2003 Cognitive representations of hand posture in ideomotor apraxia. *Neuropsychologia* **41**, 1091–1113. (doi:10.1016/S0028-3932(02)00314-7)
- 82 Watkins, K. & Paus, T. 2004 Modulation of motor excitability during speech perception: the role of Broca's area. *J. Cogn. Neurosci.* **16**, 978–987. (doi:10.1162/0898929041502616)
- 83 Meister, I. G., Wilson, S. M., Deblieck, C., Wu, A. D. & Iacoboni, M. 2007 The essential role of premotor cortex in speech perception. *Curr. Biol.* **17**, 1692–1696. (doi:10.1016/j.cub.2007.08.064)
- 84 Fadiga, L. & Craighero, L. 2006 Hand actions and speech representation in Broca's area. *Cortex* **42**, 486–490. (doi:10.1016/S0010-9452(08)70383-6)
- 85 Moro, A., Tettamanti, M., Perani, D., Donati, C., Cappa, S. F. & Fazio, F. 2001 Syntax and the brain: disentangling grammar by selective anomalies. *Neuroimage* **13**, 110–118. (doi:10.1006/nimg.2000.0668)
- 86 Friederici, A. D., Meyer, M. & von Cramon, D. Y. 2000 Auditory language comprehension: an event-related fMRI study on the processing of syntactic and lexical information. *Brain Lang.* **75**, 289–300. (doi:10.1006/brln.2000.2313)
- 87 Newman, S. D., Just, M. A., Keller, T. A., Roth, J. & Carpenter, P. A. 2003 Differential effects of syntactic and semantic processing on the subregions of Broca's area. *Brain Res. Cogn. Brain Res.* **16**, 297–307. (doi:10.1016/S0926-6410(02)00285-9)
- 88 Hickok, G. & Poeppel, D. 2000 Towards a functional neuroanatomy of speech perception. *Trends Cogn. Sci.* **4**, 131–138. (doi:10.1016/S1364-6613(00)01463-7)
- 89 Cubelli, R., Marchetti, C., Boscolo, G. & Della Sala, S. 2000 Cognition in action: testing a model of limb apraxia. *Brain Cogn.* **44**, 144–165. (doi:10.1006/brcg.2000.1226)
- 90 Halsband, U., Schmitt, J., Weyers, M., Binkofski, F., Grutzner, G. & Freund, H. J. 2001 Recognition and imitation of pantomimed motor acts after unilateral parietal and premotor lesions: a perspective on apraxia. *Neuropsychologia* **39**, 200–216. (doi:10.1016/S0028-3932(00)00088-9)
- 91 Buccino, G. et al. 2001 Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur. J. Neurosci.* **13**, 400–404.
- 92 Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F. & Fazio, F. 1997 Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain* **120**, 1763–1777. (doi:10.1093/brain/120.10.1763)
- 93 Buxbaum, L. J., Kyle, K. M. & Menon, R. 2005 On beyond mirror neurons: internal representations subserving imitation and recognition of skilled object-related actions in humans. *Brain Res. Cogn. Brain Res.* **25**, 226–239. (doi:10.1016/j.cogbrainres.2005.05.014)
- 94 Pazzaglia, M., Smania, N., Corato, E. & Aglioti, S. M. 2008 Neural underpinnings of gesture discrimination in patients with limb apraxia. *J. Neurosci.* **28**, 3030–3041. (doi:10.1523/JNEUROSCI.5748-07.2008)
- 95 Gainotti, G. & Lemmo, M. S. 1976 Comprehension of symbolic gestures in aphasia. *Brain Lang.* **3**, 451–460. (doi:10.1016/0093-934X(76)90039-0)
- 96 Duffy, R. J. & Duffy, J. R. 1981 Three studies of deficits in pantomimic expression and pantomimic recognition in aphasia. *J. Speech Hear. Res.* **24**, 70–84.
- 97 Wang, L. & Goodglass, H. 1992 Pantomime, praxis, and aphasia. *Brain Lang.* **42**, 402–418. (doi:10.1016/0093-934X(92)90076-Q)
- 98 Feyereisen, P. & Seron, X. 1982 Nonverbal communication and aphasia: a review. I. Comprehension. *Brain Lang.* **16**, 191–212. (doi:10.1016/0093-934X(82)90083-9)
- 99 Tranel, D., Kemmerer, D., Adolphs, R., Damasio, H. & Damasio, A. R. 2003 Neural correlates of conceptual knowledge for actions. *Cogn. Neuropsychol.* **20**, 409–432. (doi:10.1080/02643290244000248)
- 100 Saygin, A. P., Wilson, S. M., Dronkers, N. F. & Bates, E. 2004 Action comprehension in aphasia: linguistic and non-linguistic deficits and their lesion correlates. *Neuropsychologia* **42**, 1788–1804. (doi:10.1016/j.neuropsychologia.2004.04.016)
- 101 Fazio, P., Cantagallo, A., Craighero, L., D'Ausilio, A., Roy, A. C., Pozzo, T., Calzolari, F., Granieri, E. & Fadiga, L. 2009 Encoding of human action in Broca's area. *Brain* **132**, 1980–1988. (doi:10.1093/brain/awp118)
- 102 Martin, A., Wiggs, C. L., Ungerleider, L. G. & Haxby, J. V. 1996 Neural correlates of category-specific knowledge. *Nature* **379**, 649–652. (doi:10.1038/379649a0)
- 103 Fadiga, L., Craighero, L. & Roy, A. C. 2006 Broca's region: a speech area? In *Broca's region* (eds Y. Grodzinsky & K. Amunts). New York, NY: Oxford University Press.
- 104 Hauk, O., Johnsrude, I. & Pulvermuller, F. 2004 Somatotopic representation of action words in human motor and premotor cortex. *Neuron* **41**, 301–307. (doi:10.1016/S0896-6273(03)00838-9)
- 105 Boulenger, V., Roy, A. C., Paulignan, Y., Deprez, V., Jeannerod, M. & Nazir, T. A. 2006 Cross-talk between language processes and overt motor behavior in the first 200 msec of processing. *J. Cogn. Neurosci.* **18**, 1607–1615. (doi:10.1162/jocn.2006.18.10.1607)
- 106 Goldenberg, G. & Hagmann, S. 1997 The meaning of meaningless gestures: a study of visuo-imitative apraxia. *Neuropsychologia* **35**, 333–341. (doi:10.1016/S0028-3932(96)00085-1)
- 107 Ochipa, C., Rothi, L. J. & Heilman, K. M. 1994 Conduction apraxia. *J. Neurol. Neurosurg. Psychiat.* **57**, 1241–1244. (doi:10.1136/jnnp.57.10.1241)
- 108 Goldenberg, G. 1995 Imitating gestures and manipulating a manikin—the representation of the human body in ideomotor apraxia. *Neuropsychologia* **33**, 63–72. (doi:10.1016/0028-3932(94)00104-W)
- 109 Schwoebel, J., Buxbaum, L. J. & Coslett, B. H. 2004 Representations of the human body in the production and imitation of complex movements. *Cogn. Neuropsychol.* **21**, 285–298. (doi:10.1080/02643290342000348)
- 110 Roy, A. C., Craighero, L., Fabri-Destro, M. & Fadiga, L. 2008 Phonological and lexical motor facilitation during speech listening: a transcranial magnetic stimulation study. *J. Physiol. Paris* **102**, 101–105. (doi:10.1016/j.jphysparis.2008.03.006)
- 111 D'Ausilio, A., Pulvermuller, F., Salmas, P., Bufalari, I., Begliomini, C. & Fadiga, L. 2009 The motor somatotopy of speech perception. *Curr. Biol.* **19**, 381–385. (doi:10.1016/j.cub.2009.01.017)
- 112 Nelissen, N., Pazzaglia, M., Vandenbulcke, M., Sunaert, S., Fannes, K., Dupont, P., Aglioti, S. M. & Vandenberghe, R. 2010 Gesture discrimination in primary progressive aphasia: the intersection between gesture and language processing pathways. *J. Neurosci.* **30**, 6334–6341. (doi:10.1523/JNEUROSCI.0321-10.2010)
- 113 Goldenberg, G., Hermsdorfer, J., Glindemann, R., Rorden, C. & Karnath, H. O. 2007 Pantomime of tool use depends on integrity of left inferior frontal cortex. *Cereb. Cortex* **17**, 2769–2776. (doi:10.1093/cercor/bhm004)
- 114 Thompson, C. K. 2003 Unaccusative verb production in agrammatic aphasia: the argument structure complexity hypothesis. *J. Neurolinguist.* **16**, 151–167. (doi:10.1016/S0911-6044(02)00014-3)

- 115 den Ouden, D. B., Fix, S., Parrish, T. B. & Thompson, C. K. 2009 Argument structure effects in action verb naming in static and dynamic conditions. *J. Neurolinguist.* **22**, 196–215. (doi:10.1016/j.jneuroling.2008.10.004)
- 116 Thompson, C. K., Bonakdarpour, B., Fix, S. C., Blumenfeld, H. K., Parrish, T. B., Gitelman, D. R. & Mesulam, M. M. 2007 Neural correlates of verb argument structure processing. *J. Cogn. Neurosci.* **19**, 1753–1767. (doi:10.1162/jocn.2007.19.11.1753)
- 117 Mozaz, M., Rothi, L. J., Anderson, J. M., Crucian, G. P. & Heilman, K. M. 2002 Postural knowledge of transitive pantomimes and intransitive gestures. *J. Int. Neuropsychol. Soc.* **8**, 958–962. (doi:10.1017/S1355617702870114)
- 118 Buxbaum, L. J., Kyle, K., Grossman, M. & Coslett, H. B. 2007 Left inferior parietal representations for skilled hand–object interactions: evidence from stroke and corticobasal degeneration. *Cortex* **43**, 411–423. (doi:10.1016/S0010-9452(08)70466-0)
- 119 Heath, M., Roy, E. A., Westwood, D. & Black, S. E. 2001 Patterns of apraxia associated with the production of intransitive limb gestures following left and right hemisphere stroke. *Brain Cogn.* **46**, 165–169. (doi:10.1016/S0278-2626(01)80057-9)
- 120 Carmo, J. C. & Rumiati, R. I. 2009 Imitation of transitive and intransitive actions in healthy individuals. *Brain Cogn.* **69**, 460–464. (doi:10.1016/j.bandc.2008.09.007)
- 121 Stamenova, V., Roy, E. A. & Black, S. E. 2010 Associations and dissociations of transitive and intransitive gestures in left and right hemisphere stroke patients. *Brain Cogn.* **72**, 483–490. (doi:10.1016/j.bandc.2010.01.004)
- 122 Krolczak, G. & Frey, S. H. 2009 A common network in the left cerebral hemisphere represents planning of tool use pantomimes and familiar intransitive gestures at the hand-independent level. *Cereb. Cortex* **19**, 2396–2410. (doi:10.1093/cercor/bhn261)
- 123 McNeill, D. 1992 *Hand and mind: what gestures reveal about thought*. Chicago, IL: University of Chicago Press.
- 124 Feyereisen, P. & Seron, X. 1982 Nonverbal communication and aphasia: a review. II. Expression. *Brain Lang.* **16**, 213–236. (doi:10.1016/0093-934X(82)90084-0)
- 125 Cicone, M., Wapner, W., Foldi, N., Zurif, E. & Gardner, H. 1979 The relation between gesture and language in aphasic communication. *Brain Lang.* **8**, 324–349. (doi:10.1016/0093-934X(79)90060-9)
- 126 McNeill, D. 1985 So you think gestures are nonverbal? *Psychol. Rev.* **92**, 350–371. (doi:10.1037/0033-295X.92.3.350)
- 127 Herrmann, M., Reichle, T., Lucius-Hoene, G., Wallesch, C. W. & Johannsen-Horbach, H. 1988 Nonverbal communication as a compensative strategy for severely nonfluent aphasics? A quantitative approach. *Brain Lang.* **33**, 41–54. (doi:10.1016/0093-934X(88)90053-3)
- 128 Willems, R. M. & Hagoort, P. 2007 Neural evidence for the interplay between language, gesture, and action: a review. *Brain Lang.* **101**, 278–289. (doi:10.1016/j.bandl.2007.03.004)
- 129 Christopoulou, C. & Bonvillian, J. D. 1985 Sign language, pantomime, and gestural processing in aphasic persons: a review. *J. Commun. Disord.* **18**, 1–20. (doi:10.1016/0021-9924(85)90010-3)
- 130 Daumuller, M. & Goldenberg, G. 2010 Therapy to improve gestural expression in aphasia: a controlled clinical trial. *Clin. Rehabil.* **24**, 55–65. (doi:10.1177/0269215509343327)
- 131 Marangolo, P., Bonifazi, S., Tomaiuolo, F., Craighero, L., Coccia, M., Altoe, G., Provinciali, L. & Cantagallo, A. 2010 Improving language without words: first evidence from aphasia. *Neuropsychologia* **48**, 3824–3833. (doi:10.1016/j.neuropsychologia.2010.09.025)
- 132 Raymer, A. M., Singletary, F., Rodriguez, A., Ciampitti, M., Heilman, K. M. & Rothi, L. J. 2006 Effects of gesture + verbal treatment for noun and verb retrieval in aphasia. *J. Int. Neuropsychol. Soc.* **12**, 867–882. (doi:10.1017/S1355617706061042)
- 133 Scharp, V. L., Tompkins, C. A. & Iverson, J. M. 2007 Gesture and aphasia: helping hands? *Aphasiology* **21**, 717–725. (doi:10.1080/02687030701192273)
- 134 Poizner, H., Bellugi, U. & Iragui, V. 1984 Apraxia and aphasia for a visual-gestural language. *Am. J. Physiol.* **246**, R868–R883.
- 135 Poizner, H., Bellugi, U. & Klima, E. S. 1990 Biological foundations of language: clues from sign language. *Annu. Rev. Neurosci.* **13**, 283–307. (doi:10.1146/annurev.ne.13.030190.001435)
- 136 MacSweeney, M., Capek, C. M., Campbell, R. & Woll, B. 2008 The signing brain: the neurobiology of sign language. *Trends Cogn. Sci.* **12**, 432–440. (doi:10.1016/j.tics.2008.07.010)
- 137 Hartmann, K., Goldenberg, G., Daumuller, M. & Hermsdorfer, J. 2005 It takes the whole brain to make a cup of coffee: the neuropsychology of naturalistic actions involving technical devices. *Neuropsychologia* **43**, 625–637. (doi:10.1016/j.neuropsychologia.2004.07.015)
- 138 Rapcsak, S. Z., Gonzalez Rothi, L. J. & Heilman, K. M. 1987 Apraxia in a patient with atypical cerebral dominance. *Brain Cogn.* **6**, 450–463. (doi:10.1016/0278-2626(87)90139-4)
- 139 Coppens, P., Hungerford, S., Yamaguchi, S. & Yamadori, A. 2002 Crossed aphasia: an analysis of the symptoms, their frequency, and a comparison with left-hemisphere aphasia symptomatology. *Brain Lang.* **83**, 425–463. (doi:10.1016/S0093-934X(02)00510-2)
- 140 Meador, K. J., Loring, D. W., Lee, K., Hughes, M., Lee, G., Nichols, M. & Heilman, K. M. 1999 Cerebral lateralization: relationship of language and ideomotor praxis. *Neurology* **53**, 2028–2031.
- 141 Frey, S. H., Funnell, M. G., Gerry, V. E. & Gazzaniga, M. S. 2005 A dissociation between the representation of tool-use skills and hand dominance: insights from left- and right-handed callosotomy patients. *J. Cogn. Neurosci.* **17**, 262–272. (doi:10.1162/0898929053124974)
- 142 Goldenberg, G. & Hagmann, S. 1998 Tool use and mechanical problem solving in apraxia. *Neuropsychologia* **36**, 581–589. (doi:10.1016/S0028-3932(97)00165-6)
- 143 Osiurak, F., Jarry, C., Allain, P., Aubin, G., Etcharry-Bouyx, F., Richard, I., Bernard, I. & Le Gall, D. 2009 Unusual use of objects after unilateral brain damage: the technical reasoning model. *Cortex* **45**, 769–783. (doi:10.1016/j.cortex.2008.06.013)
- 144 Kertesz, A. & Hooper, P. 1982 Praxis and language: the extent and variety of apraxia in aphasia. *Neuropsychologia* **20**, 275–286. (doi:10.1016/0028-3932(82)90102-6)
- 145 Caramazza, A. & Badecker, W. 1989 Patient classification in neuropsychological research. *Brain Cogn.* **10**, 256–295. (doi:10.1016/0278-2626(89)90056-0)
- 146 Iacoboni, M. & Wilson, S. M. 2006 Beyond a single area: motor control and language within a neural architecture encompassing Broca's area. *Cortex* **42**, 503–506. (doi:10.1016/S0010-9452(08)70387-3)
- 147 Kimura, D. 1977 Acquisition of a motor skill after left-hemisphere damage. *Brain* **100**, 527–542. (doi:10.1093/brain/100.3.527)
- 148 Goldenberg, G. 2001 Imitation and matching of hand and finger postures. *Neuroimage* **14**, S132–S136. (doi:10.1006/nimg.2001.0820)

- 149 Warren, J. E., Wise, R. J. S. & Warren, J. D. 2005 Sounds do-able: auditory-motor transformations and the posterior temporal plane. *Trends Neurosci.* **28**, 636–643. (doi:10.1016/j.tins.2005.09.010)
- 150 Binder, J. R., Desai, R. H., Graves, W. W. & Conant, L. L. 2009 Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* **19**, 2767–2796. (doi:10.1093/cercor/bhp055)
- 151 Damasio, A. R. & Tranel, D. 1993 Nouns and verbs are retrieved with differently distributed neural systems. *Proc. Natl Acad. Sci. USA* **90**, 4957–4960. (doi:10.1073/pnas.90.11.4957)
- 152 Matzig, S., Druks, J., Masterson, J. & Vigliocco, G. 2009 Noun and verb differences in picture naming: past studies and new evidence. *Cortex* **45**, 738–758. (doi:10.1016/j.cortex.2008.10.003)
- 153 Hillis, A. E., Oh, S. & Ken, L. 2004 Deterioration of naming nouns versus verbs in primary progressive aphasia. *Ann. Neurol.* **55**, 268–275. (doi:10.1002/ana.10812)
- 154 Xu, J., Gannon, P. J., Emmorey, K., Smith, J. F. & Braun, A. R. 2009 Symbolic gestures and spoken language are processed by a common neural system. *Proc. Natl Acad. Sci. USA* **106**, 20664–20669. (doi:10.1073/pnas.0909197106)
- 155 Roy, A. C. & Arbib, M. A. 2005 The syntactic motor system. *Gesture* **1**, 7–37. (doi:10.1075/gest.5.1.03roy)
- 156 Allen, K., Ibara, S., Seymour, A., Cordova, N. & Botvinick, M. 2010 Abstract structural representations of goal-directed behavior. *Psychol. Sci.* **21**, 1518–1524. (doi:10.1177/0956797610383434)
- 157 Grodzinsky, Y. & Santi, A. 2008 The battle for Broca's region. *Trends Cogn. Sci.* **12**, 474–480. (doi:10.1016/j.tics.2008.09.001)
- 158 Hagoort, P. 2005 On Broca, brain, and binding: a new framework. *Trends Cogn. Sci.* **9**, 416–423. (doi:10.1016/j.tics.2005.07.004)
- 159 Grafton, S. T. & Hamilton, A. F. 2007 Evidence for a distributed hierarchy of action representation in the brain. *Hum. Mov. Sci.* **26**, 590–616. (doi:10.1016/j.humov.2007.05.009)
- 160 Koechlin, E. & Jubault, T. 2006 Broca's area and the hierarchical organization of human behavior. *Neuron* **50**, 963–974. (doi:10.1016/j.neuron.2006.05.017)
- 161 Goldenberg, G., Hartmann-Schmid, K., Surer, F., Daumüller, M. & Hermsdorfer, J. 2007 The impact of dysexecutive syndrome on use of tools and technical devices. *Cortex* **43**, 424–435. (doi:10.1016/S0010-9452(08)70467-2)
- 162 Sitnikova, T., Holcomb, P. J., Kiyonaga, K. A. & Kuperberg, G. R. 2008 Two neurocognitive mechanisms of semantic integration during the comprehension of visual real-world events. *J. Cogn. Neurosci.* **20**, 2037–2057. (doi:10.1162/jocn.2008.20143)
- 163 Ahlsen, E. 2008 Embodiment in communication—aphasia, apraxia and the possible role of mirroring and imitation. *Clin. Linguist. Phon.* **22**, 311–315. (doi:10.1080/02699200801918879)
- 164 Goldenberg, G., Hartmann, K. & Schlott, I. 2003 Defective pantomime of object use in left brain damage: apraxia or asymbolia? *Neuropsychologia* **41**, 1565–1573. (doi:10.1016/S0028-3932(03)00120-9)
- 165 Hutsler, J. & Galuske, R. A. 2003 Hemispheric asymmetries in cerebral cortical networks. *Trends Neurosci.* **26**, 429–435. (doi:10.1016/S0166-2236(03)00198-X)
- 166 Giraud, A. L., Kleinschmidt, A., Poeppel, D., Lund, T. E., Frackowiak, R. S. & Laufs, H. 2007 Endogenous cortical rhythms determine cerebral specialization for speech perception and production. *Neuron* **56**, 1127–1134. (doi:10.1016/j.neuron.2007.09.038)
- 167 Arbib, M. A. 2008 From grasp to language: embodied concepts and the challenge of abstraction. *J. Physiol. Paris* **102**, 4–20. (doi:10.1016/j.jphysparis.2008.03.001)