



Common functional resources for tool use and language: new horizons towards a reciprocal impact

Simon Thibault

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Résumé

L'utilisation d'outil est le produit de l'évolution humaine. En plus de sa composante sensorimotrice, dont la complexité est désormais bien caractérisée, l'habileté à utiliser un outil impacte la cognition. En effet, l'utilisation d'outil requiert d'intégrer un objet externe comme une partie corporelle, tout en incluant sa structure fonctionnelle dans le programme moteur. D'autre part, il a été proposé que les aires cérébrales impliquées dans le langage aient exploité les ressources neuronales dédiées à l'outil. Ainsi, les chercheurs ont avancé l'hypothèse de similarités entre les processus sous-tendant l'utilisation d'outil d'une part et le langage de l'autre, en plus des similarités entre action et langage auparavant suggérées par les modèles de la cognition incarnée. Ainsi, cette thèse vise à caractériser les ressources neuronales partagées et les liens comportementaux réciproques entre l'utilisation d'outil et le langage.

Dans une première étude, nous avons utilisé la neuroimagerie fonctionnelle pour tester l'existence de ressources neuronales partagées entre l'utilisation d'outil et deux fonctions langagières : la phonologie et la sémantique. Pour la phonologie, les participant.e.s devaient réaliser une tâche d'identification phonologique, tandis que pour la sémantique, une tâche d'amorçage sémantique avec décision lexicale était réalisée. Bien que l'utilisation d'outil et la phonologie recrutent des régions corticales contigües du lobule pariétal inférieur, aucune preuve n'a été trouvée en faveur de ressources neuronales partagées entre ces deux fonctions. Des analyses multivariées ont en revanche montré que l'activité neuronale induite par la sémantique est décodée au sein du réseau neuronal de l'utilisation d'outil et plus particulièrement dans le gyrus frontal inférieur gauche et le cortex occipitotemporal gauche.

Dans une seconde étude, nous avons testé l'existence de ressources partagées pour l'utilisation d'outil et la fonction syntaxique. Les participant.e.s devaient réaliser une tâche de compréhension syntaxique impliquant des phrases relatives de complexité différente. Les résultats ont montré que l'utilisation d'outil et la syntaxe complexe (i.e. relatives objet) induisaient une activité neuronale anatomiquement co-localisée au sein des ganglions de la base. De plus, des analyses multivariées ont révélé une distribution spatiale similaire pour les patterns neuronaux induits par l'utilisation d'outil et le traitement des relatives objet. En conséquence, le partage de ces ressources neurofonctionnelles se reflète au niveau comportemental par un transfert d'apprentissage entre les deux domaines : l'entraînement à l'utilisation d'outil améliore la performance linguistique pour la syntaxe complexe et réciproquement, l'entraînement à la syntaxe complexe améliore la performance motrice avec l'outil. Aucun transfert d'apprentissage n'a été observé pour les habiletés syntaxiques après un entraînement équivalent mais sans outil, ou bien pour l'utilisation d'outil après entraînement avec des structures syntaxiques plus simples (i.e. relatives sujet).

Nos résultats démontrent l'existence de ressources partagées entre utilisation d'outil et langage et indiquent l'existence d'une fonction syntaxique supramodale dédiée aux domaines moteur et langagier. Plus généralement, nos travaux ouvrent des perspectives quant à la mise en place des protocoles d'apprentissage ou de réhabilitation interdomaine tirant profit du transfert d'apprentissage. Nos résultats confortent enfin l'hypothèse d'une coévolution entre l'habileté à utiliser un outil et le langage, ayant favorisé le partage de ressources neuronales communes pour ces deux habiletés.

Mots clés : Utilisation d'outil, Phonologie, Sémantique, Syntaxe, Neuroimagerie, Transfert d'apprentissage

Abstract

Tool use is a hallmark of human evolution. Beyond its sensorimotor components, whose complexity has been extensively investigated, tool use impacts cognition. Tool use requires integrating an external object as a body part and embedding its functional structure in the motor program. Additionally, it has been proposed that brain areas involved in language have exapted neural resources devoted to tool use. Accordingly, researchers have advanced the existence of similarities between the processes underlying tool use and language, in line with the similarities for action and language suggested by the embodied cognition models. Thus, this thesis aims to further characterize the shared neural resources and reciprocal behavioral links between tool use and language.

In a first study, we used functional neuroimaging to test the existence of shared neural resources between tool use and two linguistic processes: phonology and semantics. For phonology, the participants performed a phonological identification task, whereas for semantics they underwent a semantic priming task with a lexical decision. Although tool use and phonology recruited contiguous regions in the inferior parietal lobe, no evidence for shared neural resources was found between those two functions. By contrast, multivariate analyses showed that the neural activity elicited by semantics was decoded within the tool-use neural network, in the left inferior frontal gyrus and the left occipitotemporal cortex.

In a second study, we tested the existence of shared neural substrates for tool use and syntactic processing. The participants performed a syntactic comprehension task requiring to process syntactic structures of different complexity. Results showed tool use and complex syntax (i.e. object relatives) elicited neural activity anatomically co-localized within the basal ganglia. Multivariate analyses revealed similar spatial distributions of neural patterns prompted by tool use and object relative processing. Moreover, the shared neurofunctional resources are reflected behaviorally by cross-domain learning transfer: tool-use training significantly improves linguistic performance for complex syntax, and reciprocally, complex syntax training improves motor performance with the tool. No learning transfer was observed on language syntactic abilities if participants trained without the tool, nor on tool use if participants trained with simpler syntactic structures (i.e. subject relatives).

Our findings show the existence of shared neural resources between tool use and language, pointing to the existence of a supramodal syntactic function shared between the motor and the language domains. More generally our work opens perspectives to develop learning or rehabilitation protocols taking advantage of the crossdomain learning transfer. From an evolutionary point of view, our results reinforce the hypothesis of a co-evolution between tool use and language, leading to shared neural resources for these two abilities.

Keywords: Tool use, Phonology, Semantics, Syntax, Neuroimaging, Learning Transfer

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Abbreviations list

2-AFC: Two-Alternative Forced Choice

AIP: Intraparietal Area

ATL: Anterior Temporal Lobe

DLD: Developmental Language Disorder

EBA: Extrastriate Body Area

EEG: Electroencephalography

ELAN: Early Left Anterior Negativity

ERP: Event-Related Potential

F1: First Formant

F2: Second Formant

F3: Third Formant

fMRI: functional Magnetic Resonance Imaging

iEEG: intracranial Electroencephalography

IFG: Inferior Frontal Gyrus

IPL: Inferior Parietal Lobe

IPS: Intraparietal Sulcus or **aIPS** for anterior Intraparietal Sulcus or **pIPS** for posterior Intraparietal Sulcus

ITG: Inferior Temporal Gyrus or **pITG** for posterior Inferior Temporal Gyrus

LAN: Left Anterior Negativity

LOC: Lateral Occipital Cortex

M1: Primary Motor Cortex

Mya: Million years ago

MEG: Magnetoencephalography

MEPs: Motor Evoked Potentials

mF2: monkey Dorsal Premotor Cortex

mF5: monkey Ventral Premotor Cortex

MIP: Medio-intraparietal Cortex

MVPA: MultiVoxel Pattern Analysis

MTG: Middle Temporal Gyrus or **pMTG** for posterior Middle Temporal Gyrus

MNI: Montreal Neurological Institute

mm: millimeters

ms: milliseconds or s for seconds

MT+: Middle Temporal plus

OTC: Occipitotemporal Cortex

PET: Positron Emission Tomography

PMC: Premotor Cortex
PMd: dorsal Premotor Cortex
PMv: ventral Premotor Cortex
PT: Planum Temporale
RDM: Representational Dissimilarity Matrix
ROI: Regions of Interest
RSA: Representational Similarity Analysis
SII: Second somatosensory area
SLI: Specific Language Impairment
SMG: Supramarginal Gyrus or **aSMG** for anterior Supramarginal Gyrus
sMRI: structural Magnetic Resonance Imaging
SPL: Superior Parietal Lobule
Spt area: Sylvian-parietal-temporal area
SPOC: Superior Parieto-Occipital Cortex
STG: Superior Temporal Gyrus or **pSTG** for posterior Superior Temporal Gyrus or **aSTG** for anterior Superior Temporal Gyrus
STS: Superior Temporal Sulcus or **pSTS** for posterior Superior Temporal Sulcus
TD: Typically Developing
TMS: Transcranial Magnetic Stimulation
VWFA: Visual Word Form Area

Chapter 1

-

Theoretical background

General introduction

The field of neuroscience leaves the feeling that understanding of the brain is possible only by isolating a specific cognitive process. Such a modular approach certainly helped to decipher the specificities of different cognitive processes. Indeed, by designing tasks aiming to study one specific process in isolation of others, researchers have developed several well controlled experimental paradigms that subsequently facilitated the identification of their neural bases by the mean of neuroimaging techniques. Nonetheless, this approach critically neglected the interaction between potentially interdependent cognitive functions relying on interconnected and multimodal neural networks (i.e. localizationist vs. connectivist approaches). Therefore, only relying on a modular approach might prevent the understanding of the human behavior and the central nervous system in a systemic and holistic way. Until recently, older accounts have mainly depicted the brain functional organization as rather simplistic with sensorimotor processes being relegated to low level processing and restricted to primary cortical and subcortical areas. Conversely, higher level cognitive processes have been associated to larger networks encompassing several cortical associative areas. By contrast, more recent accounts have put forward the role of both primary sensorimotor and associative cortices in a large range of functions, suggesting a thinner border between the low-level sensorimotor and higher-level cognitive functions (Goodale & Milner, 1992; Middleton & Strick, 2000). As a corollary, scholars have proposed a theory according to which cognition might be *embodied*, and which focuses on the shared neural representations between the sensorimotor and cognitive functions (Barsalou, 1999; Lakoff & Johnson, 1980; Varela et al., 1991). Embodied cognition, also called *grounded cognition*, suggests that most of the cognitive functions are grounded into the sensorimotor network. In a review, Barsalou defined the main tenets of embodied cognition as follows: “*Grounded cognition rejects traditional views that cognition is computation on amodal symbols in a modular system, independent of the brain’s modal systems for perception, action, and introspection*” (Barsalou, 2008, p. 617). Embodied cognition proposes that cognition is underlined by bodily states and situated actions. Numerous experiments put forward empirical evidence supporting embodied cognition assertions. For instance, attentional processes have been proposed to rely on the sensorimotor network. The premotor theory of attention suggests that the mechanisms of covert shifting attention are tied to the processes supporting the planning of explicit ocular movements (Rizzolatti et al., 1987). Similarly, numerical cognition, relying on the ability to represent the number magnitude, is tightly linked to the representations of space (see Walsh, 2003 for the model called *A Theory Of Magnitude*).

More recently, the contribution of the motor system to language has been extensively studied: processing syllables, words or sentences involves the sensorimotor network (for a review, see Pulvermüller & Fadiga, 2010).

The possibility that cognition is embodied within the neural systems subserving action and perception opens questions about the role of evolution in this organization. For instance, it has been suggested that phylogenetically recent cognitive functions took advantage of the various neural circuits already present in the brain (Dehaene & Cohen, 2007). In other words, under specific environmental pressures, new cognitive functions have emerged on already existing circuits thanks to neural recycling processes. Among the different functions developed in the animal reign, the abilities to move and perceive are likely among the most vital and critical for human evolution (Kuhn et al., 2016), in order to fulfill primary needs such as eating or drinking. To this aim, we can postulate the abilities to move and perceive likely appear early in the animal reign, because these abilities are already observable at the level of a single cell or even in unicellular eukaryote organisms (Fritz-Laylin, 2020). Under the pressure of environmental demands, the abilities to move and perceive have likely been refined by the emergence of new cognitive-sensorimotor functions. In this evolutionary process, neural circuits devoted to action and perception have progressively expanded (Iriki & Taoka, 2012) or been exapted (Dehaene & Cohen, 2007) from their original purpose. This process could have helped the emergence of cognitive functions within the sensorimotor circuits, such as attention, numerical cognition and even language. For instance, theoretical accounts have defended a contribution of the sensorimotor system in language emergence (Corballis, 2003; Rizzolatti & Arbib, 1998). Beyond the emergence of language, one critical advent of human evolution is our capacity to use and build tools in a way that outperforms any kind of animal species (Seed & Byrne, 2010). The emergence of this ability relies on the sensorimotor system, but moving from relatively simple manual behavior to more fine motor behavior including the control of tools is an incredible product of evolution. The evolution of tool-use behaviors may have expanded the hominid pre-existing neural territories that consequently could have been exapted to serve a different purpose and support new emergent cognitive functions (Iriki & Taoka, 2012). As a consequence, because of the exaptation process two functions can be closely related and influence each other (Mendoza & Merchant, 2014). Thus, functions supported by the actual human brain may result from their co-evolution history. Such co-evolution link has been suggested for two highly refined function in humans that are tool use and language (Ambrose, 2001; Iriki & Taoka, 2012; Ponce de León et al., 2021; Stout & Chaminade, 2012), opening the

possibility that similar neural resources could underlie the two functions. However, this prediction remains poorly tested and almost unexplored.

In this thesis we aim to fill this gap by studying the neural similarities and the behavioral links between tool use and language. The next pages of this introduction aim to critically review the literature by first presenting the neural bases of three distinct though related components of language: phonology, semantics and syntax and how they are represented within the sensorimotor systems. The second section puts forward the neural bases of tool use. Finally, a third section opens a discussion about the similarities across tool-use and language processes, as well as the possibility neural resources are shared between these two abilities.

The neural bases of language, an ability grounded in the sensorimotor network

As a result of our evolution history, human language contains communications types that differ from other species and are defined by a high degree of refinement (Hauser et al., 2002; Premack, 2007; Ujhelyi, 1996). Language is a cognitive ability that is supported by a set of specifically linguistic functions including, among others, phonology, semantics and syntax. Phonology allows to process the relevant sounds of language called phonemes. Phonemes are defined as the smallest units of language that are put together in order to form meaningful words. Semantics allows to access and process the meaning of words and sentences. The words are put together following a set of rules critical for sentence meaning. Syntax is the function that handles these rules for sentence organization. In this section we aim to review the neural correlates of these three linguistic functions.

Interestingly, numerous evidence has suggested that phonology and semantics rely on the sensorimotor network, and to a lesser extent this evidence has been provided for sentence processing preferentially taxing either the semantic or syntactic resources (for reviews, see Fischer & Zwaan, 2008; Pulvermüller & Fadiga, 2010). These observations suggest that language is an amodal function relying in part on neural circuits subserving the modal sensorimotor functions. Noteworthy, the embodiment of the sentence processing has been studied under two approaches, one more related to the semantic content of the sentence and another focusing on syntactic processing. For the sake of clarity, these two different approaches will be discussed separately.

Our hypothesis posited the existence of an overlap between tool use and language. The data have shown that tool use and some of the linguistic components, such as phonology, semantics and syntax preferentially activate the left hemisphere (Vigneau et al., 2011). Other linguistic components such as prosody and pragmatics, no less important for efficiently communicating, will not be discussed within this thesis. Prosody refers to language intonation either for language listening or production. This is sometimes presented as the musicality of language. Pragmatics refers to comprehension of language within a specific context. We think these components go beyond the scope of this thesis. Their link with sensorimotor circuits is not so obvious and they are mostly supported by the right hemisphere (Kotz et al., 2006 for prosody; Shields, 1991 for pragmatics) while tool use involve a left hemisphere dominance (Johnson-Frey, 2004). Overall, the present chapter presents a non-exhaustive set of behavioral,

neuroimaging and neuropsychological studies showing that phonology, semantics and syntax are embodied within the sensorimotor network and that language and motor functions influence each other. This evidence will be the basis for our work that aims to investigate the hypothesis of a link between tool use and language.

1. Phonology

a. Behavioral studies

In the daily life, we are perceiving speech without apparent effort. However, speech perception is a complex process involving several computational steps. As a result of this processing, verbal sounds, such as phonemes can be recognized and distinguished from non-verbal sounds, such as ringing bells. Yet, these two sounds are defined by acoustic features characterized by the variations of different frequencies across time (i.e. spectrogram). Hence, to identify which sounds are relevant for a given language, speech perception is supported by a linguistic function called phonology. Phonological processing allows to recognize speech units (i.e. the phonemes) that will be the basis for a proper comprehension. Indeed, improper phonological processing can impair our ability to understand linguistic content. For instance, the nouns *beach* and *peach* convey totally different meaning but are auditorily close and only vary from a subtle contrast between the phonemes /b/ and /p/ (this is called a minimal pair). Thus the ability to distinguish /b/ from /p/ or from any other phonemes is crucial. From this general example, speech perception and especially phonological processing can be seen as the process aiming to assign a linguistic sound into one phonemic category for a given language. Nonetheless, this perception can be challenged in real world situations requiring to minimize several sources of variability, in order to extract the linguistic features conveyed by a verbal sound (Liberman et al., 1957). Even without specific neurological and developmental impairments, these sources of variability can arise from a default of articulation of the speaker, a specific language accent, the environmental noise surrounding the listener, or simply the perception of linguistic sounds that are not part of the native language repertoire.

Two main paradigms have been employed to investigate the phonological perception and how our brain is able to recognize the phonological invariants of phonemes. These two paradigms are the phonological discrimination and identification tasks (see methodology box 1). Both rely on the perception of sounds belonging to a continuum of acoustically varying sounds (Fig. 1). A seminal study (Liberman et al., 1957) conducted on phonological processing,

employed a continuum varying from /b/ to /d/ to /g/ along 14 different stimuli. The stepwise frequency transformations applied to the first stimuli result in the creation of unique sounds characterized by allophonic differences. Allophones are phonetic variants of a phoneme (i.e. non contrastive speech segments). How do humans perceive speech sound? Liberman and colleagues first employed an identification task where the participants had to assign the 14 sounds perceived to a given phoneme category (i.e. /b/, /d/, /g/). The proportion of responses for each phoneme category was quantified and revealed that each sound stimulus was most often assigned to the same category (i.e. identification percentage close to 100%). Furthermore, the transition between two categories (e.g. /b/ from /d/) was quite steep suggesting that the participants undoubtedly assigned sounds to a given category and eliminated their allophonic differences (see Fig. 2A for a modern replication of Liberman et al., 1957). Overall, this specific psychophysical relation suggests a phenomenon known as *categorical perception*. However, this result might be explained because the participants were explicitly asked to assign one sound to one category. To address this issue the phonological discrimination task was employed. In this task, stimuli are matched by pairs separated by the same number of intervals (e.g. three steps, see methodology box 1). The participants are required to indicate whether the pairs of sounds are similar or different. As an evidence of the participants' inability to perceive allophonic differences, some pairs were classified as similar while none of them contained the exact same acoustic stimuli. Furthermore, pairs of stimuli were judged as different at percentage rate close to 100%, validating the categorical perception assumption for speech perception (Fig. 2B). Overall, these specific psychophysical relations characterize the ability of our brain to categorize linguistic sounds into discrete phonemes (Liberman et al., 1957). This behavioral effect has been replicated more recently in neuroimaging studies aiming to understand the neural bases of speech categorical perception (Chang et al., 2010; Raizada & Poldrack, 2007). Interestingly, in children suffering dyslexia this mode of speech perception is affected and dyslexics give more attention to allophonic differences (Serniclaes et al., 2004).

Later, Liberman and colleagues (Liberman et al., 1967) proposed that the categorical perception phenomenon can only be the result of a special decoder allowing to assign different speech sounds to a specific category. Liberman and colleagues defended the idea that this decoder may be found within the neural system controlling the articulatory muscles. Crucially, support to this proposition comes in part from the observation that blinded war veterans, who lost their sight, had relatively poor speech perception ability (for a short story, see Iacoboni, 2008). According to their hypothesis, because of the sight loss, these patients had more

difficulties to map a speech sound to the associated articulatory gestures that are visually conveyed. Put differently, perceiving speech sounds would consist of their categorization in virtue of the fact that they are associated to invariant speech articulatory gestures. In favor of the existence of such invariants, it is impossible to emit a sound that is halfway through two stop consonants like /b/ and /d/. Thus, Liberman and colleagues proposed that speech categorical perception is possible thanks to a decoder able to refer incoming speech sounds to their invariant motor commands. This theory is called the *motor theory of speech perception* (Liberman et al., 1967; Liberman & Mattingly, 1985; Liberman & Whalen, 2000) and suggests a core contribution of the motor system in speech perception. The next section will aim to decipher the neural bases of speech perception.

Methodology box 1: Phonological identification and discrimination tasks

The phonological identification and discrimination tasks require the creation of a perceptual phonetic continuum. This continuum is obtained by synthesizing speech stimuli with an adapted software allowing to change the formants. A formant corresponds to a specific frequency band within a sound, specifically the first formant (F1) is the lowest frequency contained in an auditory signal, whereas the second formant (F2) and third formant (F3) correspond to higher frequency bands. By changing the F2 and F3 one can shape a continuum of sounds. Such progressive modification of the original acoustic features, will be perceived as the original phoneme before switching to a different perceived phoneme at a certain degree of acoustic modification. For our study, we used the software Praat (<https://www.fon.hum.uva.nl/praat/>) to vary F2 and F3 onset frequency of the phoneme /ba/ over 14 equal steps. This resulted in a continuum going from the syllables /ba/ to /da/ with a total of 15 steps, namely from the unambiguously perceived /ba/ to the unambiguously perceived /da/ and the 13 steps in-between (Fig. 1).

This continuum can be subsequently used to set up an identification task requiring a participant to listen to a sound of the continuum and to indicate whether a /ba/ or a /da/ is heard. The number of /ba/ responses is quantified and the psychophysical curve (Fig. 2A red curve) is expected to follow a sigmoid: 100% of /ba/ responses for sounds close to the /ba/ extremity and 0% of /ba/ responses for sounds close to the /da/ extremity. For sounds localized in the middle of the continuum, the proportion of /ba/ responses is expected to tend towards 50%, corresponding to the chance level.

The continuum can also be used with an identification task where the participants are required to perform a two-alternative forced choice task (2-AFC) that allows to indicate whether they consciously perceived a fine grained difference between stimuli. By using the continuum between /ba/ and /da/, we can associate sounds by pairs, so that stimulus 1 is associated with stimulus 3, stimulus 2 with stimulus 4, stimulus 3 with stimulus 5, and so on along the continuum. Pairs of sounds both extracted from the same half of the continuum will be more likely classified as similar, whereas pairs containing sounds crossing the categorical perception boundary, will have more chance to be classified as different (i.e. one sound is perceived as /ba/ and the other as /da/; Fig. 2B).

Figure 1: Spectrograms of the stimuli used in the phonological identification task in this thesis. A) Entire spectrogram of the first stimulus (i.e. unambiguous syllable) of the continuum. (B) The first 50ms for each stimulus spectrogram is represented, highlighting the stepwise changes applied to the second and third formant frequencies, respectively F2 (in red) and F3 (in orange).

Figure 2: Psychometric curves for phonological identification and discrimination tasks. (A) Psychometric curves obtained for the proportion of /ba/ responses (in red), /da/ responses (in green) and /ga/ responses (in blue) measured during an identification task over 14 stimuli. (B) Psychometric curves for the proportion of pairs judged different during a discrimination task. The first peak corresponds to the pairs of sounds crossing the category boundary between /ba/ and /da/, while the second peak corresponds to the transition between /da/ and /ga/. Adapted from Chang et al., 2010.

b. Neuroimaging studies

What are the neural bases of speech perception? A dual stream model has been proposed for the perception of speech, with a frontoparietal pathway (i.e. dorsal stream) and a frontotemporal pathway (i.e. ventral stream) performing distinct computations (Hickok & Poeppel, 2007). First of all, this model suggests the earliest stage of speech perception involves spectrotemporal analysis occurring bilaterally in the auditory cortices, including the Heschl's gyri and the Planum Temporale (PT). Then phonological processing takes place in the bilateral (but with biased activity towards the left hemisphere) posterior portions of the middle temporal gyrus (pMTG) and superior temporal sulcus (pSTS). Finally, the system diverges into two different left-lateralized pathways. One dorsal pathway that maps sensory and phonological representations onto articulatory motor representations and one ventral pathway that maps phonological representations onto lexical conceptual representations (Fig. 3).

Figure 3: The dual stream model of speech perception. The model supports a distinction between a dorsal stream (in blue) involved in phonological integration within the articulatory system and a ventral stream (in purple) involved in phonological mapping onto lexical representations. A bilateral contribution of the posterior portions of the temporal cortex (in yellow and green) is proposed for lower level processes in speech perception. aITS: anterior inferior temporal sulcus; pITS: posterior inferior temporal sulcus aMTG: anterior middle temporal gyrus; pMTG: posterior middle temporal gyrus; STG: superior temporal gyrus; STS: superior temporal sulcus; pIFG: posterior inferior frontal gyrus; PM: premotor cortex. Adapted from Hickok & Poeppel, 2007.

A study further considered the role of the left posterior superior temporal gyrus (pSTG), a region surrounded by the left pMTG and left pSTS, in speech perception. Intracranial electroencephalography (iEEG) was performed within this area and revealed distinct neuronal

foci responding to distinct phoneme categories (/ba/, /da/ and /ga/), when participants were submitted to a continuum of acoustically varying sounds during identification and discrimination tasks (Chang et al., 2010). This means that the pSTG is involved in acoustic-to-higher order phonetic level encoding of speech sounds. This finding is consistent with a neuroimaging meta-analysis showing that the left posterior temporal cortex is involved in phonological processes (Turkeltaub & Coslett, 2010). The same identification and discrimination paradigms have been employed in a fMRI scanner and the results showed several areas are involved in the amplification of phonetic differences, namely when a sound crossed the categorical perception boundary (Raizada & Poldrack, 2007). The region that was the most significantly activated for this amplification process was the left supramarginal gyrus (SMG), a region of the inferior parietal cortex (IPL) localized at the vicinity of the pSTG. These findings suggest the two regions are closely linked for phonological processing and functional connectivity analysis confirms the activity of the left SMG correlated with the lower level speech perception areas, such as the left PT (Raizada & Poldrack, 2007). Noteworthy, other brain regions, such as the left posterior parietal cortex, the left middle frontal cortex, the right prefrontal cortex, the right cerebellum and the anterior cingulate cortex accompanied the left SMG for this neural amplification of phonetic differences. A neuroimaging meta-analysis including foci obtained from phonological categorical perception tasks corroborates the contribution of the left IPL that includes both the left SMG and left angular gyrus (Turkeltaub & Coslett, 2010). Finally, a region at the interface of both the parietal and temporal lobes, called Spt area (Sylvian-parietal-temporal area), appears critical for phonological processing. The Spt area has been suggested to map the auditory representations of speech to their associated motor representations within the dorsal stream (Hickok & Poeppel, 2007; Pa & Hickok, 2008)

The motor theory of speech (Liberman & Whalen, 2000) predicts speech articulators are involved in speech perception. What does the neuroimaging of speech perception tell us about the role of the motor and premotor circuits for speech perception? Paradigms with passive listening of sounds revealed speech perception is not restricted to the neural territories surrounding the left Sylvian fissure, such as the pSTG or the IPL. Indeed an influential fMRI study demonstrated that the premotor and motor areas for a long time thought to be merely involved into the articulatory aspects of language, are also crucial for speech perception (Wilson et al., 2004). In this study, participants had to either produce or passively listen to single syllables such as /gi/ and /pa/. Similar sensorimotor areas were recruited by the two processes, and with a stronger intensity than for non-linguistic sounds (Fig. 4).

Figure 4: Neural responses for speech perception. Neural activity for three representative participants once they were listening to syllables, mainly found around the bilateral Sylvian fissure and the premotor and motor cortices. The black outlines indicate the premotor and motor regions recruited when participants were producing syllables. (B) Percentage of signal change within the premotor and motor regions activated for linguistic and non-linguistic sounds. Crucially, the change was more important for listening to syllables rather than non-linguistic sounds. Crucially the neural response was greater for producing speech and listening to speech in comparison to listening to non-linguistic sounds. Adapted from Wilson et al., 2004.

Furthermore, the involvement of premotor and motor cortices in phonological perception goes beyond an unspecific neural response. In a fMRI study (Pulvermüller et al., 2006), participants were required to listen to syllables embedding the /p/ and /t/ phonemes, respectively involving the lips and the tongue articulators for production. Replicating the previous results, the precentral gyrus was activated. Moreover, the authors showed that activations during listening to syllables depended on place of articulation. In other words, listening to labial sounds such as /pa/ activated the region dedicated to lip motor control, whereas listening to dental sounds such as /ta/ activated the tongue motor control region. In congruence with the motor homunculus (Penfield & Boldrey, 1937), /t/ perception activated the inferior part of the precentral gyrus, whereas listening to /p/ involved the superior part of the precentral gyrus (Fig. 5). The neural response observed follows the well-known somatotopic organization of the motor system (Penfield & Boldrey, 1937).

Figure 5: Somatotopic activations for articulator movements, silent articulation and listening to syllables. (A) Left panel: Activations for movement of the tongue (green) and lips (red). Middle panel: Activations for silent production of dental syllables (i.e. tongue related, in green) and labial syllables (i.e. lips related, in red). Right panel: Activations for listening to dental syllables (green) and labial syllables (red). From Pulvermüller and Fadiga, 2010. (B) Somatotopic organization within the motor cortex, also called motor homunculus (found at: https://thebrain.mcgill.ca/flash/i/i_06/i_06_cr/i_06_cr_mou/i_06_cr_mou.html).

Neuroimaging studies showed the involvement of both motor and premotor circuits for speech perception. The still hotly debated question opens: is this activation intrinsic part of language processing, allowing speech perception or is it simply a byproduct of the automatic mental simulation of the articulatory movements required to produce the heard speech sounds (see Lotto et al., 2009)? The use of transcranial magnetic stimulation (TMS) allows to evidence the causal role of a cortical region in a specific cognitive function. This technique induces a change in cortical excitability when applied through a single pulse. As a result, it might induce a cognitive facilitation (or inhibition if the pulse is applied to decrease excitability) for the processes underlined by the stimulated cortical area (for a review on TMS, see Silvanto & Cattaneo, 2017). Otherwise, when used with a repeated pulse, this technique induces a transient

virtual lesion in neurotypical participants and allows to test whether the induced perturbation impacts a specific cognitive process (Pascual-Leone et al., 2000). In a TMS study (Fadiga et al., 2002), participants listened to words while single pulse TMS was applied over the tongue motor control area in the primary motor cortex (M1). The words contained consonants that were either a lingua-palatal fricative consonant (i.e. /r/) requiring strong tongue mobilization to be produced, or a labiodental fricative consonant (i.e. /f/) which only requires slight tongue mobilization for production. Crucially, the motor evoked potentials (MEPs) recorded on the participants' tongue were greater in amplitude for listening to words embedding a lingua-palatal fricative rather than a labiodental fricative. This effect was replicated later in another TMS study (Roy et al., 2008) where participants had to listen to pseudowords embedding consonants involving important tongue movement (i.e. /l/) to be produced, in comparison to pseudowords embedding consonants with a small tongue involvement (i.e. /b/, /m/, /f/ or /p). Such causal contribution of the motor areas to speech perception was corroborated in a study applying repetitive TMS to the premotor cortex while participants performed a phonemic discrimination task (Meister et al., 2007). Crucially, participants' ability to identify phonemes presented within a background noise, significantly worsened when the stimulation was applied to the left ventral premotor cortex (PMv) in comparison to the control conditions, without TMS and with TMS applied to the left superior temporal gyrus (STG). Given that repetitive TMS was used, it might be possible that cortical inhibition spread over a larger network beyond the PMv (Gerschlagier et al., 2001). To address this issue, in another study, single pulse TMS was applied just before the onset of speech stimuli over the tongue or lips areas within M1, so as to increase the motor neuronal excitability. The results showed a facilitation in the discrimination of dental consonants (i.e. /d/ and /t/) when TMS was applied to the tongue area and the reverse effect, with a facilitation for labial consonants (i.e. /p/ and /b/) when the TMS was applied onto the lips area (D'Ausilio et al., 2009). Interestingly, because the phonemes were presented in a noisy context, it has been proposed that the contribution of the motor areas to speech perception may depend on the presence of noise. While the previous effect was replicated for consonants embedded in noise background, the discrimination facilitation effect was abolished for consonants presented in quiet context (D'ausilio et al., 2012). Hence, the contribution of the motor areas to speech perception may be dedicated to the perception of degraded or difficult stimuli. Overall, these findings suggest that both premotor and motor areas contribute to the perception of speech sounds and not only to their articulation (for a review, see Iacoboni, 2008). Taken together these neuroimaging and TMS findings clearly support the role of the motor and premotor circuits for speech perception, reviving the original predictions of the motor theory

of speech perception (Liberman et al., 1967; Liberman & Mattingly, 1985; Liberman & Whalen, 2000).

To summarize phonological perception mostly involves cortical areas surrounding the left perisylvian region with the IPL (i.e. SMG and angular gyrus), pSTG and both the premotor cortex (PMC) and motor cortex that are highly critical for perceiving speech sounds, whereas the Heschl's gyrus and the PT are involved in lower level perception (Fig. 6). This network has been confirmed by neuroimaging meta-analyses (Turkeltaub & Coslett, 2010; Vigneau et al., 2006), also corroborating the dominance of the left hemisphere for phonological processes (Turkeltaub & Coslett, 2010; Vigneau et al., 2011). Crucially the left IPL has been associated with categorical perception processes (Möttönen & Watkins, 2009), while the PMC supports speech integration in challenging contexts involving for instance distractors or noise (Chevillet et al., 2013).

Figure 6: The phonological network. Top panel: Peak of clusters of activity are represented by blue dots obtained from neuroimaging investigations for phonology. The yellow crosses indicate the center of mass for a cluster of dots. The x and y axes represent the coordinates in millimeters (mm) in the Montreal Neurological Institute (MNI) space. Bottom panel: These centers of mass are projected in isolation onto a brain render. F3orb: *pars orbitalis*; F3td: dorsal *pars triangularis*; RolOp: Rolandic operculum; Prec: precentral gyrus; RolS: Rolandic sulcus; T1: superior temporal gyrus; T1a: anterior superior temporal gyrus; PT: planum temporale; T2m: middle part of the middle temporal gyrus; T3p: posterior inferior temporal gyrus. SMG: supramarginal gyrus. From Vigneau et al., 2006.

c. Neuropsychological studies

The seminal and influential investigations conducted by Carl Wernicke (Wernicke, 1969, english traduction of *Der Aphasische Symptomencomplex: Eine Psychologische Studie Auf Anatomischer Basis* published in German in 1874) have mostly confined the perception of speech to the left pSTG. Indeed, Wernicke's patients suffering from a lesion in the pSTG presented a deficit for language comprehension but a preserved and fluent discourse. These clinical signs are consistent with the fluent aphasia also called receptive or Wernicke's aphasia. In association with the seminal work of Paul Broca (Broca, 1861), suggesting the left inferior frontal regions are dedicated to speech production, Wernicke's observations have conducted to the definition of the Wernicke-Lichtheim-Geschwind's neurobiological model for language (Geschwind, 1970). This model suggests that speech perception occurs within the left STG, whereas speech production occurs in the left IFG; these two regions are interconnected by white matter fascicles forming a loop that associate speech perception and production. However, more recent neuropsychological studies have challenged this model. Indeed, speech sound perception did not really contribute to the auditory comprehension deficits observed in Wernicke's aphasics (Basso et al., 1977). Furthermore, the lesions of patients impaired in phonemic processing were located in the left SMG (Caplan et al., 1995) or left frontal areas (Blumstein et al., 1977), and not in Wernicke's area (i.e. pSTG). A further study showed that a lesion to the left pSTG is not systematically associated with a perception deficit but rather with a production impairment (Damasio & Damasio, 1980). These findings, together with those from neuroimaging studies reviewed in the previous section, suggest the Wernicke-Lichtheim-Geschwind's neurobiological model for language is no longer valid (see Hagoort and Swaab, 2013; Tremblay and Dick, 2016). Thus, conversely to older neuropsychological investigations, more recent ones suggest that speech perception is closely related to speech production and that the two functions do not specifically rely on clearly separated modules.

2. Semantics

a. Behavioral studies

Phonemes are the smallest relevant units for language and can be assembled in order to form words. A word is defined by a specific meaning whose retrieval involves semantic processing. One of the most common paradigms to study semantic processing at the behavioral level is semantic priming (Meyer & Schvaneveldt, 1971; Neely, 1976, see methodology box 2). Usually semantic priming requires participants to perform a lexical decision task to avoid any deliberate and explicit processing of word meaning (Binder et al., 2003; Chumbley et al., 1984) because lexical decision consists of indicating whether the stimuli presented is a legal word or not (i.e. pseudoword).

Methodology box 2: Semantic priming task with a lexical decision

In a semantic priming task (Fig. 7), one word called the *prime* is presented before a second word, the *target*. The *prime* and the *target* can belong to the same semantic category, for instance two *tool* words (e.g. *screwdriver* - *hammer*) or to different semantic categories, such as an *animal* word followed by a *tool* word (e.g. *turtle* - *hammer*). The participant is required to perform a lexical decision task requiring to indicate whether the *target* is a word (e.g. *screwdriver*) or a pseudoword (e.g. *spradromer*). The presentation of prime-target pairs belonging to the same semantic category should result in a facilitation for the lexical decision task, testified by shorter response times to the target in comparison to a pair of words belonging to different categories (Chumbley et al., 1984). In order to assess the neural bases of semantic processing we will use this task for the empirical contributions presented in this manuscript.

Figure 7: Semantic priming paradigm using a lexical decision task. Two stimuli are presented consecutively (i.e. prime followed by target) and the participant has to perform a lexical decision on the target by indicating whether it is a word or a pseudoword. Left Panel: in the pseudoword condition a word is presented as a prime before a target pseudoword. Middle Panel: in the primed word condition, two words from the same semantic category are presented. Right panel: in the unprimed word condition, two words from different semantic categories are presented. The lexical decision is expected to be faster for the primed than the unprimed condition.

Noteworthy, the priming effect is not restricted to semantics and has been found for various cognitive domains. The behavioral facilitation observed is explained by the consecutive recruitment of the same neural pool for stimuli belonging to the same category and resulting in

a neural adaptation, whereas distinct neural pools are involved for stimuli belonging to different categories (Henson, 2003). The semantic priming effect has helped to map the specific contribution of different cortical regions to different lexical and semantic categories (Copland et al., 2007; Kotz et al., 2002; Ulrich et al., 2013). In the field of the cognitive neuroscience of language, the process of single word meaning has been studied by considering mainly three different categories of words: object nouns, action verbs and abstract words. Roughly from the 1970s to the 1990s, the dominant theory regarding the manipulation of conceptual knowledge was the amodal symbolic model, suggesting that concepts, including word meanings, are abstract symbols that are represented and processed in an autonomous semantic system, separated from other modality specific systems for action and perception (Fodor, 1975). One influential idea that has emerged at the end of 1990s, suggests the opposite, namely abstract concepts are represented in the modality specific systems linked to perception and action (Barsalou, 1999). In other words, concept knowledge may be grounded within the sensorimotor system. For that reason this theoretical approach has been called grounded cognition model, embodied cognition model or simulation model. For instance, a noun referring to food, such as *nectarine* is grounded within the modality-specific systems for action and perception that are involved to process how a nectarine looks, tastes, smells, feels in the hand and how we manipulate it. Tool nouns or manipulable objects nouns, as well as action verbs have also been suggested to be grounded within the sensorimotor circuits and accordingly, they should involve the action and perception systems allowing to retrieve the knowledge about the semantic concept.

Going back to the semantic priming effect, one elegant way to evidence the link between action and language would be to precede a *target* word by a *prime* that is a real action instead of a word. Indeed, if action semantics recruits the sensorimotor systems, thus performing an action should facilitate the subsequent processing of an action word. Such a paradigm has been applied using a lexical decision task with words referring to *manipulable* and *non manipulable objects* words while participants had to intentionally turn a disk with their hand (Rueschemeyer et al., 2010). Intentional rather than passive rotation movements facilitated the performance in the lexical decision task for *manipulable objects* compared to *non manipulable objects* words. The reversed effect should also hold true, so that reading an action word before performing a motor action should impact movement. This effect has been shown in a study where participants had to read an action verb before the onset of a grasping movement. The results showed that reading action verbs in comparison to concrete, nonmanipulable nouns facilitated the grasping

action, with shorter latency of the acceleration peak (Boulenger et al., 2006). Noteworthy, when the action verb was presented right after the onset of the grasping action, the amplitude of the movement acceleration peak reduced and its latency increased in comparison to when concrete nouns were read (Boulenger et al., 2006). Furthermore, similar effects are observable in the sensory domain. Indeed, reading tactile verbs (e.g. *to touch*) in comparison to non-tactile verbs (e.g. *to replace*) speeded up the detection of tactile stimuli applied on the right forearm (Boulenger et al., 2020). In another study (Scorolli & Borghi, 2006), participants had to judge whether combinations of nouns and verbs made sense. The pairs evoked hand and mouth movements (e.g. *to unwrap the sweet* vs. *to suck the sweet*) in one block, but hand and foot movements (e.g. *to throw the ball* vs. *to kick the ball*) in the other. In the first block, the responses were delivered verbally using a microphone, while in the second block the responses were given using a foot pedal. Crucially, judging sentences sensibility for mouth-related pairs facilitated the responses delivered through the microphone, while foot-related pairs facilitated the responses delivered through the foot pedal. This study suggests that body-related semantics is grounded within somatotopic sensorimotor representations. Taken together, these findings suggest a cross talk between language and overt sensorimotor behaviors (for a review, see Borghi et al., 2010).

In the previous studies, semantic processing was behaviorally tested at the single word level, but understanding a sentence of course also requires semantic processing, namely integrating the meaning of constituent words. In a behavioral study (Glenberg & Kaschak, 2002), participants had to read sentences describing transfer either away (e.g. *You delivered the pizza to Andy*) or toward the body (e.g. *Andy delivered the pizza to you*). Their task required to make a sentence sensibility judgment consisting of indicating whether the sentence made sense. The responses were given by movements either away from or toward the body. Critically, Glenberg & Kaschak found the so-called *action-sentence compatibility effect* (ACE) reflected by the facilitation of the response times for sentences describing a transfer away from the body when the response was given in the same direction (i.e. away from the body). The same compatibility effect was observed when the response movement was performed toward the body and the sentences described the same direction. The ACE was present for sentences describing a concrete (e.g. *Andy delivered the pizza to you*) and abstract transfer (e.g. *Liz told you the story*), as well as for imperative sentences (e.g. *Close the drawer*). The ACE did not depend on the hand used, as the effect was found when the movement was performed with both the right and left arms. However the ACE was clearly dependent on the realization of a

movement with the arm. Indeed, when participants were required to give button press responses without arm movement the compatibility effect was abolished. For Glenberg & Kaschak, these findings underline that sentence comprehension is grounded into bodily experiences. Interestingly, the ACE is dependent on a first person perspective (e.g. *You gave a pizza to Louis*) because for sentences with a third person perspective (e.g. *Léa gave a pizza to Louis*), the effect is abolished (Gianelli et al., 2011). However, when the agent and recipient of the action (i.e. *Léa* and *Louis*) were assigned to a spatial position (i.e. left or right), the ACE was restored for third person perspective sentences. This is because the participants took the perspective of the agent (i.e. they put themselves in the agent's shoes). These findings suggest the ACE is flexible and depends on the spatial position of our body in order to embody language processes.

Another behavioral study tested whether the meaning conveyed by a sentence describing a movement direction could be impacted by a motor training performed in one specific direction (Glenberg et al., 2008). Participants were trained to move beans from a wide mouthed-container to a narrow mouthed-container for 20-minutes. The training condition was either toward or away from the body. After training, participants performed a judgement sensibility task by indicating whether visually-presented (or read) sentences described a toward (e.g. *Mark deals you the cards*) or an away (e.g. *You deal Mark the cards*) transfer. The training direction was found to interfere with the direction of both concrete (e.g. *You deal Mark the cards*) and abstract (e.g. *You delegate the responsibilities to Anna*) sentences: training to move beans away from the body slowed the processing of sentence describing an away movement and vice versa for the toward direction. For the authors, this effect resulted from the use-induced plasticity within the sensorimotor network, eventually affecting language processing that is grounded within this network. They also discussed this interference effect as resulting from fatigue-related, overlearning effect induced by the training or preferential tuning of stimulus-response behaviors to the motor rather than the language task. More broadly, this study supports that comprehension of sentences describing concrete and abstract movements relies on the sensorimotor system. Following this study, the role of the sensorimotor network in sentence processing has been further testified by a similar approach. Participants were trained during 3-weeks on complex manual tasks, such as origami, tying or sewing, and tested before and after for their sentence processing abilities (Locatelli et al., 2012). The sentences were simple structures presented at third singular person and describing an action (e.g. *That person draws*), so that language performance was rather reflected by semantic processing. The semantic task consisted of a sentence-picture semantic congruency judgment task, with training-related

congruent sentence-picture pairs (i.e. verbs describing actions performed during the training), training-unrelated congruent pairs (i.e. verbs describing actions not performed during the training) and incongruent pairs. After training, response times were reduced to a greater extent for training-related pairs rather than training-unrelated pairs. This suggests that the manual training improved the processing of sentences describing actions performed during training as compared to sentences describing actions that were not performed during training. These results suggest that sensorimotor expertise impacts semantic processing abilities in language (see also Beilock, 2009; Beilock et al., 2008; Holt and Beilock, 2006). Overall, these studies support a contribution of the sensorimotor system in semantic processing. The next section aims to decipher the neural bases of semantics and the involvement of the sensorimotor circuits in this process.

b. Neuroimaging studies

- The neural bases of semantic processing

Meta-analyses of neuroimaging studies focusing on semantic processing revealed that the core semantic network mostly relies on the temporal and frontal regions, as well as the IPL with the angular gyrus of the left hemisphere (Binder et al., 2009; Price, 2010, 2012; Vigneau et al., 2006). These meta-analyses focused on tasks ranging from words reading, listening or generation. For instance, Vigneau and colleagues (Vigneau et al., 2006) identified two routes within the temporal lobe for semantic processing either in the visual or auditory modalities (Fig. 8). The ventrotemporal route performs semantic processing for visually presented words, whereas the dorsotemporal route is involved in the semantics of auditorily presented words. The ventrotemporal stream relies on left posterior inferior temporal gyrus (pITG) that encompasses the visual word form area (VWFA) located in the left fusiform gyrus and projecting to the left anterior temporal lobe (ATL). The dorsotemporal route involves the left pSTG that projects onto the lateral and middle part of the MTG, then projecting onto the anterior part of the superior temporal gyrus. These two streams are linked together posteriorly in the left angular gyrus and anteriorly in the left IFG, suggested to be amodal semantic hubs respectively involved in conceptual knowledge and semantic retrieval. Vigneau and colleagues mostly interpreted the involvement of these regions as the result of an integrative amodal semantic system that processes different types of semantic categories similarly in the parietal (i.e. left

angular gyrus) and frontal regions (i.e. left IFG). This system is also able to encode in different networks the modality of word presentation (i.e. visual or auditory).

Figure 8: The semantic network. Top panel: Peak of clusters of activity are represented by red dots obtained from neuroimaging investigations for semantics. The yellow crosses indicate the center of mass for a cluster of dots. The x and y axes represent the coordinates in mm in the MNI space. Bottom panel: These centers of mass are projected in isolation onto a brain render. F3orb: *pars orbitalis*; F3tv: ventral *pars triangularis*; F3opd: dorsal *pars opercularis*; PrF3op: junction of precentral gyrus and *pars opercularis*; Pole: temporal pole; T1a: anterior superior temporal gyrus; T1p: posterior superior temporal gyrus; T2ml: middle and lateral part of the middle temporal gyrus; T3p: posterior inferior temporal gyrus. Fusa: anterior fusiform gyrus; AG: angular gyrus. From Vigneau et al., 2006.

In addition to brain mapping, numerous investigations have been led to understand the time course of the brain activations for semantic processing. By the mean of EEG recordings, one main event-related potentials (ERPs) have been associated with semantics and is called N400 (i.e. corresponding to a negative evoked response occurring 400ms after the onset of a word). The N400 has been discovered in the context of sentence comprehension. Indeed, the amplitude of this neurophysiological response increases particularly when a sentence contains a semantic ambiguity or violation, such as *He shaved off his mustache and city* (Kutas & Federmeier, 2000). This neural response appears to be involved in the incremental build-up of a sentence for comprehension. Indeed, when a linear sentence unfolds word by word the N400 response tends to reduce for the last word (Kutas & Federmeier, 2000). In other words, the N400 response is linked to the expectation for a given word to appear, which is shaped by the general meaning at the sentence beginning. The N400 response will thus increase if the final word of a sentence does not respect the word expectation. For instance, in the sentence *They wanted to make the hotel look more like a tropical resort, so along the driveway they planted rows of palms/pines/tulips*, the two unexpected words *tulips* and *pines* provoked the strongest N400 response (Kutas & Federmeier, 2000). In other words, N400 is part of the sentence comprehension but rather reflects semantic processes for sentence comprehension. The neural bases of the N400 have been investigated and are supported by the left IFG, left MTG and left STG (Friederici & Kotz, 2003).

Nonetheless, this semantic network (Fig. 8) and its suggested amodal function does not specifically fit with the behavioral data presented above. Indeed, the reviewed behavioral investigations tend to confirm the theoretical accounts of the grounded cognition theory. However, the aforementioned semantic network does not take into account the fact that language concepts can be represented in modality-specific systems for action and perception.

One way to evidence this would be to directly study the neuroanatomical correlates of processing different semantic categories that evoke specific sensorimotor modalities not considered in the meta-analysis by Vigneau and colleagues (Vigneau et al., 2006). One of the easiest ways to study the neural underpinnings of different semantic categories is passive word reading or picture naming tasks in a fMRI scanner. Object nouns can tax various semantic categories, such as manipulable objects (e.g. *hammer*), non-manipulable objects (e.g. *house*), food (e.g. *nectarine*), animals (e.g. *turtle*), or landscapes (e.g. *mountains*). These categories can stress different sensorimotor features, such as shape, color, motion, motor, tactile, auditory, olfactory and gustatory features. The cortical areas involved in processing these different features are well known. Thus, if the modal sensorimotor system participated in the processing of object concepts, these modal areas should be recruited by semantic processing.

- The role of the sensorimotor circuits for object nouns

As a matter of example, tools and animals are characterized by different shapes or motion patterns. Indeed, a four-legged animal presents a quadrupedal movement pattern that is clearly different from the shape and motion of most of the tools. Observing motion provokes responses in a portion of the temporal lobe that is slightly anterior to the transverse and lateral occipital sulci. This area is called the middle temporal plus (MT+) and responds without exception to the observations of various biological and non-biological motion patterns (Zeki, 1991; Zihl et al., 1991). Furthermore, this area projects anteriorly towards the posterior temporal cortices that respond preferentially to different motion modalities. Indeed, the posterior superior temporal sulcus (pSTS) preferentially responds to the sight of biological motions, such as motion of living species (Saygin, 2013), whereas the posterior middle temporal gyrus (pMTG) is activated to the sight of non-biological motions, such as motion of a tool (Beauchamp & Martin, 2007). It has also been suggested that the ventral occipitotemporal cortex (OTC) is critical for encoding shape features (Ishai et al., 1999). In an influential study (Chao et al., 1999), participants were required in different tasks to view, match and name pictures of tools and animals (in addition to pictures of houses and faces for viewing and matching tasks). In a last condition, they had to silently read nouns of tools and animals. Interestingly, for picture viewing and matching both the ventral and lateral temporal cortices were activated. Critically, the medial fusiform gyrus and the pMTG responded preferentially for pictures of tools, whereas the lateral fusiform gyrus and pSTS were involved for pictures of animals. These findings testify that perceptual features such as shape and motion, can be

encoded in contiguous but separated neural regions. For the more conceptual tasks, namely picture naming and noun reading, the activations involved exactly the same cortical regions. Indeed, tool nouns relied more on the pMTG and the medial fusiform gyrus, whereas the pSTS and lateral fusiform gyrus were more activated for animal nouns. This evidence supports the grounded cognition theory because the semantic and conceptual tasks involved the same neural territories that encode distinct shape and motion properties during visual perception tasks.

Beyond shape and motion, the words meaning can also be associated to sensorimotor events. For instance, performing an action mostly relies on the dorsal cortical areas (Goodale & Milner, 1992). Thus, the grounded cognition model suggests that the motor system should be more important for the semantic encoding of manipulable object nouns, such as tools, than for non-manipulable objects nouns. Viewing and naming tool pictures rather than animals, faces and houses pictures revealed an involvement of the left PMv and the left posterior parietal cortex (Chao & Martin, 2000). These observations have been replicated in a picture naming task with manipulable and non-manipulable objects nouns (Saccuman et al., 2006), and furthermore corroborated by a neuroimaging meta-analysis of studies employing picture naming of tools and animals (Chouinard & Goodale, 2010). Nonetheless, because the viewing and naming tasks were based on visual presentation of pictures it is possible that even for naming task, the activity might be rather explained by mental imagery of object manipulation rather than pure conceptual processing. To address this issue, Boronat and colleagues (Boronat et al., 2005) asked participants to judge pictures or written words pairs of manipulable objects by indicating in separate runs whether each pair denoted a similar function (e.g. match – lighter) or a similar manipulation (e.g. keyboard – piano). Crucially, regardless of the modality of presentation (i.e. pictures or words), the left parietal regions were activated for the judgement about manipulability (Boronat et al., 2005). This finding was replicated in a repetitive TMS study, where stimulation of the left IPL yielded longer responses times in a semantic decision task requiring to make manipulation judgments (Ishibashi et al., 2011). Overall, these findings reflected a common network for the processing of tool nouns that is independent of their visual presentation modality (i.e. pictures and words). This observation suggest that viewing picture did not only activate an action mental representation, but also conceptual features shared with nouns processing.

Furthermore, tools and animals can be distinguishable by their auditory features. For instance dog and cats produce distinctive vocal sounds, whereas a hammer and a saw are characterized by specific mechanical sounds. Thus the grounded cognition model predicts that

the systems involved in auditory perception will be also involved for conceptual processing of nouns evoking high acoustic features (e.g. *telephone*) in comparison to nouns that do not evoke high acoustic features (e.g. *cup*). In a lexical decision task, Kiefer and colleagues (Kiefer et al., 2008) asked participants to read nouns referring to natural (i.e. animals, plants and fruits) or artifact categories (tools, musical instruments and transportations) with different acoustic features. Reading words with high acoustic features activated the pSTG and pMTG within 150ms as revealed by a study combining fMRI and EEG experiments (Kiefer et al., 2008). Because the clusters of activity overlapped with the network involved for actual processing of sounds (i.e. animal and tool sounds) and the involvement of these regions was early, it suggests that the modality-specific systems are recruited automatically during the processing of auditory conceptual features. Further studies confirmed these findings both for the localization (Kiefer et al., 2012), and the earliness of cortical activations (Trumpp, Traub, & Kiefer, 2013; Trumpp, Traub, Pulvermüller, et al., 2013).

To summarize, the described findings provide evidence for the grounded cognition model suggesting conceptual representations rely on the action and perception systems. Further evidence have been found for gustatory or olfactory features (Goldberg et al., 2006a, 2006b; González et al., 2006), as well as color features (Simmons et al., 2007), suggesting that the whole modal brain systems are involved for conceptual processing. Nonetheless, the findings leave questions open regarding how these anatomically distributed modality-specific features for an object noun are bound together. The *hub-and-spoke* model suggests that the bilateral ATL is an integrative region for all these features (Lambon Ralph et al., 2010; Patterson et al., 2007). We will not further present this model here since we are interested in specifically highlighting the role of the sensorimotor areas in the processing of words particularly referring to manipulable objects.

- The role of the sensorimotor circuits for action verbs

Object nouns are not the only words to represent sensorimotor features, indeed a large range of verbs refer to actions that represent sensorimotor features of different body parts. The semantic processing of action verbs has been extensively studied. One important finding comes from an fMRI study showing that reading hand- (e.g. *pick*), foot- (e.g. *kick*) or mouth-related (e.g. *lick*) action verbs activated premotor and motor areas in a somatotopic fashion (Hauk et al., 2004; Fig. 9A). In other words, reading the verb *pick* activated the hand area, the verb *kick*

the foot area and the verb *lick* the mouth area. Importantly, the same areas were involved when the same participants actually performed an action with the hand, foot or tongue (Fig. 9B). Later, these findings on action verbs have been largely corroborated, for instance an involvement of the motor areas was found for the comprehension of action verbs, such as *grasp*, as compared to abstract verbs, such as *think* (Rüschmeyer et al., 2007). In a different experiment, neural activity increased within the left premotor cortex for reading literal (e.g. *grasping the pen*) but not metaphorical (e.g. *grasping the idea*) phrases evoking hand, mouth and foot movements (Aziz-Zadeh et al., 2006). Noteworthy in this latter study, the regions of interest (ROIs) considered for the analysis corresponded to the areas activated by observation of mouth, hand and foot actions. This ensured that the left premotor cortex found active in the reading task was part of the motor control and perception system. In the study conducted by Aziz-Zadeh and colleagues, the absence of motor related activations for metaphorical sentences (or idioms) might be explained by the relatively small number of trials performed. To address this issue Boulenger and colleagues (Boulenger et al., 2009) ran an experiment with more repetitions. By testing hand and foot related metaphorical sentences (e.g. *he grasped the idea* vs. *he kicked the habit*), they found somatotopic activations along the motor strip: the hand motor area was activated by hand-related idiomatic sentences, while the foot motor areas was activated by foot-related idiomatic ones (see also, Desai et al., 2010). Overall these data suggest that both concrete and metaphorical sentences evoking motor representations are grounded within the sensorimotor system (for a review and meta-analysis, see Jirak et al., 2010).

Figure 9: Somatotopic activations for action verb reading. (A) Participants had to silently read action verbs referring to three different body parts, such as the legs (in blue), the arm (in red) and the face (in green). The results revealed a somatotopic organization within the premotor and motor areas. (B) The same participants performed foot (in blue), finger (in red) and tongue movements (in green), revealing the same somatotopic organization of the functional activations within the premotor and motor areas. Adapted from Hauk et al., 2004.

Another way to evidence that language is grounded within the sensorimotor network is to assess the long term effect of studying a language onto the cortical structure. Similarly to a motor training (Draganski et al., 2004; Quallo et al., 2009; Wenger et al., 2016), study of the from a foreign language vocabulary learning can modify the cortical structure (Mårtensson et al., 2012). Thus, if the sensorimotor network is involved in processing action verbs, the structure of this network should undergo reorganization after a training with action verbs. One study brought preliminary results supporting this hypothesis (Ghio et al., 2018). Participants were trained on eight different cognitive tasks involving the same ten words evoking

movements performed either by the distal (e.g. *pinch*) or the proximal (e.g. *catch*) musculature. The authors quantified the structural changes within ROIs selected for their involvement in the motor domain. Crucially, the linguistic training triggered grey matter structural changes within the left dorsal premotor cortex (PMd) for the group trained with verbs evoking proximal movements and within the right lobule VIIa of the cerebellum for the group trained with verbs that evoke distal actions. According to the authors, these results showed that language learning can modulate the cortical structure of the sensorimotor network since previous studies uncovered the involvement of these regions in sensorimotor processing. Even though interesting, these findings have to be interpreted with caution with respect to the structural magnetic resonance imaging (sMRI) techniques the authors used (Lorio et al., 2016), especially with their small sample size (i.e. $n=10$ for each group). The ROIs the authors selected were based on previous experiments, whereas the use of a functional localizer would have been more appropriate to identify the motor-related areas within this group of participants, rather than considering independent acquisition. This comment holds particularly true with regard to recent insights about the cerebellum. Indeed, a fine grained mapping of the cerebellar functions suggest that the lobule VIIa is involved in general language processes (M. King et al., 2019), but not that much in hand motor control which rather involves the lobule V (Diedrichsen & Zotow, 2015).

The whole of the aforementioned neuroimaging studies reflect the contribution of a large neural network for semantic processing of both action verbs and manipulable object nouns. This network includes, among other, regions such as pMTG, the pITG, the IPL and the left IFG. Within this network, the neural activations elicited by action verbs and manipulable object nouns should be closely related because they both convey sensorimotor features. Conversely, the neural activity elicited by an animal noun and action verbs should be less related given that the sensorimotor features are less prominent for animal nouns. To test these neural similarities and dissimilarities between different semantic categories a multivariate technique called the representational similarity analysis (RSA, see methodology box 3) has been employed (Carota et al., 2017). In a fMRI experiment, the authors utilized different semantic categories with action verbs (i.e. referring to leg, arm and face movements) and object nouns (i.e. food, tools and animals). The neural dissimilarities between each of these categories was recorded within several ROIs (e.g. left precentral gyrus and left pITG; Fig. 10A). A model of latent semantic similarity between each words stimuli was estimated from the analysis of a texts corpus. For instance, this model showed, in language, action verbs are most often associated

together in a text, whereas leg related action verbs are rarely associated with food nouns (Fig. 10B). Thus, this model integrated the textual similarities between different semantic categories and leaving the question open regarding the contribution of the brain to encode these similarities at the neural level. The RSA revealed, this model explained the neural activity elicited by the left IFG, left pMTG and left precentral gyri. These results suggest the sensorimotor components weighting words relation in texts is also represented within neural activity for a set of brain regions involved in sensorimotor processing and rejected the possibility of amodal processing within these areas.

Methodology box 3: The representational similarity analysis (RSA)

The RSA is a multivariate analysis approach employed in the field of neuroimaging that takes into account the spatial organization of neural activations across several voxels rather than the pure difference in terms of signal intensity changes (Diedrichsen & Kriegeskorte, 2017; Kriegeskorte et al., 2008). As such, the RSA will test how well the activation patterns fit with a theoretical model. Taking as an example the study by Carota and colleagues (Carota et al., 2017), the brain activity patterns for six semantic categories were measured so to quantify the distance between each neural pattern from the other. The distance between the neural patterns is calculated with an index of dissimilarity that is $1 - r$ (i.e. one minus the Pearson correlation score between two conditions). The estimated distances are entered in a representational dissimilarity matrix (RDM, Fig. 10A). This RDM is then compared to a theoretical model that is obtained from independent data (i.e. computational or behavioral model) or defined *a priori*. Carota and colleagues aimed to test whether the semantic similarity/dissimilarity is encoded within specific brain areas. To do that, they defined a model with a latent semantic similarity between the six semantic categories studied (Fig. 10B). This similarity was obtained from the co-occurrence in pool of texts of one word from one semantic category (e.g. *knife* for tool nouns) with another from another category (e.g. *carve* for arm-related action verbs). Thus if specific brain regions are representing this semantic similarity then the correlation score between the model and the RDM should be high. At the group level, to estimate if this effect is robust across participants, the mean correlation score is compared against zero with parametric or non-parametric tests. The authors also tested *a priori* models assuming differences between the semantic categories. For instance, it is possible to test whether brain regions are representing the similarities between each action verbs category, dissimilarities between each object nouns category and between verbs and nouns (Fig. 10C).

Figure 10: Insights about the RSA procedure. (A) Two RDMs obtained from neural activity elicited by six semantic categories within the left precentral cortex (left panel) and the left pITG (right panel). Each colored square corresponds to a dissimilarity score ($1 - r$). Dark blue corresponds to a dissimilarity score of 0, meaning the neural activities are perfectly similar, whereas yellow indicates a dissimilarity score of 1 meaning the neural activities are perfectly dissimilar. (B) Theoretical model obtained from data indexing the semantic similarity/dissimilarity between the six semantic conditions. Visually, we can notice the closer similarity between the model and the RDM for the left precentral gyrus rather than the RDM for the left pITG. This similarity is measured with a correlation score. (C) Theoretical model defined to test an *a priori* hypothesis regarding strong

representational similarity among actions verbs and dissimilarity between object nouns and action verbs. Adapted from Carota et al., 2017.

- The specificity of the sensorimotor activations for language processing

Such kind of results obtained from fMRI studies are indeed exciting, yet they do not clearly indicate whether the described sensorimotor activations are relevant for language processing or if they are merely a byproduct resulting from mental imagery at a later stage of processing. A debate is still open in the field of cognitive neuroscience of language regarding the role of mental imagery for language processing (Cayol & Nazir, 2020; Mahon & Caramazza, 2008). A study using magnetoencephalography (MEG) replicated previous results by showing that listening to action verbs related to foot and face movements somatotopically activated the left frontocentral cortical strip (Pulvermüller, Shtyrov, et al., 2005). Critically, the participants were asked to focus their attention on a distraction task (i.e. silent movie watching) and not on the action words. Furthermore the frontocentral activations when an action verb was played occurred within 200ms after word onset. Overall, these results suggest the motor activations for language are early and likely happen during the semantic access to words, thus being incompatible with post-conceptual mental imagery. Another study using electroencephalography (EEG) showed that the readiness potential recorded during movement preparation reduced when an action word was subliminally and simultaneously presented to the participants (Boulenger, Silber, et al., 2008). The subliminal presentation of an action word aimed to rule out the potential contribution of voluntary mental imagery that might occur when an action word is consciously perceived. However, motor imagery has been suggested to be involved during the covert computational stages occurring before an overt actions (Jeannerod, 1994, 1995). Thus, the earliness of the functional activations only excludes that the sensorimotor activations are reflecting voluntary mental imagery, but does not does not imply that motor regions play a functional contribution to language processing.

To uncover the causal role of sensorimotor activations for language processing, one of the best tools is TMS. In a semantic decision task, single pulse TMS applied to the left PMv, a region involved in tool use (see Brandi et al., 2014), prevented the facilitating priming effect for tool nouns but not for animal nouns (Cattaneo et al., 2010). Furthermore, the application of TMS over the left PMd (also involved for tool use; see Brandi et al., 2014) or the absence of TMS stimulation did not preclude the priming effect for both tool and animal nouns. The effect found for the PMv but not for the PMd is consistent with a previous positron emission

tomography (PET) study, where participants viewed pictures of tools (Perani et al., 1999). This suggests that tool nouns could be preferentially grounded within specific regions of the entire sensorimotor network supporting tool use. Another TMS study, where participants had to perform a lexical decision task with action verbs, showed a facilitation effect when the single TMS pulse was applied to the left motor areas related to the effector implied by the action verbs (Pulvermüller, Hauk, et al., 2005). In other words, the semantic priming was more important for hand-related than leg-related action verbs when the TMS was applied to the hand motor areas, and the reverse was found for leg-related verbs when TMS was applied to the leg motor areas. Finally, in a similar study (Tremblay et al., 2012), participants had to perform a semantic decision task by indicating whether a target word was congruent with a prime sentence. The sentences described either a manual action (e.g. *I squeeze the ball*), a manipulable object (e.g. *The ball is red*), a non-manipulable object (e.g. *The nursery is pink*) or an orofacial movement (e.g. *I bit my lower lip*). Repetitive TMS was applied over the left PMv at the level of the inferior frontal sulcus. The results showed the virtual lesion resulted in the abolishment of the priming effect only for the sentences describing a manual action. This effect was also accompanied by a compensation in the TMS condition in comparison to the sham condition. Indeed, the proportion of incongruent responses reduced and resulted in a higher sensitivity (i.e. sensitivity index or d'). Overall, these findings tend to confirm that motor regions are functionally relevant for language processing and that their involvement is not a byproduct of mental imagery.

c. Neuropsychological studies

From the neuropsychological perspective, the grounded cognition model indeed predicts deficits about conceptual knowledge would occur after lesions that affect various cortical regions and not only one single module in the brain. For instance, a patient with a lesion localized onto the hand premotor and motor areas would be expected to have more difficulty to process action verbs evoking a hand movement. Aphasia and apraxia are two deficits resulting from a brain lesion and respectively affecting the ability to efficiently produce or understand language and to perform actions (in particular with tools). Neuropsychological investigations have often reported that the severity of apraxia matches with the severity of aphasia (Dee et al., 1970; Kertesz & Hooper, 1982). For instance in group of aphasics the language performance correlated with the ability to pantomime tool use (Goldenberg et al., 2003). Along with the association between apraxia and aphasia (Roby-Brami et al., 2012), lesions affecting the motor and premotor cortices were also found to affect the processing of action words. Motor neuron

disease is a movement disorder originating in part from the degeneration of the frontal motor areas. Interestingly, these patients have a deficit for action related semantic processing (Bak & Chandran, 2012; Bak & Hodges, 2001, 2004; Grossman et al., 2008). This observation is consistent with previous evidence showing patients with lesions in the left IFG have more difficulty to process manipulable than non-manipulable action verbs (Arévalo et al., 2007). A similar finding has been found for a large sample of patients (i.e. n=127). The patients tested had lesions affecting various localizations in both hemispheres and performed tasks requiring conceptual knowledge of actions. The stimuli were mostly action verbs related to arm and hand actions. Crucially, the patients' deficit to process these words was mainly related to left IFG lesions in the presumed hand area (Kemmerer et al., 2012). This effect does not appear only restricted to cortical areas, indeed patients suffering from Parkinson's disease, a neurodegenerative trouble mostly affecting the basal ganglia (BG), also had an impairment for processing action verbs (Boulenger, Mechtouff, et al., 2008). Patients underwent a lexical decision task in semantic priming paradigm, with prime and target words belonging to two different lexico-semantic categories: action verbs or concrete non-manipulable nouns. While the control group showed the well-known semantic priming effect for each word category, the parkinsonian patients off dopaminergic treatment did not show such facilitation for action verbs only. Interestingly, patients recovered the priming effect when they received their dopaminergic treatment before the experiment. Similar deficits have been observed in parkinsonian patients for action-related semantic processing (Fernandino et al., 2012; Johari et al., 2019). Beyond action verbs, the semantic processing of tool nouns seems to be specifically encoded within the network subserving tool use. For instance, in patients with left hemisphere lesions, both the action knowledge about an artifact and the semantic ability to find the thematic relation between two artifacts (e.g. *hammer-nail*) were impaired and mainly explained by lesions affecting the left occipitotemporal cortex (OTC) and the human MT+ localized posteriorly (Kalénine & Buxbaum, 2016). These results are consistent with another investigation showing that apraxia patients have deficit in processing declarative information regarding tool manipulation knowledge, consistent with a semantic organization for tool nouns within the tool-use left frontoparietal network (Buxbaum & Saffran, 2002). Overall these findings support the hypothesis that conceptual knowledge is grounded within the action and sensory systems subserving motor control or multisensory integration.

Nonetheless, a set of neuropsychological investigations showed that lesion to the sensorimotor circuits did not systematically cause a language deficit. For instance, two patients

with limb apraxia did not show any deficit to recognize tools or to identify tools from their function knowledge (Rumiati et al., 2001). In another study, twelve left damaged patients performed tool-use and action imitation tasks, as well as a language task requiring to comprehend action verbs and tool nouns (Papeo et al., 2010). Crucially, a double dissociation was observed, meaning that the lexical-semantic processing of action words was independent of the ability to imitate actions or use a tool. These findings clearly challenge the grounded cognition theory.

How can these diverging findings be reconciled? According to Papeo & Hochmann (2012), the main limitation of the neuropsychological studies supporting the embodied cognition model, relies on the lack of sensorimotor evaluation when language deficits are shown. Thus, while patients have a deficit to process action verbs or tool nouns, there is no direct evidence these patients have also specific sensorimotor deficit. From this perspective the authors considered that conceptual representation about movement might not be grounded in the sensorimotor network. Although this interpretation makes sense, the large range of behavioral and neuroimaging studies that reveals the earliness of sensorimotor activations for language makes it not fully convincing. The type of stimuli used to assess motor and language deficit is of particular importance. To address this issue, Mengotti and colleagues (Mengotti et al., 2013) tested left brain damaged patients on the imitation of meaningful movements (e.g. tool pantomime) in comparison to meaningless ones (e.g. a random trajectory with the hand with no meaning). The imitation of meaningful movements involved conceptual features, such as lexical-semantic representations. Crucially, patients impaired to imitate meaningful movements were also impaired for the repetition and imitation language tasks. Hence, in neuropsychological studies, the corroboration of the embodied cognition predictions may rely on the sharing of conceptual features for both language and action.

In our opinion, patient idiosyncrasies might also account for these diverging results. Indeed, in general one of the limitations of neuropsychological studies performed twenty years ago relies on the relatively small sample size. Small sample size may prevent a clear understanding of general brain processes because a small set of participants might not be representative of the general population deficit. Indeed, the likelihood that two patients will suffer from exactly the same lesion and cognitive deficits is almost null. This is of further interest because both action and language involve distributed neural networks, opening the possibility for compensations when one part of the network is lesioned but another remains intact. Because of these idiosyncrasies, the compensations could selectively concern the motor

domain but not language (or vice versa), thus resulting in the performance dissociation previously observed in patients assessed on both tool use and tool nouns. Another mechanism that could account for these differences, is the patient ability to recover quickly after a stroke. For instance patient impairments are most important in the first days after a stroke, then the patients start to recover (Prabhakaran et al., 2008). Thus, it is very likely that after a stroke, patients impaired in both language and action will not systematically recover the two abilities at similar pace (Ginex et al., 2020). To summarize, an apraxia patient with a focal lesion may have a deficit to use a tool but preserved conceptual representation of the tool because this representation is grounded in a larger and spared sensorimotor network.

3. Syntax

a. Behavioral studies

Processing a sentence involves several linguistic components such as the phonology, for discriminating the relevant sounds of language and semantics for extracting the meaning conveyed by the constituent words. However, understanding a sentence does not simply rely on the semantic and phonological content but also on the hierarchical organization of the sentence components. Such hierarchical processing is handled by the syntactic function. Indeed, two sentences can have the same semantic content but different meanings because of different hierarchical organizations. Thus, studying syntactic processing requires to employ tasks controlling for the influence of the semantic content. Most of the behavioral investigations focusing on syntax have employed at least four paradigms. These paradigms are called syntactic violation detection, garden path sentences, *Jabberwocky* sentences and syntactic comprehension.

The syntactic violation detection task requires to detect a syntactic anomaly within a sentence. To be considered as syntactic, an anomaly has to impact the hierarchical organization of the sentence, namely this violation is not an orthographic mistake. Instead syntactic violation can impact the phrase structure, for instance a sentence like *Bill admired Susan's picture of the park* is correct, whereas *Bill admired Susan's of picture the park* is incorrect. The second sentence violates the classical preposition noun order within the sentence (Neville et al., 1991). Phrase structure violations are not the only violations that have been studied. Indeed, violations in a sentence might be morphosyntactic (i.e. violation of the word morphonology or form), such as verb tense violations. For instance, an incorrect sentence like *It seems that the cats won't*

usually eating the food we put on the porch provoked more eye movements towards the words preceding the violation in comparison to an correct sentence like *It seems that the cats won't usually eat the food we put on the porch* (Ni et al., 1998). Similarly, sentences with subject-verb agreement violations (i.e. *he have* instead of *he has*) provoked longer reading times at the level of the violation in comparison to correct sentences (De Vincenzi et al., 2003). Furthermore, the violations can also impact the formation of a question (i.e. unnecessary addition of question pronoun), the pronoun gender (i.e. *him* for a woman), the pronoun case (i.e. reversal between *we* and *us*). These violations also led to a greater complexity for processing incorrect sentences rather than correct sentences (see Neville et al., 1991). Crucially, irrespective of the violation type, the correct and control sentences have to contain similar semantic content with respect to the incorrect sentences. This experimental manipulation aims to reduce the impact of semantics in order to isolate the syntactic processing.

The garden path sentence is another paradigm used to assess syntactic processing. A garden path sentence is grammatically correct but contains a syntactic ambiguity (Kaan & Swaab, 2003). The most likely interpretation of a garden path sentence is incorrect. To deal with this interpretation error, the reader will have to reanalyze this sentence from the beginning. For instance, there are two ways to analyze the sentence *They told the boy that the girl met the story*. The first way consists in analyzing the sentence as follows *They told [the boy] [that the girl met the story]*. This analysis appears to be a dead end (i.e. *to be led down the garden path*) and yields an unintended meaning reflected by the pragmatic ambiguity *the girl met the story*. The other and correct interpretation for the sentence is as follows *They told [the boy that the girl met][the story]*. At the behavioral level, processing garden path sentences provokes longer response times and more errors than non-garden path sentences (Kaan & Swaab, 2003).

In the attempt to disentangle semantics from syntactic processing experimental protocols featuring *Jabberwocky* sentences emerged. In a *Jabberwocky* sentence words are replaced with pseudowords, but keeping the morphosyntactic markers. This paradigm has been inspired by an eponym poem written by Lewis Carroll in 1971, whose the first quatrain was the following:

*Tw'as brillig, and the slithy toves
Did Gyre and gimble in the wabe;
All mimsy were the Borogoves,
And the mome raths outgrabe.*

Syntactic violations are included and have to be detected by the participants. For instance, a syntactically correct *Jabberwocky* sentence is *The wibon was being rished*, whereas *The plover was being in-the rished* is a syntactically incorrect *Jabberwocky* sentence. Interestingly, when asked to judge the syntactic correctness of a sentence, participants made more errors for syntactically incorrect structures than syntactically correct ones, but the rate of errors was equivalent between correct *Jabberwocky* and regular sentences (Hahne & Jescheniak, 2001). However, the *Jabberwocky* though preventing a common and standard interpretation does not prevent attempts of semantic interpretations. This limitation may be one reason why the *Jabberwocky* paradigm has not been considered as a gold standard for studying syntactic processing.

The last paradigm is the syntactic comprehension task. This paradigm will be used for our experimental contribution and is presented in the methodology box 4. The whole of the paradigms aim to understand the syntactic processing at the behavioral level. These tasks have also been employed with neuroimaging tools. The next section aims to review the neural bases of syntactic processing.

Methodology box 4: The syntactic comprehension task

The syntactic comprehension task consists of manipulating different syntactic structures with equivalent semantic content in order to control for the influence of semantics while highlighting the differences in hierarchical organization. For instance three syntactic structures have often been studied in the neuroscience of language: coordinated, center-embedded subject relative and object relative clauses. An object relative clause such as *The writer that the poet admires writes the paper* conveys a different meaning than a subject relative clause such as *The writer that admires the poet writes the paper* or coordinated clause such as *The writer admires the poet and writes the paper*. So that if an affirmation such as *The writer admires the poet* is presented, this latter will be true for the coordinated and subject relative but false for the object relative. Both the coordinated and subject relative sentences respect the canonical subject-object order of the English language so that *The writer admires the poet*, whereas with the object relative sentence there is an interruption of this canonical order, so that the same affirmation *The writer admires the poet* is no more true (i.e. *The poet admires the writer* is true). Thus, to understand this sentence our brain has to decode its hierarchy and the different long-distance dependencies. Most importantly, these different syntactic structures are known to imply different degrees of processing difficulty. At the behavioral level, this is evidenced by an increase of the response time and decrease of the accuracy to process the object relative sentences in comparison to subject relative and coordinated sentences (Caplan & Waters, 1999; Just & Carpenter, 1993; J. King & Just, 1991).

b. Neuroimaging studies

Two seminal neuroimaging investigations gave clear insights regarding the neuroanatomical correlates of syntactic processing. In a PET study (Stromswold et al., 1996), participants had to perform a semantic plausibility judgment on sentences of different syntactic structures. The authors evidenced the greater contribution of the left IFG (i.e. Broca's area) for the most complex syntactic structure, namely the center embedded relative clauses (e.g. *The juice that the child spilled stained the rug*) in comparison to right branching clauses (e.g. *The child spilled the juice that stained the rug*). The same year a fMRI study also based on ROIs analysis, confirmed the role of the left IFG for syntactic comprehension of object relative in comparison to subject relatives and coordinated clauses (Just et al., 1996). Furthermore, the left pSTG (i.e. Wernicke's area) contributed to syntactic processes. By contrast, the involvement of the homologous regions in the right hemisphere was negligible. Afterwards, other neuroimaging studies have corroborated these seminal findings by uncovering the role of the left IFG in syntactic processing (Ben-Shachar et al., 2003; Makuuchi et al., 2009; Moro et al., 2001). A first meta-analysis attempt gives an overview about the network supporting syntactic processing, by revealing the involvement of the left IFG and regions surrounding the left pSTS (Fig. 11 upper panel, light green). Noteworthy the network identified by the authors also included results from studies focusing of sentence comprehension, such as text comprehension or sentence completion tasks. These tasks did not specifically test syntactic processing but rather sentence comprehension as a general processing including both syntax and semantics.

Figure 11: The sentence comprehension network. Top panel: Peak of clusters of activity are represented by green dots obtained from neuroimaging investigations for sentence comprehension. Light green represents the peaks for the contrasts investigating syntactic comprehension. The yellow crosses indicate the center of mass for a cluster of dots. The x and y axes represent the coordinates in mm in the MNI space. Bottom panel: These centers of mass are projected in isolation onto a brain render. F3tv: ventral *pars triangularis*; F3opd: dorsal *pars opercularis*; F2p: posterior middle frontal gyrus; Pole: temporal pole; T1a: anterior superior temporal gyrus; T2ml: middle and lateral part of the middle temporal gyrus; T2p: posterior middle temporal gyrus; STSp: posterior superior temporal sulcus. From Vigneau et al., 2006.

A more recent neuroimaging meta-analysis (Walenski et al., 2019) investigated the contrasts for comprehension of non-canonical (e.g. object relatives) versus canonical (e.g. subject relatives) structures obtained from 37 studies. This revealed the involvement of seven clusters found within the left IFG, left middle frontal gyrus, left superior frontal gyrus, left pMTG, left angular gyrus and right insula (Fig. 12).

Figure 12: The complex syntax network. Meta-analysis of the clusters significantly activated for the processing of non-canonical versus canonical sentence for left hemisphere view (left panel), superior view (middle panel) and right hemisphere view (right panel). The clusters activated are the *pars orbitalis* (1), the *pars opercularis* and *triangularis* (2) of the left IFG, the left middle frontal gyrus (3), the left superior frontal gyrus (4), the right insula (5), the left pMTG (6) and the left angular gyrus (7). From Walenski et al., 2019.

These meta-analyses showed that a larger network than left IFG and left pSTG is involved in complex syntactic processing. Most of the neuroimaging studies focusing on syntax do not report a role of the subcortical structures but this might be explained by methodological choice and especially the selection of ROIs for fMRI analysis. Indeed, an experiment has reported the contribution of subcortical structures to syntactic processing (Moro et al., 2001). Participants had to covertly read sentences with syntactic (i.e. wrong order) or morphosyntactic (i.e. wrong agreement: e.g. *he have* instead of *he has*) anomalies. Whereas the two tasks commonly activated the left and right IFG, the syntactic task recruited in addition the left caudate nucleus of the basal ganglia. The authors suggested that the BG might be involved in checking the sentence words order, as well as in handling the hierarchical structure of the sentence. The contribution of the BG was also found in another study where participants had to detect syntactic violations (Friederici et al., 2003).

At the neurophysiological level, the EEG investigations revealed the specific contribution of an ERP, called P600 (i.e. corresponding to a positive evoked response occurring 600ms after the onset of a word), and reflecting the syntactic processing. The P600 response has been mostly linked to the processing of syntactic violations affecting the phrase structure. For instance, the incorrect sentence *Bill admired Susan's of picture the park* will elicit a stronger P600 than the correct sentence *Bill admired Susan's Picture of the park* (Neville et al., 1991). The P600 is also involved in other syntactic and morphosyntactic violations, such as subject-verb agreement, pronoun case, pronoun gender, verb tense or question formation. The P600 is not only restricted to syntactic violations. Indeed, P600 responses are also observed for syntactic processing involving complex structures. In an EEG experiment (Kaan et al., 2000),

participants were submitted to sentences with similar semantic content but combined within different structures. For instance, one sentence was a simpler structure to process (e.g. *Emily wondered whether the performer in the concert had imitated a pop star for the audience's amusement*) in comparison to another more complex structure (e.g. *Emily wondered who the performer in the concert had imitated for the audience's amusement*). The verb *imitated* is linked to the actor *the performer* for each sentence. In addition, for the more complex structure, another linking operation has to be performed on the top of the first one. Indeed *who* referred to the object (i.e. the pop star) which is distant from the verb by several words. On the occurrence of the verb (i.e. *imitated*), a stronger P600 response was elicited by the complex structure in comparison to the simpler one (Kaan et al., 2000). The P600 neural response is also observed for processing garden path sentences. In comparison to the non-garden path sentence, garden-path sentences involved stronger P600 responses (Kaan & Swaab, 2003). Overall the P600 response represents the processes involved in syntactic integration and likely allows reanalysis and repairing process to handle syntactic complexity, ambiguity or violation. Other ERPs components such as the early left anterior negativity (ELAN) and the left anterior negativity (LAN) occurring respectively around 200ms and 300ms from word onset are supporting syntactic processing, however their functional significance has been a matter of debate (Steinhauer & Drury, 2012). The P600 is likely under the control of the BG and the left pSTG (Friederici & Kotz, 2003). The role of the subcortical structures in syntactic processing was later investigated in humans via iEEG recordings (Wahl et al., 2008). The syntactic violations consisted in the lack of a noun at the end of the sentence (e.g. correct: *The pizza was eaten in the restaurant* vs. incorrect: *The ice cream was eaten in*), while the syntactic complexity was not manipulated. The results revealed the contribution of the thalamus to process syntactic violations, while the BG (i.e. globus pallidus and subthalamic nuclei) did not show any syntax related activity. These results suggest that the role of the BG for syntactic processing is not totally devoted to the identification of syntactic violations. Instead, the BG might subserve the integration of syntactic difficulties (Friederici & Kotz, 2003), requiring to extract sentence meaning from the analysis of the long distance dependencies and the hierarchical organization.

Based on this literature review, the neural bases of syntax appears to rely on cortical areas such as the left IFG and the left pSTG, as well as subcortical areas such as the BG. These regions are likely involved in the combinatorial process of words within a sentence, as well as in handling the long-distance interdependent relations between these words. As for semantics and phonology, one influential idea that has been proposed is that syntactic processing can be

embodied within the sensorimotor system (Greenfield, 1991; Maffongelli et al., 2019; Pulvermüller, 2014; Pulvermüller & Fadiga, 2010; Roy & Arbib, 2005). These theoretical accounts start from a simple observation: actions display a similar hierarchical organization as sentences do. Thus, a similar function has been assumed to handle hierarchies in both the linguistic and the motor domains: for a center embedded relative sentence such as [*The man [that the dog chased] ran away*] or a motor structure such as [*open the door [switch on the light] close the door*]. If this hypothesis holds true, similarities should be observed at the neural level between motor and language hierarchical processes. Some of the most appealing evidence in favor of this hypothesis comes from ERPs studies. In a study, participants were asked to observe motor sequences presenting either a content error (e.g. making coffee with cola) or structure error (e.g. pour pasta into a pan before pouring it with water). Crucially, the content error induced a stronger N400 response whereas the structure error produced stronger LAN and P600 responses (Maffongelli et al., 2015). Thus the ERPs evoked by the observation of motor sequences are similar to the neural responses evoked by the detection of semantic or structural errors in language (see also Sitnikova et al., 2008, 2003). However, the neural response similarity between action observation and sentence comprehension does not prevent the possibility that different mechanisms are at stake when the action has to be produced. In an attempt to take this issue into consideration, a research team investigated how the execution of a motor sequence interacted with syntactic processing (Casado et al., 2018). In their task, sentences were self-administered by the subject following a linear rule (i.e. three consecutive finger presses) or non-linear rule (i.e. two finger presses were interrupted by one foot press). The sentences included relative clauses with a subject-verb morphosyntactic disagreement, in such a way the singular or plural verb agreement was incorrectly applied (e.g. presented in Spanish, the sentence *The water [Noun, Singular], that overflowed the dam, flooded [Verb, Plural, 3rd person] the village.* included morphosyntactic disagreement between the singular noun *water* and the verb *flood* conjugated in 3rd person plural, instead of 3rd person singular). The EEG recordings revealed an attenuation of the LAN and increase of the P600 responses when sentences with the grammatical violations were non-linearly rather than linearly self-administered (Casado et al., 2018). This non-linear self-administration aimed to induce a different complexity into the action structure. This motor action is hypothesized to be analogous to an embedded structure in language, in turn impacting syntax-related electrophysiological responses (i.e. LAN and P600). Furthermore, these findings suggest the existence of shared neural resources for processing linguistic sequences and motor sequences. Interestingly, the investigations of the neural bases subserving the execution of a hierarchically organized motor

sequence most often revealed the role of the BG (Martins, Bianco, et al., 2019) and left IFG (Koechlin & Jubault, 2006), comforting the hypothesis that shared neural resources can process complex structure either in the motor or language domains.

Crucially, the ability to handle grammatical rule-governed combinations, such as syntactic rules, has been proposed to be supported by the procedural system rooted within the frontal cortex and the BG (Ullman, 2001, 2004, 2006). The procedural system is well known for its contribution in the motor domain and especially to support learning and control of new motor skills (Kreitzer, 2009). In addition, language has grammar rules that do not have to be violated at the risk of impairing the meaning conveyed. The rules might be subserved by the procedural memory system rather than the declarative memory system. To further explain its rationale, Ullman takes the example of the verb tense agreement. Indeed, in English there are regular and irregular verbs. For the regular ones the rule to handle requires to add the suffix –*ed* to the infinitive form of the verb: *walk* is conjugated in *walked* for the past tense. Conversely irregular verbs (i.e. *take* in the infinitive form and *took* in the past tense) requires to memorize the past tense form that can be assigned to a given rule. This ability to memorize irregular form is suggested to rely upon the declarative system and more specifically the hippocampus. This dissociation between the procedural and declarative system has been recently supported by a neuroimaging meta-analysis on novel language learning (Tagarelli et al., 2019). Only contrasts testing grammatical or lexical learning were considered in this study. While both types of learning relied on the activity within the left IFG and the posterior parietal regions, the grammar learning only activated the BG. In their meta-analysis, Tagarelli and colleagues separated studies relying on declarative memory (i.e. explicit learning) and procedural memory (i.e. implicit learning) and found the specific contribution of the parahippocampal cortex to explicit learning whereas implicit learning was supported by the BG.

In parallel, the contribution of the IFG to syntactic processing has been a matter of debate (Fadiga et al., 2006). Indeed, complex syntax is likely supported by executive processing involving working memory. Being able to understand a sentence with interdependent elements also relies on the ability to store them in memory. Thus, the increase of neural activity within the left IFG for more complex syntactic structures may solely result from the requirement to store sentence elements into working memory. To address this question, the structure of sentences were manipulated in terms of complexity and length (Makuuchi et al., 2009). Interestingly, the neural correlates for processing complex syntactic structures involved the left *pars opercularis*, whereas sentences with longer structure requiring to hold elements into

working memory involved the inferior frontal sulcus. This observation has been in part replicated in a study looking at the localization of several functions, such as sentence comprehension and working memory within the left IFG. The results revealed that most of the functions studied relied on the left IFG but stood apart in language-specific and domain-general hubs (Fedorenko et al., 2012). Even though these two neural nodes are anatomically distinct, they are likely interconnected and the role of working memory for syntax cannot be totally ignored (Makuuchi & Friederici, 2013; Santi & Grodzinsky, 2007).

c. Neuropsychological studies

The postmortem brain observations performed on fluent and non-fluent patients by Paul Broca and Carl Wernicke showed that lesions in these patients are respectively localized in the left pSTG and left IFG. Paul Broca characterized non-fluent aphasia as a deficit in language production ability resulting from a lesion to the left IFG (Broca, 1861). Conversely Carl Wernicke describe fluent aphasia as a language comprehension deficit originating from a lesion to the left pSTG (Wernicke, 1881). Patients with fluent and non-fluent aphasia were tested on their ability to comprehend sentences putting forward the semantic content or the syntactic rules (Caramazza & Zurif, 1976). Interestingly, non-fluent aphasia patients' comprehension was relatively spared in comparison to fluent aphasia patients when the semantic content has to be used. However, as soon as the patients had to handle syntactic rules their comprehension dropped and was equivalent to that of fluent aphasia patients (Caramazza & Zurif, 1976). Hence, before neuroimaging findings, neuropsychology already revealed the contribution of the left IFG and left pSTG for syntactic comprehension. Noteworthy, the two renowned Paul Broca's patients (i.e. Misters Leborgne and Lelong) had their brain conserved. Using structural neuroimaging, the lesions were shown to not only affect the left IFG but also deeper structures such as the insula and the BG (Dronkers et al., 2007). This finding corroborates previous neuropsychological investigations showing aphasia profiles correlated with the lesion in the BG and surrounding white matter tracts (Alexander et al., 1987). Further studies run in patients with lesions to various left frontal and subcortical lesions showed they were impaired for processing non-canonical structures as compared to controls (Teichmann et al., 2015). The authors suggested that the ability to process complex syntactic structures relies on a white matter tract joining the left IFG and the BG. Further studies conducted in parkinsonian patients revealed a deficit for processing syntactic structures as compared to controls (Johari et al., 2019). Huntington disease is also a neurodegenerative disease impacting the BG. Patients

suffering Huntington disease were found impaired in the rule application across various domains, such as syntax, morphology and arithmetic (Teichmann et al., 2005, 2008). Critically, the syntactic impairment induced by the BG neurodegeneration did not appear related to potential confounding executive processing such as working memory (Sambin et al., 2012). Both the Parkinson and Huntington diseases are known to severely impact the motor functions.

Similarly, the left IFG is critical for action execution or observation (Rizzolatti et al., 1996) and the left pSTG is an important area for the perception of biological motion (Beauchamp & Martin, 2007). Accordingly, it might be possible that the syntactic system is grounded within the sensorimotor territories, so that patients with lesions to these areas are impaired for both language and action. As for neuroimaging, few neuropsychological studies addressed this question and assumed that syntactic impairment observed in these patients should not be link to a gross motor impairment but rather to a difficulty in processing action sequence. Fazio and colleagues (Fazio et al., 2009) asked non-fluent aphasic patients to reorder a sequence of human actions (e.g. sequence for reaching a bottle of water) and sequence for non-biological movements (e.g. sequence of a bicycle falling on the floor) presented with pictures. The authors' prediction was straightforward: if syntax and action sequences share neural resources, participants with left IFG lesion should have a deficit in reordering human action sequences but not non-biological event sequences. This prediction was verified and patients were worst in rearranging a visually presented human motor sequence in comparison to neurotypical controls. Crucially, this deficit was not simply explained by a general inability to reorganize sequences, as patients were equally capable with respect to controls to reconstruct physical events sequences. This study fundamentally evidenced the role of Broca's area in processing hierarchies beyond its well described role for language, in turn suggesting the implication of this area for the same function but at the service of the motor system.

The study by Fazio and colleagues opens the possibility that action sequence production and not only observation is impaired in patients suffering from syntactic language impairments. This question has been addressed with children (i.e. around 11 years old) suffering from a specific language impairment (SLI, also called developmental language disorder - DLD, see Bishop, 2017) that impacts their abilities to handle syntactic dependencies (Roy et al., 2013). These children were compared to typically developing (TD) children. Crucially, these young participants had to displace a bottle, whose weight was either known or unknown, while their movement kinematics was recorded. This manipulation allowed to test whether the motor action is hierarchically organized, by controlling whether the different action components (i.e.

reach, grasp, lift and move) are embedded (i.e. Grasp TO Displace) or simply juxtaposed (i.e. Grasp AND Displace). When the bottle weight was known the TD children anticipated this information in the grasping phase before lifting the object, suggesting the reliance over the embedded strategy. Conversely the SLI children did not show such anticipation and the kinematics was only modified by object's weight during the moving phase. The SLI children strategy is consistent with the use of a juxtaposition, in such a way the grasping and moving phases are distinguishable. To rule out the contribution of a broad cognitive impairment to this effect an additional group of patients was included. These patients were young adults with fragile-X syndrome characterized by delayed language abilities but spared ability to deal with syntactic dependencies. The patients, while slower to perform the motor task in comparison to healthy adults (i.e. around 25 years old), used the embedded strategy when the bottle weight was known (as adults controls did). Overall, these experiments suggest shared hierarchical processes might be at stake between the motor and language domains. Taken together, these findings suggest the existence of a syntax-like process for action that may share components with the linguistic syntax. Finally, the entire language section offers an overview regarding the network involved in language processing. Because we assume neural similarities between language and tool use, the next section will review the neural bases of tool use.

The neural bases of tool use

Tool use is one of the most complex motor ability and an incredible hallmark of human evolution. The widely-accepted definition for tool use describes the use of an object “*to alter [...] the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use*” (Beck, 1980 in Seed & Byrne, 2010, p. R1032). Even though animals are able to use tools (Seed & Byrne, 2010), as well as to shape manufactured tools as demonstrated for chimpanzees (McGrew & Collins, 1985) and Caledonian crows (Hunt, 1996), humans’ ability to use tool and conceive new tools outperforms that of animals. Crucially, humans’ tool use represents a level of sophistication of the motor system that is unique within the animal reign. Strikingly, such a level of sophistication is also a characteristic of the human communication system represented by language. Given these sophisticated processes, the possibility of co-evolution history between tool use and language has been proposed (Ponce de León et al., 2021). In this view, a co-localization of neural resources between tool use and language resulting from this co-evolution process has been suggested (Stout & Chaminade, 2012), so that syntax, semantics and phonology might be closely linked to the ability to use a tool. Thus, the tool will allow to test our predictions on the relation between tool use and language that is until now mainly theoretical.

Tool use often consists of reaching and grasping an object impossible or difficult to handle with the bare hand. Reaching and grasping are also the two main components of a manual action performed without a tool (Jeannerod, 1999; Jeannerod et al., 1995). In the daily life, reaching and grasping objects such as a glass of water or a piece of food with the hand are ubiquitous actions. Even though this action seems in appearance simple and well mastered, it requires involvement of several cortical and subcortical areas. Seminal works from Ungerleider’s team (Mishkin et al., 1983; Ungerleider & Mishkin, 1982) lately refined by Goodale’s team (Goodale & Milner, 1992) suggest the co-existence of two separate processing streams, one ventral and one dorsal, originating from the visual cortex. The dorsal stream recruits frontoparietal areas and is dedicated to goal directed actions by processing the object localization (i.e. *where*) and its three dimensional features in order to select an adapted motor plan (i.e. *how*) to act upon the object. The ventral stream projects onto the inferotemporal areas and is rather dedicated to the processing of conceptual knowledge (i.e. *what*), such as semantic representations about texture, shape, size and color of an object. This two-stream organization is found in both monkeys and humans and also supports tool use. In the next sections, from both non-human and human primates’ studies, we will review the critical neural components

involved in tool use, by first describing the reach-to-grasp network for manual actions and then how this network is specifically reinvested and extended for tool-use actions. Critically, we will present the ability to skillfully control a tool is not supported by a single motor area but rather by a large network involving primary sensorimotor and associative areas, as well as subcortical regions such as the BG and cerebellum.

1. The neural organization of tool use in monkeys

a. The neural organization of reaching and grasping in monkeys

Seminal investigations of the dorsal stream have been performed by iEEG recordings on monkeys' left hemisphere during reach-to-grasp movements. A reach-to-grasp movement generally encompasses three main interdependent components: arm reaching, wrist orientation and hand grasping (Jeannerod et al., 1995). The dorsal stream supports these components. Specifically, previous studies in monkeys (for a review, see Jeannerod et al., 1995) have highlighted the role of the anterior intraparietal area (AIP), the monkey ventral premotor area (mF5) and the primary motor area (M1) for goal-directed movements. Crucially, the AIP codes for the global structure of an action given the intrinsic properties (e.g. size and shape) of the object to grasp. The mF5 area rather codes for specific sub-components within the global action plan, such as the grip type (e.g. thumb-index fingers opposition) required to grasp the object. This refined motor plan is then sent to M1 subsequently sending a motor command to the spinal cord motor neurons in order to execute the movement. The role of these different neurocognitive nodes has further been extended by integrating the contribution of different parietal regions such as the medio-intraparietal area (MIP), and frontal regions such as the monkey dorsal premotor area (mF2). More specifically, the MIP and mF2 areas are contained within a dorsomedial stream coupling together the reaching and grasping components. Conversely, the AIP and mF5 are part of the dorsolateral stream that is rather critical for specifying reaching and grasping components (for a review see, Davare et al., 2011). These circuits (Fig. 13) also receive inputs from additional neural nodes located in the dorsal and ventral streams, with a specific contribution of regions at the junction of parietal, temporal and occipital regions (Davare et al., 2011; Goodale & Milner, 1992).

Figure 13: Complete overview of the monkey's action network. In red is represented the core grasping circuit involving the dorsolateral stream with AIP and mF5 (F5 on the figure). In blue is represented the reach-to-grasp circuit, involving the dorsomedial stream with the MIP and mF2 (PMd on the figure), as well various medial cortical areas. In green is represented the inputs from the ventral to the dorsal stream and in purple various dorsal

cortical regions implied in the reach-to-grasp circuits. 46: dorsolateral prefrontal cortex; F5: ventral premotor cortex; FEF: frontal eye field; PMd: dorsal premotor cortex; PMdr: rostral dorsal premotor area; SMA: supplementary motor area; CMAd: dorsal cingulate motor area; M1: primary motor cortex; AIP: anterior intraparietal sulcus, SII: second somatosensory area; LIP: lateral intraparietal sulcus; MIP: medial intraparietal sulcus; MST: medial superior temporal; PF: part of rostral inferior parietal convexity; PFG: part of rostral inferior parietal convexity; PG: part of caudal inferior parietal convexity; PGm: precuneate cortex; PEc: parietal area PEc; V6Av: ventral visual area V6A; V6Ad: dorsal visual area V6A; TEa/TEm: anterior and middle inferotemporal cortex; TEp: posterior inferotemporal cortex; TEO: inferior occipitotemporal cortex. From Davare et al., 2011.

b. Tool use in monkeys is supported by the a dorsal stream and subcortical areas

Some non-humans primates, such as chimpanzees or macaques, are able to use tools. Thus, monkeys have been a fruitful model for understanding the neural bases of tool use. Because tool use requires to integrate an external object into the motor plan, it presents a different degree of complexity in comparison to a free-hand action, namely an action performed with the bare hand. As for free-hand actions, tool use mostly involves the same interdependent components that are reaching and grasping phases (Gentilucci et al., 2004) supported by the dorsal stream (for a review and a meta-analysis, see Lewis, 2006). Nonetheless, beyond this similarity, tool use substantially differs from free-hand actions because using a tool requires to reach and handle an object with an external and functional object (i.e. the tool) controlled by the hand. This organization adds a different constraint onto the motor control system that can be observable at the behavioral, kinematic and neural levels. Are the same neurocognitive hubs recruited for an action with the bare hand and with the tool? Does tool use differently involve the manual reach-to-grasp dorsal stream?

From the study of intracranial recordings, tool use has been found to update the body and space representations (Iriki et al., 1996 and for a review, see Maravita and Iriki, 2004). The monkeys were required to use a long-held rake to retrieve piece of food. After using this tool, the response of visuotactile neurons located in the parietal cortex was modified. Indeed, as shown by previous studies (Colby & Duhamel, 1991; Leinonen et al., 1979), visuotactile neurons fired for both visual and tactile modalities when a visual target was approaching the body. Crucially, after using a tool, the bimodal neurons of monkeys fired when the visual targets approached the tool tip, as if the neurons' receptive fields shifted toward, or enlarged till to englobe, the functional tip of the tool. Interestingly, passive holding of the tool did not provoke such changes in the neuronal responses, suggesting that the updating of the spatial representation, taken as proxy of a change of the body schema, only occurs when the tool is actively manipulated.

The previous findings clearly put forward that the online control of tool use involves a different network than free-hand action. To further address this question, two monkeys were scanned by mean of a PET scanner while using long-held rake. The neural recordings of tool use were compared to the manipulation of a stick. Using a tool recruited a large network involving the left premotor cortex (i.e. both mF2 and mF5), the left intraparietal sulcus (IPS), the bilateral posterior portions of the inferior temporal cortices, the bilateral BG and cerebellum,

as well as the bilateral supplementary motor area (Obayashi et al., 2001). The authors mostly discussed these activations with respect to the previous findings on the updating of the body schema established after tool use. Given the presence of bimodal neurons, the IPS likely integrates both the somatosensory and visual inputs of the tool action, before sending it to the premotor cortex involved in specifying the action motor goal. The cerebellum is suggested to play a role in the reconstruction of an acquired body image built upon long-term memory for tool use (Obayashi et al., 2001). The BG and the SMA are rather involved in maintaining and updating the body representation throughout the spatiotemporal organization of the tool-use motor sequence. Lastly, the inferior temporal cortices are part of the ventral stream and involved in object recognition (Goodale & Milner, 1992; Mishkin et al., 1983; Ungerleider & Mishkin, 1982), so that the involvement of these regions in tool use is likely representing the updating of conceptual body representations. Overall, this mostly left lateralized network, is hypothesized to support the online sensorimotor transformations imposed by the embedding of the tool into the motor plan. For monkeys, these sensorimotor transformations imply the updating of the body representations allowing the precise guidance of the hand-held rake toward the distant food reward.

A long-held rake is a specific tool allowing to reach objects that are out of reach. However, tools might also subserve a different purpose. For instance pliers allow to finely reach an object that under certain circumstances is difficult to handle with the bare hand (i.e. too small or too fragile object). Pliers can be distinguished between classic and reverse pliers. Classic pliers involve parallel kinematics between the hand and the tool, whereas reverse pliers involve opposite kinematics (Fig. 14). Indeed, with reverse pliers when the hand is opening, the tool is closing. Albeit both classic and reverse pliers support a similar goal, different kinematic requirements are at stake, opening questions about the neural substrates encoding tool and hand kinematics. Such topic has been addressed in a study conducted in monkeys (Umiltà et al., 2008). Crucially, neurons located in monkeys' left mF5 and M1 areas, firing for the grasping component of free-hand actions, also coded for the aperture of the tool tip. The same mF5 neuronal pool discharged for the opening of both classic and reverse pliers, even though hand kinematics were opposite. Interestingly, a subset of neurons in M1 responded only to the hand configuration, regardless of the type of pliers used. Indeed, these neurons fired only when the hand was closing. Thus, these findings suggest the neurons of the monkey ventral premotor cortex encode the action goal rather than hand configuration during an action. Importantly,

these results also suggest that tool use can be incorporated into the body representations supported by the premotor cortex, in such a way pliers become fingers.

Figure 14: Normal and reverse pliers. A) The normal pliers' kinematics is congruent with the kinematics of the hand so that the tool is opened when the hand is opened. B) The reverse pliers' kinematics is incongruent with the kinematics of the hand so that the tool is closed when the hand is opened. From Umiltà et al., 2008.

One further way to evidence the neural network of tool use beyond fMRI and intracranial recordings, is sMRI. Indeed, learning a new task is known to impact the grey matter structure and these changes can be non-invasively estimated thanks to sMRI (Draganski et al., 2004). In a study (Quallo et al., 2009), three monkeys were intensively trained to use a long-held rake during two weeks and the structural modifications were measured at different time points. The results showed the grey matter changed mainly in the right hemisphere for the IPS, STS and second somatosensory area (SII) and at a lenient threshold in their left hemisphere homologues. Furthermore white matter changes were measured in the cerebellar lobule V. Again these findings stressed the role of areas involved in multisensory integration for tool use. According to the authors, the IPS is likely involved in the integration of visuomotor information during the grasping control with a tool (Iriki et al., 1996). SII is an area of tactile integration (Murray & Mishkin, 1984) and might support the incorporation of a tool into the body schema. The STS is at the interface of both the dorsal and ventral stream (Goodale & Milner, 1992) and might support more conceptual aspects about the tool-use task, such as tool recognition. Critically, these results also highlight the involvement of the two hemispheres for tool-use learning, while previous studies rather suggested a reliance over the left hemisphere during online control of a tool (Obayashi et al., 2001). In addition, the role of the cerebellum might subserve the acquisition of new motor skills and more specifically the integration of internal models about the novel tool (Imamizu et al., 2000).

To summarize, these findings in monkeys show the tool-use network is vast because supported by several cortical and subcortical areas. The core functional network for online control of a tool appears mainly supported by the left dorsal stream including both parietal and frontal areas. For instance, the left IPS integrates visual and somatosensory inputs in order to update the body representation, whereas the left premotor cortex specifies the action goal. In addition, the right frontoparietal homologues support tool-use learning. Tool use is also supported by the ventral stream and the bilateral posterior temporal cortices, whose function likely consists of processing tool conceptual representation. Furthermore, the subcortical areas

including the BG and the cerebellum are also involved in tool use. Their role is not clear but it has been suggested to subserve the execution of motor sequences or the integration of an internal model about the tool action.

2. The neural organization of tool use in humans

Nearly one decade after the seminal investigations in monkeys (for a review, see Jeannerod et al., 1995), the human neural bases of reach-to-grasp actions started to be investigated thanks to fMRI and TMS. The neural activity elicited was very close to the neural activity found in monkeys. Indeed, for a reach-to-grasp action, the anterior intraparietal sulcus (aIPS), putatively corresponding to the monkey's AIP, and the posterior intraparietal sulcus (pIPS), roughly corresponding to the monkey's MIP, were found active in human's parietal areas. Furthermore, the PMv, supposed to be homologue to the monkey's mF5, as well as the PMd, similarly considered as homologue to the monkey's mF2, were found involved within the frontal lobe. Thus, human reach-to-grasp activity relies on the dorsal stream encompassing a dorsomedial and a dorsolateral substream. In line with studies in monkeys, the human dorsal stream encodes the spatial representations supporting goal directed movements (for reviews, see Culham and Valyear, 2006; Filimon, 2010; Grafton, 2010; Davare et al., 2011). What is the role of this network when a tool has to be handled? Similar neural bases to monkeys but also interspecies differences might be expected for human tool use. Indeed, studies in monkeys mostly focused on the use of a long-held rake, whereas studies in humans have tested the neural bases for a larger set of tools. Furthermore, the investigations led on humans could be considered as more robust, given the larger sample tested thanks to the generalization of fMRI. In this section, we will first present behavioral evidence showing that tool use updates the body representations. Finally, we will highlight the neural bases of human tool use through both neuroimaging and neuropsychological investigations.

a. Tool use in humans induces plasticity and updates the body schema

Using a tool is a very specific action that goes beyond reach-to-grasp free-hand actions. Previously, from monkeys studies, we mentioned tool use is supported by stronger activations of both dorsal and ventral streams, as well as a greater spatial covering of the cortical surface in comparison to action without a tool (Obayashi et al., 2001). Furthermore, tool use can imply reverse kinematics of the tool with respect to the hand (e.g. reverse pliers). Yet, the action goal remains the same as for a pair of classic pliers, where the kinematics of the hand and the tool are seemingly. Behaviorally, when humans have to deal with a reverse mapping between the hand and tool kinematics, this results in a slower planning of the tool-use action (Massen & Prinz, 2007). Interestingly, fine analyses of movement kinematics did not show striking

differences between free-hand and tool-use actions requiring to handle a mechanical grabber (Gentilucci et al., 2004). Nonetheless, further evidence suggested that the control of the aperture was different between the tool and the hand, especially when the tool was not skillfully mastered (Itaguchi & Fukuzawa, 2014). Overall, these results show that tool use can present a certain degree of complexity that our brain has to deal with in order to rapidly perform a successful action. One mechanism that could account for these differences between tool-use and free-hand actions, is the need to incorporate the tool within the body schema. Using a tool puts forward an additional constraint onto the neural circuits supporting multisensory integration. Indeed, we previously mentioned parietal bimodal neurons in monkeys increased or shifted their receptive field after tool use (Iriki et al., 1996), thus inducing a change in space and body representations. Behavioral investigations in humans also suggested a remapping of the body and space representations after tool use. For instance, training for a short period of time (i.e. about 30 minutes) with a mechanical grabber slowed down the kinematics of subsequent free-hand movements, in such a way that the participants acted as if their arm was longer (Cardinali et al., 2009; Martel et al., 2021; for a review see Martel et al., 2016). Nonetheless, this idea of tool incorporation (also called embodiment) has been recently challenged by a fMRI study. Indeed, the neural activity elicited by the observation of tool-use actions was found more dissimilar to the free-hand neural activity for expert tool-users (i.e. litter picker) than novice tool-users (Schone et al., 2021). These findings were obtained from the analysis of brain areas previously known for their involvement in multisensory integration, like the left OTC (Brozzoli et al., 2011, 2012; Gentile et al., 2013) and left parietal cortex (Maravita & Iriki, 2004). The authors interpreted these patterns of neural dissimilarity as the lack of tool incorporation into the body representations. Indeed, according to them, expert tool-users because of their regular tool-use practice, should represent their hand more like a tool if the tool would have been incorporated. Instead the neural activity suggested the experts represented their hand less like a tool in comparison to novices. This absence of incorporation can be in part explained by the fact that the authors used a passive task, in which tool-use actions were visually presented and did not require any direct manipulation of a tool. Indeed, when visual information are discarded, the incorporation of the tool still happened, suggesting the somatosensory information are the most crucial for updating the body representations (Martel et al., 2019). Furthermore, when participants are asked to hold a tool, the integration of sensory information afferents at the level of the hand suggests the tool structure is incorporated within the body representations (Miller et al., 2018). This experiment revealed that participants were able to correctly localize different stroke sites over a tool, even though the same

mechanoreceptors were at stake for the hand holding the tool. This behavioral faculty is likely explained by the role of the somatosensory cortex, which produced a unique neural response depending on the stroke site over the tool. Overall, this set of evidence supports the idea of tool incorporation, especially when visual, tactile and proprioceptive modalities are involved. This incorporation is imposed by the requirement to integrate an external object, the tool, into the body representations. As revealed by previous studies in monkeys, this faculty of incorporation is likely supported by the plastic abilities of the left frontoparietal areas (Iriki et al., 1996; Umiltà et al., 2008).

b. Tool use in humans is supported by a cortical and subcortical network

- The left frontoparietal network

Neuroimaging studies testing the network supporting the use of a tool have been mainly performed thanks to fMRI. However, using a tool in a fMRI scanner is challenging because of the restricted space. To overcome this limitation, the first studies focused on pantomimes rather than actual use of tools. Pantomimes consist of reproducing the spatiotemporal features of a tool action but without a tool. Hence, to uncover the network supporting tool use, pantomimes neural activity was compared to the neural activity elicited by meaningless manual actions (e.g. finger tapping). The experiments implementing such a design, revealed that pantomimes specifically recruited the left IPS with the inferior and superior parietal lobules (SPL and IPL), as well as the PMd cortex (Choi et al., 2001; Moll et al., 2000). These left hemisphere areas were also preferentially activated regardless of the hand (i.e. right or left) used for pantomime, suggesting tool use is a left lateralized function. The neural substrates subserving pantomimes planning and execution have been considered separately (Johnson-Frey et al., 2005). The results showed planning to pantomime recruit left frontoparietal areas including the left SMG and left PMv. The execution is supported by the same core network in addition to the left SPL and left PMd, as well as the left prefrontal cortex. Interestingly, the right hemisphere was similarly activated than the left one for execution but not for planning. Again these activations did not depend on the hand used, because both right and left hand pantomimes exhibited a similar network, with a left frontoparietal dominance for planning and bilateral activation for execution. More recently, a study (Garcea & Buxbaum, 2019) considered the neural activities elicited for pantomiming tool use and for transporting (i.e. displacing) tools. In line with the previous studies, planning to pantomime tool use involved a left frontoparietal network

encompassing the left SMG, the left PMv that extends onto the insula, as well as the left pMTG. Whole brain connectivity analyses were performed with the left SMG as a seed. The left SMG connectivity was maximal with the left ventral ATL and left IFG for gesturing tool use, while for transporting a tool, the connectivity was greater with the left SPL and the bilateral fusiform gyri. This observation is consistent with the existence of two different pathways for processing respectively online sensory-information (i.e. tool transport) and object properties or conceptual knowledge (i.e. tool use).

Despite the space constraints in the fMRI scanner, a set of studies have tried to use designs that require the actual use of a tool. In a study participants were required to plan and execute actions with a large set of tools including a hammer, a pen, tweezers, scissors, a knife, a spoon, a screwdriver, a key, a lighter and a bottle opener (Brandi et al., 2014). The neural activity elicited when using these tools was compared to the use of non-functional objects (i.e. a set of cylindrical bars). In line with the pantomimes studies, tool use involved a left frontoparietal network for both planning and execution. However, the activations for planning were mostly confined within the left SMG and SPL, whereas the frontal cluster found in the PMd was relatively small (Fig. 15 top panel). For execution the entire left IPS was activated in addition to the SMG and the SPL (Fig. 15 bottom panel). Furthermore, more intense activations were observed in the frontal areas with the recruitment of both the PMd and PMv. The right hemisphere homologues of these areas also supported tool-use but to a smaller extent than the left hemisphere. The function of each of these neural hubs is still unclear but the parietal areas, with the left IPS, likely support multisensory integration involved in tool use (Iriki et al., 1996). Among the parietal areas, the function of the left SMG is still a matter of debate and could subserve the retrieving of knowledge about how to use a tool (Buxbaum, 2001) or conversely support technical reasoning regarding the way the tool has to be used (Reynaud et al., 2016). The left premotor cortex (i.e. PMv and PMd) might rather support the goal of the action (Umiltà et al., 2008).

Figure 15: The tool-use network. For each hemisphere, the neural activities elicited by tool-use planning (top panel) and tool-use execution (bottom panel) are reported. The color scale indicates the activation intensity with the range of the t-values from low values in dark red to high values in white. MFG: middle frontal gyrus; PMd: dorsal premotor cortex; PMv: ventral premotor cortex; AIP: anterior intraparietal sulcus; SMG: supramarginal gyrus; SPL: superior parietal lobule; LOC: lateral occipital cortex; FG: fusiform gyrus; IOG: inferior occipital gyrus; MOG: middle occipital gyrus; MTG: middle temporal gyrus. From Brandi et al., 2014.

Further neuroimaging studies have been performed, giving a clear insight about the core network involved in tool use. Most of these studies have been either summarized in reviews and meta-analyses (Ishibashi et al., 2016; Johnson-Frey, 2004; Lewis, 2006; Peeters et al., 2013; Reynaud et al., 2016; Valyear et al., 2017). These studies confirm that the tool-use network is mainly left lateralized and supported by the free-hand reach-to-grasp network. However, using a tool appears to recruit this stream with stronger intensity than free-hand actions. Furthermore tool use also appears to recruit additional areas all around the core network supporting free-hand actions (Fig. 16). While free-hand actions are mostly supported by the left IPS and the PMd (and also PMv, see Filimon, 2010), tool use involves a larger network encompassing y further resources within the SPL and IPL as well the PMv.

Figure 16: Tool-use and free-hand grasping networks. (A) Left panel: A meta-analysis of 11 neuroimaging studies involving actual tool use and pantomimes. Right panel: A meta-analysis of 16 neuroimaging studies involving a grasping movement with free hand. From Valyear et al., 2017. (B) The network from a meta-analysis of 70 contrasts from 59 tool-relevant studies including action, naming and recognition. From Ishibashi et al., 2016.

Does tool use recruit brain regions that are specifically devoted for this purpose? From neuroimaging meta-analysis the response seems that it does. However the involvement of the SPL, IPL or PMv is also found for free-actions but might represent computations whose neural intensity is smaller than tool use. To address this issue, a study compared the neural patterns elicited for planning to reach or grasp an object with either a tool (i.e. reverse pliers) or the free hand (Gallivan et al., 2013). Testing the differences between neural patterns required to take advantage of multivariate rather than univariate analysis differences. To evidence these neural resources, the authors employed a multivariate technique called classification-based multivariate pattern analysis (MVPA, see methodology box 5). As a first step of analysis, the authors identified a general network activated for both tool use and free hand-actions thanks to univariate analysis (i.e. based on the signal intensity). Within this network, the authors selected ROIs in the left hemisphere based on their previously documented contribution to reach-to-grasp actions. Overall, several classifiers were trained and tested on the neural patterns elicited by planning to reach or grasp an object: one was trained and tested on the reaching and grasping neural patterns only for tool use, another only for free-hand actions and a last one was trained with the data from one effector (i.e. hand or tool) but tested on the other effector. In other words, this latter classifier aims to identify the neural hubs where the neural patterns for reaching and grasping are shared across effectors, so that reaching or grasping can be decoded regardless of

the effector used. Interestingly, the cross-effector classification approach revealed that neural activity for planning of reaching or grasping can be decoded regardless of the effector used within the PMd, the PMv, and both the middle and posterior IPS. These findings suggest the neural patterns for reaching or for grasping are similar across the two effectors within these areas. Such findings corroborate previous studies in monkeys (Umiltà et al., 2008) and show the premotor cortex encodes the goal of the action (i.e. reach or grasp) regardless of the effector (i.e. tool or hand) used. Indeed, because reverse pliers were used as a tool, the hand kinematics differed between tool use and free hand but the action goal remains the same. In addition, the posterior portion of the IPS, which is a multisensory area, may encode common representations about the action goal rather than information about the different muscles to mobilize for an action. This specification about the muscles to recruit might be performed by the aIPS and M1 as suggested by the significant classification of both tool and free-hand actions but the nonsignificant cross-effector classification. Again these findings clearly corroborate what was known in monkeys, such as the findings showing that the pool of neurons in M1 responded only to hand closing (Umiltà et al., 2008). Of further interest, the SMG only decoded the neural activity elicited by tool use but not by manual actions, suggesting this area is specifically devoted for tool use. The SMG might be the site where tool use knowledge is retrieved (Buxbaum, 2001). A similar result was found in the left pMTG, which according to Gallivan and colleagues (Gallivan et al., 2013) might reflect the sensory prediction of upcoming actions. Finally, two regions decoded only the neural activity for free-hand actions: the extrastriate body area (EBA) and the superior parieto-occipital cortex (SPOC). According to the authors, the EBA and SPOC support visual-perceptual processing of arm and hand movements (see Orlov et al., 2010), as well sensory prediction mechanisms. These results are of particular interest and help to better understand how tool use is supported by the brain with respect to the network involved in free-hand action (Fig. 17).

Figure 17: The frontoparietal action network. The regions supporting tool-use actions only are represented in blue. The regions supporting free-hand actions only are represented in red. The regions supporting both tool-use and free-hand actions are represented in pink and purple. Crucially the purple network represent the regions where similar processes occur regardless of the effector used, likely to support the encoding of the action goal. The pink network represents regions where different computations occur, likely to support the recruitment of different muscles because of different hand kinematics between the tool and the free-hand action. From Gallivan et al., 2013.

Methodology box 5: The classification-based MVPA

The classification-based MVPA is a multivariate technique, which like the RSA, considers the spatial organization of the neural activations rather than differences in terms of signal intensity. Conversely to the RSA, the classification-based MVPA does not measure a neural distance between the functional activations. Instead this technique consists of classifying neural patterns across different conditions of interest. Using machine learning algorithms, a classifier is trained onto a dataset and tested over an independent dataset of neural patterns never used for the training. Originally this technique has been implemented to study the neural representation of various object categories within the occipital cortex. Indeed, object categories usually elicit similar intensity level but the spatial organization of the neural activity can differ between objects from different categories, such as pictures of faces and houses (Haxby et al., 2001). Let us take an example with a classifier trained to classify neural patterns elicited by the perception of pictures of a bottle or a shoe (Norman et al., 2006). Once trained the classifier is then tested on new neural patterns of bottle and shoe pictures that did not serve for the training. The classifier will assign these novel neural patterns to one category. This assignment can be correct or wrong, in such a way it is possible to estimate the quality of the classification by measuring the total number of correct classifications over the total number of category assignments performed (for the whole procedure, see Fig. 18). Neural patterns are considered different if the classifier accuracy is significantly above the chance level, corresponding for a design including two categories to 50%. When the classification accuracy does not differ from chance, it means the neural patterns for the two conditions are indistinguishable from each other, suggesting the lack of neural activity difference.

Figure 18: The classification-based MVPA. The procedure can be summarized as follows: A) Pictures of a shoe and a bottle are presented and the neural activity elicited is recorded at the level of the whole brain. A set of voxels, called *feature*, is selected. B) The data is organized into a training set and a test set that are independent (i.e. different runs or subjects). Noteworthy the grey and white circles represent the neural activity intensity. C) The feature selected are then fed to a classifier for the training allowing to identify a decision boundary. D) This decision boundary represented by the red dashed line allows to classify the feature for the test set. Noteworthy, a feature can be misclassified as depicted by the blue dot, corresponding to neural activity elicited by the shoe picture, but classified by the classifier as a pattern of activity matching the activity elicited by a bottle picture. Adapted from Norman et al., 2006.

What may be the specific role of the SMG for tool use? Both univariate and multivariate neuroimaging studies put forward the specific contribution of the left SMG for tool use. The SMG is a gyrus localized within the anterior part of the IPL and localized below the IPS. Interestingly, the studies conducted in monkeys do not reveal any activation within the IPL in the monkey's brain (Obayashi et al., 2001), while the rest of the network remains consistent with the human tool-use network. The lack of activity within this area may be explained because it is a very rudimental structure in monkey's brain (see Geschwind, 1965). This assumption is still a matter of debate but of course raises questions about a potential link between the evolution of the IPL and tool-use behaviors in humans (Iriki & Taoka, 2012). In order to evidence the human SMG specificity for tool use, both monkeys and humans were asked to observe free-hand and tool-use actions in a scanner. In both species, the observation of actions activated bilaterally the IPS, the PMv and the occipitotemporal cortices. In humans, the observation of actions with a tool additionally involved a cluster of activity in the anterior part of the left SMG (aSMG), while no activity in the IPL was elicited in monkeys (Peeters et al., 2009). These findings were later replicated in humans showing that the aSMG was also activated for the observation of actions without a tool but mimicking the tool kinematics (Peeters et al., 2013). Overall, these results suggest the SMG is specifically devoted to tool-use actions and may encode visual information about the kinematics of a tool action.

The seminal neuropsychological investigations about tool use helped to understand the contribution of the SMG. About one hundred years before the use of neuroimaging, the neural network supporting tool use was quite well identified thanks to post-mortem neuropsychological investigations. Indeed, apraxics patients exhibited a loss of praxis or tool-use behaviors after a cerebral vascular accident. Apraxia is highlighted by the patients' difficulty to use their limb for a set of actions that most often involve a tool. The seminal investigations led by Hugo Liepmann have suggested the existence of at least three types of apraxia, respectively called ideational apraxia, ideokinetic apraxia and limb-kinetic apraxia (Liepmann, 1908, 1920). Later the ideokinetic apraxia has been renamed ideomotor apraxia, a terminology that continues to be used nowadays (Goldenberg, 2003). Each of these apraxia types is characterized by different behavioral impairments provoked by lesions affecting brain areas within the left hemisphere (Fig. 19).

Figure 19: The three apraxia types. Lesions to the junction of occipital, temporal and parietal lobes (region 3) result in ideational apraxia. Lesions to the IPL result in ideomotor apraxia (region 2). Lesions to the precentral and postcentral gyri result in limb-kinetic apraxia (region 1). F. sup.: superior frontal gyrus; F. med.: middle frontal gyrus; F. inf.: inferior frontal gyrus; Op.f.: frontal operculum; Op.R: Rolandic operculum; C.a. anterior central

gyrus; Cp: posterior central gyrus. a.sm: anterior supramarginal gyrus. O.s.: superior occipital cortex. O.m.: middle occipital cortex; O.inf. inferior occipital cortex; Tsup.: superior temporal gyrus; Tm.: middle temporal gyrus; Tinf.: inferior temporal gyrus. From Johnson-Frey, 2004 and inspired from Liepmann, 1920.

Limb-kinetic apraxia designates the inability to make precise, independent and coordinated movements with the fingers and the hand after a lesion affecting the motor and premotor areas (Park, 2017). Ideational apraxia, also called conceptual apraxia refers to an inability to name a tool and also correctly perform tool-use action sequences, so that patients can use a comb to brush their teeth or a toothbrush to brush their hair (Ochipa et al., 1989). Patients' lesions are localized at the junction of parietal, temporal and occipital lobes. Ideomotor apraxia arises after a lesion of the left IPL and in particular the SMG. The ideomotor apraxia patients have difficulty in producing motor skills retrieved from memory, such as symbolic gestures (i.e. waving their hand for a goodbye) and using a tool or pantomiming the use of tool. Importantly, this deficit is generally not attributable to gross sensorimotor impairments or cognitive deficits (Buxbaum, 2001). The ideomotor apraxia behavioral impairments seem to indicate that the SMG is specifically dedicated to storing manipulation knowledge (Buxbaum, 2001). In other words, if patients with ideomotor apraxia are impaired for tool-use knowledge, it is mainly because the representation about how to perform a tool action has been erased. This latter view about the role of the SMG for tool use is still a matter of debate (Buxbaum, 2017; Osiurak & Badets, 2016). The left frontoparietal network processes the online sensorimotor transformations imposed by the tool to support the realization of the action goal (Lewis, 2006). With respect to these computations, the role of the SMG has also been suggested to support technical reasoning about how to use a tool (Osiurak et al., 2011; Reynaud et al., 2016). Noteworthy, limb apraxia arises from lesions to the left hemisphere and corroborates the left-hemisphere dominance observed in functional neuroimaging (Liepmann, 1908, 1920). The impact of right hemisphere lesions on the ability to use a tool is less known. Nonetheless, some studies revealed lesions over the right frontoparietal network might cause limb apraxia especially for gestures imitation (Goldenberg, 1996, 1999). However, the deficits observed in those patients might result from difficulty with visuospatial processing (Dressing et al., 2020). Taken together, the neuroimaging and neuropsychological investigations inform us about the specific role of the left frontoparietal stream in tool-use actions.

- The left occipitotemporal junction

In previous section, we mentioned ideomotor apraxia is associated with knowledge deficit about how to use tools, whereas ideational apraxia rather impacts the conceptual association between a tool and its function. The ideational apraxia impairments are associated with lesions localized to the junction of the occipital, temporal and parietal lobes. Initial investigations of the visual streams already suggested both ventral and dorsal streams interacted through regions at their interface like the pSTS (Goodale & Milner, 1992). Interestingly neuroimaging studies we presented above reported activations of the OTC (see Fig. 15, 16 and 17) with the involvement of the pMTG (i.e. posterior temporal cortex) or the lateral occipital cortex (LOC, i.e. anterolateral occipital cortex). The role of this region has been associated to tool recognition. Indeed, previous neuroimaging work revealed the pMTG and also the medial fusiform gyrus respond to the observation of pictures of tools, tool naming and even reading the name of a tool (Chao et al., 1999; Martin et al., 1996). As we discussed before, these conceptual representations about tools are grounded into the sensorimotor system involved in the perception of tool motion and tool shape (Beauchamp & Martin, 2007; Ishai et al., 1999). Previously, a review (Johnson-Frey, 2004) about tool use assigned the OTC only to conceptual processing but given the strong involvement of this area for actual use its role might be multiple. Indeed, the OTC is also involved in multisensory integration (Brozzoli et al., 2011, 2012; Gentile et al., 2013). Given the involvement of the OTC for conceptual and sensorimotor modalities, it might imply a functional interaction between these two modalities. For instance, a study recently revealed that novel tools receiving a verbal label were facilitated for their use in comparison to unlabeled tools (Foerster et al., 2020). This behavioral effect was accompanied by electrophysiological modulations occurring at the level of the centro-occipito-temporal circuits where a decrease of the power in the sensorimotor beta-band was observed. This finding supports the assumption that the OTC is a zone of convergence for tool conceptual and sensorimotor processing.

- The subcortical areas

Extensively studied for their role in motor functions, the BG have also been reported in the neuroimaging studies of tool-use pantomime (Choi et al., 2001; Garcea & Buxbaum, 2019; Johnson-Frey et al., 2005) in humans, but also in monkeys for online tool use (Obayashi et al., 2001) and during tool-use learning (Yamazaki et al., 2016). The role of the BG for tool use

likely supports the realization of a motor sequence more complex than for free-hand movement (Choi et al., 2001). This interpretation may come from studies revealing the role of the BG in the action sequence (Lehéricy et al., 2005), as well as in *chunking* processes (Graybiel, 1998; Wymbs et al., 2012). Chunking refers to the ability to combine motor elements into an integrated unit in order to facilitate movement production. This integration can be serial, such as a single motor act (i.e. a finger tap) is associated with another one and so on. This organization can also include a further hierarchical complexity with the implementation of a recursive rule, strengthening the interdependent relation between each motor act. The implementation of such rule seems to specifically rely on the BG (Martins, Bianco, et al., 2019), even though previous evidences (Koechlin & Jubault, 2006) and theoretical works (Fadiga et al., 2006; Maffongelli et al., 2019; Pulvermüller & Fadiga, 2010) pointed towards a role the left IFG for processing more complex hierarchical motor sequence. Hence, we can speculate that when the BG activate during tool use, it might reflect the processing of specific hierarchical rules imposed by the tool in order to successfully combine the action sub-components. Furthermore neuropsychological studies have also reported tool use deficits in patients with lesion to the BG (Agostoni et al., 1983) or lesion affecting both the BG and the surroundings white matter tracts (Pramstaller et al., 1996). However, because the lesions are rarely focal, it is possible the observed deficits might rather be explained by involvement of a larger network.

In addition to the BG, the cerebellum has also been reported to be active during tool use, especially for tool-use pantomimes (Choi et al., 2001; Johnson-Frey et al., 2005) and tool-use learning (Imamizu et al., 2000). For instance, after participants learned a new spatial relation rule between a computer mouse and its cursor (i.e. rotational perturbation), they exhibited higher activity within the phylogenetically recent cerebellar circuits near the posterior superior fissure (Imamizu et al., 2000). These results open the possibility that learning a new sensorimotor transformation rule to use a tool does not only rely on the cerebral cortex but also involves the cerebellum. A pantomime study rather suggests that the cerebellar involvement reflects the increased difficulty imposed by tool use (Choi et al., 2001). Indeed, tool use in comparison to simple hand movements likely involves multi-joint movements and also a different integration of proprioceptive information, for which the role of the cerebellum might be critical (Thach et al., 1992). However, a more recent study did not find any specific contribution of the cerebellum for proprioceptive integration related to tool use with respect to manual actions (Pazen et al., 2020). Other researchers proposed that the contribution of the cerebellum might be due to the storage and retrieval of tool-use knowledge through the numerous

projections the cerebellum has with the parietal cortex (Imamizu et al., 2000, 2003). Studying the role of the cerebellum for tool use might be critical for future studies, especially since the recent discovery that the cerebellar surface in humans represents 80 % of the cerebral surface, whereas in monkeys this value only reaches 50 % (Serenio et al., 2020). This difference is likely explained by different evolutionary consequences and for that reason, it is very likely that the phylogenetically recent parts of the cerebellum, as for the cortex, evolved in order to support the refined human abilities such as tool use or language. Nonetheless, the contribution of the cerebellum for tool use remains elusive, indeed to the best of our knowledge there is no clear evidence of patients with cerebellar lesions that present a deficit in tool use such as in limb apraxia. Thus the contribution of the cerebellum might only subserve the general learning process and the retrieval of learned internal models.

Taken together, tool use is not only supported by the left frontoparietal areas. Indeed, the ventral stream is also critical for tool use and subserve visual recognition of tools, as well as conceptual processing about tools. Furthermore, subcortical areas such as the basal ganglia and the cerebellum are also crucial for tool-use but the purpose of their contribution remain largely unknown.

On the similarities between tool use and language

The suggestion of the similarity between tool use and language appeared well before the first archeological and neuroimaging records. Indeed, since the nineteenth century, Charles Darwin was fascinated by the level of sophistication of the motor and language abilities in humans and wrote: “*A man-like animal who possessed a hand and arm sufficiently perfect to throw a stone with precision to form a flint into a rude tool, could, it can hardly be doubted, with sufficient practice make almost anything, as far as mechanical skill alone is concerned, which a civilised man can make. The structure of the hand in this respect may be compared with that of the vocal organs, which in the apes are used for uttering various signal-cries, or, as in one species, musical cadences; but in man closely similar vocal organs have become adapted through the inherited effects of use for the utterance of articulate language*” (Darwin, 1871, p.133-134). Then, why might tool use and language be considered similar beyond the level of sophistication of the functions? To provide elements of response, we will first review a set of theoretical accounts or empirical contributions suggesting a link between tool use and language in general. Then in the next section we will go into deeper details by characterizing the potential link between tool use and each linguistic component of interest in the present thesis, which are phonology, semantics and syntax.

1. General links between tool use and language

Since Charles Darwin’s observation, it has been suggested that tool use and language may have co-evolved. The human brain may have evolved in association to our proficiency to use and make tools, allowing the emergence of a *language ready brain* (Ambrose, 2001; Ponce de León et al., 2021). Indeed, the cortex (Ponce de León et al., 2021) but also subcortical regions like the cerebellum (Serenio et al., 2020) have expanded during the course of human evolution. As previously stated, tool use implies a specific constraint on the cortical and subcortical areas, resulting in the increase of the neural resources in both gray and white matter after a short period of learning (Quallo et al., 2009). Would it thus be possible that the expansion of cortical circuits observed at the ontogenetic level have transferred from one generation to another? In others words, do isolated structural modifications of the brain structure have led to modifications of the brain structure at the phylogenetic level? There is no direct evidence in favor of such a process but it has been previously suggested as a possible scenario (Iriki & Taoka, 2012). Crucially, these novel resources have been also suggested to form a neural niche for the

emergence of new cognitive function such as language (Iriki & Taoka, 2012). The reuse of neural circuits devoted to a specific function and progressively reoriented towards a new function have also been proposed with the *neural recycling* hypothesis (Anderson, 2016; Dehaene & Cohen, 2007). Neural recycling would have occurred for the emergence of functions that are culturally recent in humans such as reading. Reading is a pretty recent ability (i.e. writing appears about 3400 years ago, see Walker, 1987) and until recently, even in our western societies, a small part of the population was able to read. Because of its recentness, reading may be anchored in different structures originally subserving a different function. The role of brain plasticity for absorbing any kind of cultural evolution is likely crucial. A cultural acquisition will find its neural niche in brain circuits that are sufficiently close and plastic to be reoriented towards a novel use. The evolutionary older neural circuits are invaded by novel cultural objects but their prior function is not totally erased, resulting in the sharing of neural resources. Considering reading, this cultural evolution has likely appeared because of the recycling of neural circuits found within the ventral stream in order to facilitate the recognition of language abstract symbols (Dehaene & Cohen, 2007). A set of cognitive functions in human may have evolved similarly, among them language and tool use. Albeit these functions are older than reading, it has been suggested that primates may have a pre-existing system that has evolved by neural recycling over the course of human evolution (Iriki & Taoka, 2012). For instance, in co-evolution scenario between tool use and language, we can speculate the tool-use behavior may have been supported by the action-specific dorsal pathway, then recycling and forming novel neural niches to deserve different purpose, such as language. In turn, language recycled neural circuits resulting in the creation of a new neural niche for more complex and refined tool-use behaviors.

This notion of reciprocal influence between novel cultural objects, such as tool use and language has likely been critical in human evolution. In a behavioral study (Morgan et al., 2015), the efficacy of stone tool-making transmission was evaluated along chains of humans using five different transmission mechanisms, ranging among others from simple imitation to verbal teaching. Critically the quality of the transmission was better for verbal teaching than imitation. Interestingly, archeological records suggest that older stone tool technology, such as the Oldowan tool made in the Morgan et and colleagues' experiment, followed a stasis for about 700,000 years before the emergence of more advanced technologies such as the Acheulean technology about 1.5 million years ago (Mya; see Lepre et al., 2011). For Morgan and colleagues, this stasis resulted from the reliance on low-fidelity social transmission like

imitation, before the emergence of teaching with proto-language that may have been the prerequisite for the emergence of the more advanced Acheulean technology (Morgan et al., 2015).

Beyond the archeological records (Ambrose, 2001; Ponce de León et al., 2021), it has been suggested that, because of their co-evolution history, tool use and language may share neural resources in the modern human brain. The link between tool use and language has been extensively discussed from neuroimaging studies focusing either on language or action (Stout & Chaminade, 2012). However, beyond the suggestion, this link remains largely unexplored. To the best of our knowledge, only two studies have endeavored to uncover shared neural resources between tool use and language. In a first study, in a fMRI scanner, the participants were asked to execute a tool-use task and language perception task requiring to listen a story. The results revealed overlapping neural activity between the two tasks within the left IFG *pars opercularis* (Higuchi et al., 2009). Although these results appear exciting, there are in our opinion some methodological limitations that preclude the possibility to generalize the present results to the brain working. Indeed, the tool-use neural activity was obtained from a comparison with a low-level baseline consisting in passively holding the tool. This contrast prevents the possibility to clearly identify the voxels involved in tool use with respect to a manual action without a tool. Furthermore, the language task used prevents the possibility to identify, among phonology, semantics and syntax, which linguistic component is the most susceptible to explain this overlap. In our opinion, considering the contribution of each linguistic component to the overlap with tool use is of major interest. Noteworthy, the results by Higuchi and colleagues were obtained from a ROI analysis approach including only the left IFG, preventing the possibility to test whether different brain regions are involved in the overlap.

In the second study (Uomini & Meyer, 2013), the participants were asked to make a stone tool as our ancestors did (i.e. an Acheulean handaxe) in one task and, in another task they had to perform cued verb generation. During these tasks performed separately, participants' neural activity was recorded by the mean of functional transcranial Doppler ultrasonography, allowing to estimate changes in the blood flow at the level of the probes (or sensors). The hemodynamic response for the two tasks correlated and the authors interpreted this common blood flow signature as evidence of shared neural resources (Uomini & Meyer, 2013). However, the interpretation of shared neural resources appears too optimistic to us given that transcranial Doppler ultrasound has poor spatial resolution, allowing to record the blood flow in each hemisphere without specifically identifying the neural sources of these hemodynamic

modulations. Furthermore, the authors did not control whether this correlation could be explained by confounding factors, such as the involvement of more attentional resources to achieve a large set of tasks not only restricted to tool use and language.

Beyond these attempts to evidence shared neural resources between tool use and language, a recent behavioral study found very encouraging results regarding the link between tool use and language (Brozzoli et al., 2019). In this experiment, the participants were assessed on a tool-use task and a sentence production task. The tool use task required participants to insert pegs on a board by the mean of pliers and the linguistic production task required them to form a sentence in a prompted syntactic form from three words. The performance in the tool-use task was predictive of the linguistic production abilities, while the same motor task performed with the bare hand was not. Furthermore, as an additional control the participants performed a linguistic repetition task, requiring to repeat a sentence. Tool use was not predictive of the sentence repetition performance (Brozzoli et al., 2019). These results suggest the existence of a shared cognitive component between tool use and language. Given that tool use was predictive of linguistic production abilities but not predictive of sentence repetition abilities, this shared component might be a shared form of syntax rather than shared executive processes involving, for instance, working memory.

These studies are encouraging to explore the existence of shared neural resources between tool use and language. However because of the methodological approaches used so far it is difficult to fully decipher this link. Indeed, we think it is important to study the overlap between tool use and each of the linguistic component that are phonology, semantics and syntax. The contribution of each of these linguistic components and their relations with tool use is likely different, with for instance distinct circuits involved. These circuits may be found within the IFG, the IPL and the posterior temporal lobe as suggested in a previous review (Stout & Chaminade, 2012). To fill this gap, we aim to test the existence of shared neural resources between tool use and phonology, semantics and syntax separately. To show the relevance of such a choice, we will review evidence showing that tool use and each of these linguistic components might share computational functions, as well as neural resources.

2. Tool use and phonology

Although the similarities between tool use and phonology are not striking at first glance, these two functions require integration of sensory information. Indeed, phonology participates

in the perception of the smallest relevant units for language (Lieberman et al., 1957). In addition, tool use involves the integration of tactile all along the tool structure (Miller et al., 2018), as well as multisensory integration of visual and tactile information (Iriki et al., 1996). This perception first relies on the primary sensory areas respectively coding tactile, visual or auditory information in distinct neural circuits. However, both speech and tool use require the contribution of additional circuits aiming to refine the processing of these sensory information. This additional sensory processing most often occurs in the multisensory integration territories found within the left IPL for phonology (Raizada & Poldrack, 2007) or tool use (Iriki et al., 1996). Furthermore, the left IPL is one of the brain regions which cortical surface has likely expanded over the course of human evolution (Iriki & Taoka, 2012; Ponce de León et al., 2021), leaving the opportunity for communication abilities to recycle these novel circuits in order to support language emergence. An evolutionary process like neural recycling might explain why the left IPL is an area of convergence for multiple sensory signals, participating to various multisensory transformations (Serenó & Huang, 2014). However, it is not clear whether the IPL holds a convergence zone where sensory information for tool use and speech are processed. For instance, it has been suggested similar computational functions for tool use and language (Stout & Chaminade, 2012). However, these computations would occur in distinct neural circuits of the left IPL, mostly because each process involves different effectors, namely the upper limb for tool use and the vocal tract for language (Stout & Chaminade, 2012). For instance, humming a melody and playing it on the piano involve close but separated clusters in the parietal cortex: Spt area for humming and aIPS for piano (Pa & Hickok, 2008). Phonological processing is not only restricted to the left IPL but also involves the left motor and premotor areas (Wilson et al., 2004), with activations following a somatotopic gradient (Pulvermüller et al., 2006). Among the premotor areas, the left IFG is thought to be part of the auditory articulatory network (Hickok & Poeppel, 2007) but also appears critical for the perceptual phonological processing (Poldrack et al., 1999). Given the involvement of the left IFG in tool use (Brandi et al., 2014) a potential overlap may occur between the two functions. Overall, some uncertainties remain regarding the existence of shared neural territories between tool use and phonology. This issue has still to be explored and is the foundation for our first hypothesis (Fig. 20 in blue).

First hypothesis:

Tool use and phonology share neural resources within the left IFG and left IPL.

3. Tool use and semantics

The existence of shared neural resources between tool use and semantics has been suggested by a large range of studies. Given the predictions of the embodied cognition theory, the semantic category that is suggested to present more similarities with the tool-use network is obviously the category of tool nouns or more generally categories referring to actions. For instance, tool conceptual processing involves cortical territories within the left posterior temporal cortex also known for its role in the perception of artifacts motion (Chao et al., 1999). Furthermore, other regions, such as the left IPL, known for processing tool function knowledge, or the left IFG for the implementation of action goal are also involved in conceptual processing of tool nouns (Cattaneo et al., 2010; Chao & Martin, 2000). Nonetheless, one of the main limitations of the aforementioned studies relies on the absence of a direct evaluation of the tool-use network. In others words the authors made the assumption that the network observed for processing conceptual information about the tool in their experiment is the same network as the one underlying action with a tool without directly measuring it. Internal validation with empirical evidence would much strongly sustain these assumptions, given that neuropsychological studies seriously challenged this view (for reviews, see Mahon & Caramazza, 2008; Papeo & Hochmann, 2012). Furthermore, a meta-analysis of neuroimaging studies involving tool use or conceptual processing about a tool (i.e. naming and recognition tasks) did not reveal any shared neural resources (Ishibashi et al., 2016). While the left frontoparietal areas were involved in tool use, conceptual processing about tools rather recruited ventral territories with the left OTC as well as a cluster in the left IFG found ventrally of the tool-use cluster. This organization suggests a separation between a dorsal stream for tool use and a ventral stream for conceptual processing about tools (Johnson-Frey, 2004). Nonetheless, functional interactions are suggested within these two streams (Johnson-Frey, 2004). Interestingly the left IFG, left OTC and left IPL are regions that have been suggested to have dramatically increased in association with the refinement tool making technologies during human evolution, opening the possibility for these novel resources to be recruited for a different purpose, such as conceptual semantic processing (Larsson, 2015). However, the existence of shared neural processes between tool use and semantics lacks empirical evidence. This question is addressed by our second hypothesis (Fig. 20 in red).

Second hypothesis:

Tool use and semantics share neural resources within the left IFG, left OTC and left IPL.

4. Tool use and syntax

Why may using a tool use be considered a syntactic process? Actions are hierarchically organized and require to associate action sub-components into a correctly organized motor sequence. Empirical evidence suggests that goal-directed actions towards an object are organized into a motor sequence (Jeannerod, 1999; Jeannerod et al., 1995). This motor sequence might present similarities both at the behavioral and neural levels with linguistic processing when requiring to handle the structure of a sentence. An action involving a tool is more likely to uncover this relation and highlight a hierarchical organization than an action with the free hand. Indeed tool use adds a further level that has to be embedded into the motor plan. As a metaphor, embedding a tool within a motor sequence has been suggested to correspond to the embedding of a relative clause within a main clause for language (Greenfield, 1991; Pulvermüller, 2014; Pulvermüller & Fadiga, 2010). To better illustrate this, we can take the following action performed with the free-hand as an example [*move your hand [grasp a peg and insert the peg] move back your hand*]. We can consider this action is hierarchically organized because a grasp-to-insert component is embedded within a reaching component. Now let us consider the same sequence performed with a tool, such as the sequence becomes [*move your hand [grasp a tool [grasp a peg and insert the peg] release the tool] move back your hand*], this sequence implies a further level imposed by the use of the tool. Overall, the sequence with a tool becomes more hierarchically organized than the sequence with the free hand.

Given that both motor actions and sentences can be hierarchically organized, it is possible that syntactic processing for language is embodied within the sensorimotor network responsible for planning hierarchically organized motor actions, or at least that similar neural resources could be at stake for supporting a supramodal syntactic function. This possibility has been extensively discussed in a series of theoretical work (Pulvermüller, 2014; Pulvermüller & Fadiga, 2010; Roy & Arbib, 2005). Interestingly, this link has also been suggested to be particularly prominent between tool use and syntax (Greenfield, 1991; Pastra & Aloimonos, 2012; Steele et al., 2012; Stout & Chaminade, 2012). Indeed, as we mentioned, using a tool results in planning a more complex motor sequence than for a simple reaching task with the bare hand. Similarly to syntax in language, where words are combined together, a parallel has been proposed for tool-use actions, where external objects has to combine together (Greenfield, 1991).

Until now there is no evidence to our knowledge showing that tool use might share neural resources with the most complex syntactic structures in language, but previous evidence

we already mentioned are encouraging (Higuchi et al., 2009) and invite to explore this hypothesis. Which neural resources can be shared between tool use and syntax? Processing of hierarchical structures in language clearly points toward the role of the left IFG (Just et al., 1996; Walenski et al., 2019) and the BG (Moro et al., 2001; Teichmann et al., 2015), two regions susceptible to be also recruited by hierarchically organized motor actions with the free-hand (Koechlin and Jubault, 2006 for IFG; Wymbs et al., 2012 for BG) or with a tool (Choi et al., 2001 for BG; Brandi et al., 2014 for IFG). Again the role of evolution in the emergence of such a shared network is likely non negligible (Stout et al., 2021). Interestingly, from an ontogenetic perspective, it has been proposed that combinatorial behaviors with objects occur within the same developmental period (i.e. from 1 to 2 years old) than combination of words to form phrases or combination of speech sounds to form words (Greenfield, 1991). Interestingly the development of these abilities is suggested to occur within the same neural area corresponding to the left IFG until the child is two years old (see Greenfield, 1991). From this age, the left IFG starts to be specialized and the dorsal part of the left IFG becomes specialized for action, whereas its ventral part plays a major role for processing language (see Greenfield, 1991). Because much has to be explored in this domain, we tested the existence of links between tool use and syntax at the neural (Fig. 20 in green) and behavioral level, by addressing respectively a third and a fourth hypothesis.

Third hypothesis:

Tool use and syntax share neural resources within the left IFG and the BG.

Fourth hypothesis:

At the behavioral level, tool use and syntax reciprocally impact each other.

Figure 20: The hypothetic shared network between tool use and language. Expected overlap for tool use and phonology in the left IFG and left IPL (in blue), for tool use and semantics in the left IFG, left OTC and left IPL (in red) for tool use and syntax in the left IFG and the BG (in green).

Chapter 2

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Experimental contribution: Tool use, semantics and phonology¹

¹ The paper presented is entitled *The tool-use cortical network contributes to semantic but not phonological neural representations* and is currently in preparation.

The tool-use cortical network contributes to semantic but not phonological neural representations

Abbreviated title: The link between tool use and language

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Abstract

Tool use and language are two highly refined human abilities. Scholars suggested they co-evolved, thus resulting in neural commonalities. We recently provided evidence of shared neural resources between tool use and syntax. However, the debate is still open on whether phonology and semantics also recruit neurofunctional supplies common to tool use. Here we tested the hypothesis that activity within the tool-use network contributes to phonological and semantic representations. To this aim, we identified the tool-use network by asking twenty participants (10 females) to use a tool, or the bare hand as control, to move pegs on a board, in the fMRI scanner. To study phonological and semantic activations, in different runs, the same participants had to identify speech sounds from a 5-step continuum between /ba/ and /da/, and underwent a semantic priming task with animal and tool nouns. Through a series of representational similarity analyses we tested whether activity in tool-use clusters contributed to neural representations of phonological and semantic stimuli. As a result, semantic activity patterns within the left inferior frontal gyrus and left occipitotemporal cortex, also activated by tool use, displayed significant within-category similarity and between-category dissimilarity. Therefore, activity in tool-use related areas contributes to semantic processing. By contrast, no significant relationship was observed between activity patterns elicited by phonological stimuli within the tool-use network. Overall, our findings show that semantics, but not phonology, is grounded within the tool-use network reinforcing the hypothesis of a functional link between semantics and tool use.

Key words: tool use, phonology, semantics, language, fMRI, neurotypical adults

Significance Statement

Paleoneurobiology has brought evidence of the co-evolution of tool use and language. As a consequence a functional link between the two functions might still be observable in the brain. Recently, we showed common neurofunctional resources for tool use and syntax, but similar direct evidence is crucially missing for semantics and phonology. Here, using functional neuroimaging in neurotypical adults, we showed that activity within the tool-use cerebral network (left inferior frontal gyrus and left occipitotemporal cortex) contributes to the neural representation of semantic categories. We did not find evidence for common neural resources for phonology and tool use. Our findings suggest that tool use and language might impact each other, opening new strategies for rehabilitation or learning.

Introduction

Tool use and language are highly sophisticated human abilities which, according to some scholars, might have co-evolved. Indirect evidence for the proposed evolutionary link comes from the metric analyses of skull endocasts. Such investigations showed that the increased complexity of manufactured tools triggered an expansion of brain areas linked to linguistic processing in the human ancestors (Ponce de León et al., 2021). As a corollary of their potential co-evolution, tool use may share neural territories and cognitive resources with linguistic processes (Stout and Chaminade, 2012). Tool use involves a left frontoparietal network, encompassing the left inferior parietal lobule (IPL) and the left inferior frontal gyrus (IFG; Brandi et al., 2014), as well as the basal ganglia (BG; Choi et al., 2001). In addition, the occipitotemporal cortex (OTC) including the left posterior middle temporal gyrus and the left lateral occipital cortex also sustains tool-use actions (Brandi et al., 2014), likely related to tool visual recognition (Schone et al., 2021). The aforementioned regions are of particular interest given their involvement in linguistic processes as well. Indeed, both the left IPL and IFG are critical for phonological processing. In particular, the parietal cortex plays a role in the neural amplification for categorical perception of speech sounds (Raizada and Poldrack, 2007), while the left IFG is engaged in the perception of phonemes, especially in noisy contexts (Meister et al., 2012). The left IFG is also a critical neural node for semantics (Binder et al., 2009), in particular for processing tool nouns (Cattaneo et al., 2010) and action verbs (Aziz-Zadeh et al., 2006). The left OTC, beyond its involvement in tool-use actions and recognition, is also of key importance for semantic processing of words referring to tools (Chao et al., 1999).

Despite the encouraging findings reviewed above, empirical evidence is missing in the debate, since the neural similarities between tool use and language have been barely investigated within the same protocol and/or the same participants. Previous studies pointing to common neural resources for tool use and language employed an unspecific linguistic comprehension task (Higuchi et al., 2009; Uomini and Meyer, 2013). This task however

prevented to clarify both the precise contribution of distinct linguistic components to the brain activity, and their specific relationship with tool use. Recently, Thibault and colleagues examined whether tool use shares cognitive processes with linguistic syntax (Thibault et al., under review). Brain activity of a group of neurotypical participants was recorded while solving a syntactic task and a motor task either with a tool or with their bare hand as control. Results showed that the network activated for tool use encompasses language-related areas such as the BG, left OTC and IPL in addition to a cluster located in the left IFG. Most importantly, multivariate approaches showed that tool-use planning and syntactic processing in language induce similar patterns of brain activity within the BG. Such shared neural resources for the two abilities are reflected behaviorally: not only individual tool-use dexterity predicts syntactic performance (Brozzoli et al., 2019) but training one ability significantly improves the other (Thibault et al., under review). These findings support the existence of a supramodal syntactic functions underlying both motor and linguistic processes. This in turn corroborates the possibility of a co-evolutionary trajectory for tool use and language.

Here, we took a step further by investigating whether phonology as well as semantics share functional resources with tool use (Stout and Chaminade, 2012). To this aim, we tested for potential anatomical overlap of functional brain activity induced by tool use on one side, and by either phonology or semantics on the other. Furthermore, we tested the hypothesis that tool use shares neural territories with phonology or semantics, by studying the representational similarities of the activity elicited by phonological or semantic processes within the tool-use network.

Materials and Methods

Participant

The sample of participants, the motor task and fMRI acquisition parameters for this dataset have been described in a previous publication (Thibault et al., under review). fMRI acquisition included 24 (11 females and 13 males) right-handed, French native participants. All had normal or corrected-to-normal vision, and they reported no history of neurological, auditory, language or sensorimotor deficits. Four participants were excluded, two did not fulfill the familiarization performance requirements before any neuroimaging acquisition, one dropped out after the inclusion phase and one was removed from analyses due to substantial head movements (several runs with movements above 1.5 mm). Hence, we analyzed the data of 20 participants with the following sociodemographic characteristics and manual preference: 10 females and 10 males; mean age \pm SD: 24 ± 4 years old; higher education level: 3 ± 2 years; mean score on the Edinburgh handedness inventory (Oldfield, 1971): 0.93 ± 0.09 . The protocol conformed to the Helsinki declaration and was approved by a national ethical committee (46/17, OUEST IV). All participants gave their written consent prior to the study and received compensation of 110 euros.

Tasks

Tool-use task

The motor task employed here has been previously described in Thibault et al., under review. The participants were asked to use a pair of 30-cm-long pliers with their right hand in order to move a peg on a plastic board (Quercetti, Torino, Italy) where two fixed visual landmarks, separated by a 9-cm distance, indicated the start and end points (Fig. 1A). The participants were lying in a resting position and were instructed to wait for a pure tone signal delivered through a MRI compatible device (Optoacoustics OptoACTIVE-two way noise cancellation communication system, Mazor, Israel). A single pure tone required the participant

to prepare the movement, while a double presentation 4s later indicated the Go for the action. In order to perform the requested movements, the described sequence was repeated twice: grasping the peg to displace it from the start to the end point and then grasping it again to move it back to its initial position. The whole sequence (4-s planning – 4-s execution – 4-s planning – 4-s execution – 10-s rest) was repeated 15 times in a single run. The participants had to press a button with their left index finger if a peg fell, to indicate the missed sequence and then grab a new peg from the left side of the plastic board. The few missed trials (lower than 0.5%) were modeled separately. As a control, in a distinct run, the same task was performed with the free hand. This allowed to define the contrast aimed to identify the tool-specific neural network. The motor task device was placed at a reachable distance in front of the participants and made visible with a double mirror mounted onto the head coil. To minimize elbow and shoulder movements, the participants' right upper arm was strapped to the trunk. The scripts controlling the audio sequence of instructions in the scanner were delivered with Presentation software (NBS, Berkeley, USA).

Phonological identification Test

A two-alternative forced choice (2-AFC) phonological identification task was designed to assess phonological processing. Stimuli were isolated syllables synthesized with Praat (<https://www.fon.hum.uva.nl/praat/>) and varied by stepwise transformations in the second and third formants over 15 steps spanning a continuum between the syllables /ba/ and /da/. Each stimulus had a duration of 343 ms.

Five stimuli out of the 15 of the continuum (i.e. stimuli 1, 5, 8, 11 and 15) were selected for presentation to the participants. One trial consisted in the presentation of the same syllable three consecutive times with a stimulus onset asynchrony (SOA; time interval between the onsets of the stimuli) of 400 ms. The participants had a maximum of 2 seconds after the onset of the third repetition to identify the stimulus as /ba/ or /da/. They were instructed to wait for

the third repetition to give their response as quickly and correctly as possible via a button press using their left index and middle fingers. The button-response association was counterbalanced across participants. All syllables were delivered through the same MRI compatible device as the one used for the tool-use task. Each stimulus was presented 11 times (11 trials), resulting in a total of 55 trials (11×5 stimuli) presented in a randomized order during the experiment. The intertrial period was jittered between 5 and 7s (Fig. 1B). To warn participants of an upcoming trial, a fixation dot was presented 500 ms beforehand and remained during stimulus presentation until the response interval. The dot was visible through the mirror oriented towards the screen placed on the back of the scanner bore. The task script was programmed onto Psychtoolbox (PTB-3) running on MATLAB (Mathworks, Natick, USA).

Semantic Priming Task

A semantic priming paradigm with a lexical decision task allowed to assess semantic processing. In such a paradigm, prime-target words pairs that are semantically related or not are presented and participants have to make a lexical decision on the target. Stimuli used as primes and targets were French words belonging to two distinct semantic categories: animal and tool nouns. Pseudowords were created by changing two letters from tool and animal nouns while following the French phonotactic rules (i.e. they remained pronounceable and orthographically legal). Pseudowords were only presented as targets, never as primes. The selection of word stimuli was based on an anonymized online survey. A total of French native 574 participants (mean age \pm SD = 23.92 ± 4.39) judged the imageability and manipulability of a subset of a larger sample of 374 object nouns, on a 7-point Likert scale. They could also report whether a word was unknown to them. Additional 246 participants (mean age \pm SD = 26.59 ± 6.01) judged the imageability of a subset of 220 animal nouns. Because the participants received only a subset of words and not the full list, each word was quoted by 82 times (i.e. by 82 participants).

Overall, 147 Object nouns with manipulability and imageability scores equal or above five (out of seven) were selected as tool nouns. Furthermore, 172 animal nouns with an imageability score equal or above five were retained. Words from the two semantic categories were selected to obtain two lists of 70 tool nouns and 70 animal nouns matched for psycholinguistic variables (written and oral frequencies, numbers of syllables, letters and orthographic neighbours) as verified with the Lexique 3.80 database (New et al., 2004; Table 1). The two lists of animal and tool nouns were then each divided into 5 lists of 14 words each. The resulting 10 lists (5 animal nouns and 5 tool nouns) were matched for the aforementioned psycholinguistic variables (Table 1). Each list was uniquely assigned to a function in the priming paradigm (either prime or target) so as to create five experimental conditions: Tool Primed, Tool Unprimed, Animal Primed, Animal Unprimed and Pseudowords.

	Tool Nouns	Animal Nouns	Semantic Categories Statistics	Word Lists Statistics
Letters	6.76 ± 1.86	6.26 ± 1.98	$W = 2109.5, p = 0.15$	$F_{(9,130)} = 0.87, p = 0.56$
Syllables	1.96 ± 0.81	1.86 ± 0.82	$W = 2277.5, p = 0.44$	$\chi^2_{(9)} = 9.79, p = 0.37$
Orthographic Neighbors	3.40 ± 4.21	2.60 ± 4.02	$W = 2045, p = 0.08$	$\chi^2_{(9)} = 8.91, p = 0.45$
Written Frequency	7.27 ± 8.98	6.82 ± 6.23	$W = 2720.5, p = 0.26$	$F_{(9,130)} = 1.18, p = 0.31$
Oral Frequency	4.65 ± 7.42	5.45 ± 6.53	$t_{(138)} = 1.57, p = 0.12$	$F_{(9,130)} = 1.12, p = 0.35$
Unknown Words	0.59 ± 0.92	0.34 ± 0.74	$W = 2080, p = 0.06$	$\chi^2_{(9)} = 12.83, p = 0.17$
Imageability	6.59 ± 0.30	6.44 ± 0.60	$W = 2313.5, p = 0.57$	$\chi^2_{(9)} = 9.80, p = 0.37$

Manipulability	5.90 ± 0.35	×	×	$F_{(4,65)} = 0.69, p = 0.60$
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Table 1. Statistics for tool and animal nouns. Means ± SD are reported respectively for tool and animal nouns on several psycholinguistic variables: number of letters, number of syllables, number of orthographic neighbors, written and oral frequencies, the times a word is unknown, imageability and, for tool nouns, manipulability. Statistics are reported for the comparison between the two semantic categories (i.e. 2 levels, animals vs. tools; two-sample t-test or Wilcoxon sum rank test as well as between the 10 lists of words used either as primes or targets across the five experimental conditions (i.e. 10 levels; ANOVA or Kruskal-Wallis test performed according to the residuals normality).

For words, primes and targets were associated by pairs in four conditions: a prime could be followed by either a target from the same semantic category (i.e. Tool Primed and Animal Primed) or a target from a different semantic category (i.e. Tool Unprimed and Animal Unprimed). In case of primed conditions, the words belonging to the same semantic category were always different. In a fifth condition, the target was a Pseudoword, following either an Animal or a Tool prime. The prime-target pairs were the same for all participants.

During the experiment, following a fixation dot presented for 500 ms a prime word was visually presented in uppercase for 300 ms and immediately followed by a target word in lowercase for 500 ms. Participants were instructed to indicate as quickly and correctly as possible whether the target was a word or a pseudoword by pressing one of two buttons with their left index and middle fingers. They had a maximum of 2 seconds after the target onset to respond. The button-response association was counterbalanced across participants. The intertrial period was jittered between 5 and 7 seconds (Fig. 1C).

Overall, participants underwent 84 trials across the five experimental conditions: 14 prime-target pairs were presented for each of the four word conditions and 28 prime-target pairs

for pseudowords (Appendix). The stimuli were visible through the mirror and the task script was programmed onto *Psychtoolbox* (PTB-3) running on MATLAB (Mathworks, Natick, USA).

Procedure

The experiment consisted of an inclusion session to familiarize participants with the tasks and to ensure that the individual level of performance met the inclusion criteria. Short versions of the semantic and phonological tasks and of the motor task were proposed. The requirements to perform the fMRI session were at least 6 correct responses in the lexical decision task (over 9 trials including 6 words and 3 pseudo-words) and at least 5 correct categorization of the syllables located at the continuum extremums (over 8 repetitions). This procedure aimed to maximize the chances of collecting a sufficient number of correct and analyzable trials in each task during the neuroimaging acquisition. The motor task for inclusion consisted of performing two blocks with each effector (two tool-use blocks and two free-hand block). In each block, the participants performed the task on the Grooved Pegboard test and were instructed to insert ten pegs as quickly as possible on the two first rows. To be included in the experiment, they were required to insert the 10 pegs for the two tool-use blocks in less than 5 minutes on average and the two free-hand blocks in less than 1 minute on average. The participants took part to two different fMRI sessions separated by two days. For each session, the participants performed an anatomical acquisition (T1-weighted), followed by motor (tool-use and free-hand) and linguistic runs in a counterbalanced order. The phonological and semantic tasks were presented on the same session, while two additional tasks, one assessing syntactic processing and the other working memory, were performed in the other session. The results for these additional tasks, together with an analysis of the data relative to the motor task, are presented in a separate report (Thibault et al., under review). Here, we present novel and unpublished results for the neuroimaging data of the motor runs, reanalyzed employing a

different pipeline for the preprocessing, as well as of the semantic and phonological runs. The session order was counterbalanced between participants.

Functional and anatomical MRIs were acquired with a Siemens Prisma 3T scanner (Siemens Medical systems, Erlangen, Germany) with a gradient echo EPI sequence, with TE = 30 ms and TR = 2400 ms. Volumes were acquired with 44 interleaved slices of 3.3 mm thickness ($3 \times 3 \times 3.3$ mm voxel size) aligned to the AC-PC plane. Overall, 171 volumes were acquired for each motor block, 303 for the semantic task and 215 for the phonological task. T1-weighted images were acquired with a 1-mm isotropic voxel and a GeneRalized Autocalibrating Partial Parallel Acquisition (GRAPPA) acceleration factor of 2 (TE = 3.8 ms, TR = 3000 ms).

Analyses

Behavioral analyses

For the phonological identification task, the proportion of /ba/ responses was quantified for each of the five stimuli of the continuum going from /ba/ to /da/. We then calculated the average proportion at the group level and reported it as mean \pm SEM. We quantified the goodness of fit of both linear and sigmoidal model on these data by computing the root mean square error (RMSE). The fitting of the two models were statistically compared with the R built-in function *anova*.

For the semantic task, response times (RTs; i.e. time interval from the display of the target word to the participant's response) and response accuracy were measured to index semantic performance. Statistics on these data were run in R-studio with the *afex* package (Singmann et al., 2020). A linear mixed model (LMM) was used on RTs and included *Semantic Category* (Tool nouns vs. Animal nouns) and *Priming* (Unprimed vs. Primed) as fixed-effect within-subject factors. These factors were also included as random slopes in addition to the random intercept for *Subjects* (Baayen et al., 2008). Planned comparisons of RTs between

primed and unprimed conditions for each semantic category were performed with LMMs including *Priming* as fixed-effect within-subject factor and *Subjects* as random intercept. The *Priming* factor was also added as random slope only for the animal nouns. This difference between the two LMMs is explained because random effects and their impact on model fit were introduced and assessed sequentially, so that the one with significantly better fitting was chosen (see Blini et al., 2018 for a similar procedure). A generalized linear mixed model (GLMM) with a binomial law was performed on response accuracy. Both *Semantic Category* and *Priming* were used as fixed-effect within-subject factors, *Semantic Category* was considered as random slope and *Subjects* as random intercept. For all analyses, Tukey post hoc comparisons were performed to further explore significant interactions. All results are reported as the mean \pm SEM.

fMRI preprocessing. For preprocessing of the fMRI data, we used fMRIPrep (<https://fmriprep.org/en/stable/>), a pipeline aiming to conduct robust and reproducible preprocessing of fMRI data (Esteban et al., 2019). The fMRIPrep pipeline generates a file describing the preprocessing procedure applied that is available for downloading (<https://osf.io/yr394/>).

fMRI univariate analyses. The Statistical Parametric Map 12 (SPM12, <https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>) was used for the univariate analysis. Data were smoothed with a Gaussian kernel of $8 \times 8 \times 8$ mm. At the first level, each participant's hemodynamic responses were modeled by the convolution of the canonical hemodynamic response with a box-car function. Each motor block was designed with planning, execution, rest and missed trials and head movements. Both directions of the movements (back and forth) were taken into consideration together. For the phonological identification task, we modeled together the three consecutive repetitions of the same syllable (i.e. 1.2s from the onset of the

first repetition) and separately for each of the five syllable stimuli from the continuum. The remaining response time (i.e. 1.6s) was modeled apart, as the same was done for head movements. For the semantic priming task, we modeled the prime - target association (i.e. 0.8s from the prime onset) separately for Tool Primed, Tool Unprimed, Animal Primed, Animal Unprimed and Pseudowords. The head movements, incorrect trials as well as the remaining time allotted to give a response (i.e. 1.5s) were modelled in separate regressors.

At the second level, we conducted within-subjects ANOVAs to identify the general network underlying the motor task. To do so, we entered the parameter estimates (i.e. beta) against baseline obtained for each condition of interest and each subject. We computed the interaction contrast highlighting the specific tool-use planning neural network with respect to free-hand planning and the overall execution network:

$$\text{Tool-use Planning Network} = [(\text{Tool-use}_{\text{Planning}} - \text{Free-Hand}_{\text{Planning}}) - (\text{Tool-use}_{\text{Execution}} - \text{Free-Hand}_{\text{Execution}})].$$

To investigate the network activated during action execution, we computed the following contrast:

$$\text{Tool-use Execution Network} = [(\text{Tool-use}_{\text{Execution}} - \text{Free-Hand}_{\text{Execution}}) - (\text{Tool-use}_{\text{Planning}} - \text{Free-Hand}_{\text{Planning}})]$$

To assess the phonological network, we used a different strategy. We weighted the contrasts on the individual behavioral performance in the phonological identification task, similarly as done in a previous study of phonological perception (Raizada and Poldrack, 2007). We aimed to uncover the brain regions specifically activated for processing speech sounds. Two neural processes can be studied for speech perception, one depending on the boundary between the perceived categories of speech sounds and another depending on the perception of

fine-grained acoustic features across speech stimuli (i.e. allophonic differences). Identifying the brain regions involved in speech categorical perception requires testing for neural differences between speech sounds that are perceived either unambiguously or ambiguously. To do so, we used the proportion of /ba/ responses during the phonological identification task: ambiguous syllables are stimuli with a proportion of /ba/ responses tending towards the chance level at 50%. Conversely, unambiguous sounds correspond to stimuli with a proportion of /ba/ responses tending towards 100% or 0%, the latter case meaning that participants categorized the syllable unambiguously as /da/. Thus, for each participant, we defined a contrast weighted on their individual performance and then we used it for the first level analyses. To find brain regions specifically responding to unambiguously perceived speech sounds, we needed to estimate signal changes displaying a U-shape relation with the interval of stimuli. Such a contrast would therefore attribute the maximum weight to the categorization performance at the extremes (i.e. 100%, namely unambiguously perceived /ba/, and 0%, unambiguously perceived /da/), and, at the opposite, the minimum weight to stimuli producing a performance at chance level (50%). To this aim, we performed a calculation over the proportion of /ba/ responses for each of the five stimuli presented (Equation 1).

$$abs(stimuli_categoriation - chance_level) \text{ (Equation 1)}$$

Equation 1. Stimuli categorization is the proportion of /ba/ responses recorded for each of the five speech stimuli of the continuum. We subtracted the chance level and transformed the resulting value in absolute value.

For identifying brain regions better responding to ambiguous phonemes, we needed to obtain the reverse relation, that is an inverted U-shape curve. Thus, we obtained the relative weighted contrast by computing the inverse of Equation 1 (Equation 2).

$$-abs(stimuli_categoriation - chance_level) \text{ (Equation 2)}$$

Equation 2. The same calculation as in Equation 1 was applied and transformed to a negative value.

The scores obtained were then normalized in order to have a contrast centered on zero.

To identify brain regions responding to fine-grained acoustic features, we defined a contrast taking into consideration the raw proportion of /ba/ responses, without applying any transformation, except for the normalization to get a zero-centered contrast. Thus, to test the neural modulations in response to allophonic features, we employed two contrasts: one taking into consideration the signal changes proportional to the rate of identification of /ba/, and the other, at the opposite, testing the signal changes proportional to the rate of identification of /da/.

The first level analyses resulted in four contrast estimates that we entered at the second level in one-sample t-tests. This aimed at uncovering the brain areas responding preferentially to unambiguous or ambiguous speech sounds and to the perception of fine-grained acoustic features from /ba/ to /da/ or /da/ to /ba/.

To assess the semantic neural network, we conducted within-subjects ANOVAs to identify the general network underlying the semantic task. To do so, we entered the parameter estimates (i.e. beta) against baseline obtained for each condition of interest and each subject. We first studied the main effect of semantic priming as follows:

$$\text{Semantic Priming Network} = [\text{Unprimed nouns} - \text{Primed nouns}]$$

Then we studied the main of effect semantic category separately for tool and animal nouns as follows:

$$\text{Semantic Tool Category Network} = [\text{Tool nouns} - \text{Animal nouns}]$$

and

$$\text{Semantic Animal Category Network} = [\text{Animal nouns} - \text{Tool nouns}]$$

Finally, we studied the semantic priming effect for each semantic category separately using the following:

$$\text{Semantic Tool Priming Network} = [\text{Unprimed Tool nouns} - \text{Primed Tool nouns}]$$

and

$$\text{Semantic Animal Priming Network} = [\text{Unprimed Animal nouns} - \text{Primed Animal nouns}]$$

To guarantee the reliability of the results, for each analysis, we reported each cluster at the whole brain level, containing more than 10 contiguous voxels, with a *p-value* below the 0.001 threshold uncorrected for multiple comparisons. Furthermore, the two motor contrasts were submitted to an exclusive mask defined at 0.05 uncorrected for multiple comparisons aiming to rule out the contribution of the interaction second component (i.e., for Tool-use Planning Network, the contribution Hand Execution > Tool Execution was masked). This mask was also used for the conjunction analyses (described below). Clusters passing the family-wise error (FWE) correction for multiple comparisons at the cluster level are highlighted with a ^{FWE} mention in the Tables. To test the existence of shared neural resources between tool use and, separately, the two linguistic processes under investigation, we performed series of conjunction analyses between the tool use network and each of the linguistic contrasts.

fMRI multivariate representational similarity analysis (RSA)

We selected regions of interest (ROIs) from the tool-use related neural activity. To this aim, we saved a mask of all the significant voxels ($p < 0.001$ uncorrected) for clusters of interest. Overall, we retained three ROIs of the tool-use planning network also known for their involvement either in phonology or semantics or in both. The three tool-use clusters were the left IPL (size = 150 voxels), left OTC (size = 76 voxels) and left IFG (size = 28 voxels). For the

two linguistic tasks, first-level analyses were run again on non-smoothed data and included the same regressors as for the univariate analyses. We used the CoSMoMVPA toolbox (Oosterhof et al., 2016) to extract, for each participant, the t -value at each voxel within a given ROI. The RSA consists of testing whether the representational similarity hypothesized in a model fits with the neural activity patterns recorded across various stimuli types (Kriegeskorte et al., 2008). The RSA consists of testing whether the neural dissimilarity (i.e. $1 - \text{Pearson's correlation score}$) across a set of conditions, computed within a representational dissimilarity matrix (RDM), corroborates a model.

For the phonological identification task, we considered a model aiming to test whether the speech category boundary is represented at the neural level. The model was designed at the individual level, to take into account interindividual differences of the categorical perception boundary. The model assumed that stimuli whose proportion of /ba/ is above the chance level (i.e. 50%) would be similarly represented at neural level as would be the stimuli whose proportion of /ba/ responses is under the chance level. On the contrary, neural activity elicited by sounds perceived as belonging to different sides of the boundary would be considered dissimilar (Fig. 1D).

For the semantic priming task, we considered four conditions of interest (i.e. Tool Primed, Tool Unprimed, Animal Primed, Unprimed Animal). Similarly, at the neural level, a distance was calculated across these four conditions and entered in a RDM. We tested an *a priori* model assuming that primed and unprimed tool nouns were similarly represented, the same rationale was applied for primed and unprimed animal nouns. The two semantic categories were on the other hand expected to be dissimilarly represented. In others words, we tested a model assuming stronger similarity of neural activity patterns within but dissimilarity between each semantic category (Fig. 1E).

To assess if the model fitted with the RDM, we computed a Pearson's correlation for each participant. To test the significance of the mean correlation score, we performed 10,000 permutations by randomly flipping the sign of the participant's correlation scores in order to obtain a null distribution. The probability for observing a significant effect under the null hypothesis was thresholded at 0.05 right-tailed and calculated from the proportion of values of the null distribution superior to the observed *Pearson's correlation score*. Thus if this proportion is smaller than 0.05, the observed *Pearson's correlation score* is considered significant and different from the chance level set at zero.

Figure 1. Overview of the set up and RSA models (A) Set-up and experimental design of the tool-use and free-hand motor tasks. (B and C) Set-up and experimental design of the two linguistics tasks: (B) phonological identification task (C) and semantic priming task. (D) The RSA model for phonology tested for dissimilarity between speech stimuli crossing the category boundary (in yellow) and similarity for stimuli lying on the same side of the boundary (in blue). This model was obtained only for visualization purposes from the group mean behavioral performance in the identification task, individual data resulting in an individual model were used for analysis. (E) The RSA model for semantics tested for dissimilarity between words belonging to different semantic categories (i.e. tool and animal nouns) and for similarity for words belonging to the same semantic category.

Results

Tool-use network

Planning an action with a tool recruited a network (Fig. 2 and Table 2A) encompassing both cortical and subcortical areas such as the BG, left OTC and left IPL ($p_{s-fwe} < 0.05$ at the cluster level) in addition to a cluster located in the left IFG ($p < 0.001$ unc.). Additional clusters of activity were also found in the right hemisphere homologues of these cortical areas. Executing an action with a tool did not activate any specific cluster with respect to free-hand execution, except for a cluster in the left visual areas (Table 2B). These results are in line with those described in Thibault et al. (under review) using different fMRI preprocessing analyses.

Figure 2. Tool-use planning network. Statistical maps thresholded at $p < 0.001$, unc., for sagittal (top) and axial views (bottom).

Region	BA	Peak MNI coordinates			Cluster size (<i>k</i>)	Z-value
		<i>x</i>	<i>y</i>	<i>z</i>		

(A) Tool-use Planning Network: (Tool-use Planning – Free-Hand Planning) - (Tool-use Execution – Free-Hand Execution)

L Postcentral Gyrus (extending onto Inferior Parietal Lobule)^{FWE}	BA1, 2, 3, 40	-66	-16	27	150	4.64
L Caudate (extending onto Globus Pallidus) ^{FWE}	-	-18	20	-13	112	4.31
L Occipitotemporal Cortex^{FWE}	BA19, 37	-54	-72	-9	76	4.53
L Putamen	-	-28	-4	-6	46	4.03
L Inferior Frontal Gyrus (Precentral Sulcus)	BA6	-58	12	27	28	3.99
L Intraparietal Sulcus	BA40	-36	-36	44	26	4.18
L Putamen	-	-24	8	-16	21	4.34
L Insula	BA13	-42	-4	4	19	3.74
L Ventral Anterior Cingulate Cortex	BA24	-10	30	11	17	4.40
L Inferior Frontal Gyrus (Ventral Premotor Cortex)	BA6	-64	0	30	11	4.15

R Putamen (cluster extending onto Globus Pallidus and Caudate Nucleus) ^{FWE}	-	26	-13	-3	772	5.21
R Inferior Frontal Gyrus (extending onto Postcentral and Supramarginal Gyri) ^{FWE}	BA1,2,3, 4,6,40	62	6	30	177	4.37
R Occipitotemporal Cortex ^{FWE}	BA19, 37	50	-58	-9	140	4.72
R Intraparietal Sulcus	BA7	36	-42	47	130	4.55
R Secondary Visual Area	BA18	26	-100	-6	13	3.65
R Cerebellum Crus I	-	26	-46	-39	11	3.65

(B) Tool-use Execution Network: (Tool-use Execution – Free-Hand Execution) - (Tool-use Planning – Free-Hand Planning)

L Secondary Visual Area ^{FWE}	BA18	-12	-76	-3	329	4.96
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Table 2. (A) Brain areas activated for tool-use planning (A) and too-use execution (B). All presented clusters contain more than 10 contiguous voxels and are below the statistics threshold $p < 0.001$, unc. Clusters passing the family-wise error correction with $p < 0.05$ at the cluster level are indicated with the mention ^{FWE}. The three regions highlighted are the ROIs used for the RSA focusing on the neural activity elicited by the phonological identification and semantic priming tasks.

Behavioral results and functional network activated by phonological processes

The proportion of /ba/ responses for the group sample was fitted with two distinct functions, respectively a sigmoid and a linear model. The sigmoid model fitted better with the data than the linear model (Fig. 3A). Indeed, the RMSE was smaller for the sigmoidal than the linear fitting (Sigmoid RMSE = 0.025 vs. Linear RMSE = 0.109). The comparison between the two models performed with an ANOVA revealed a significantly better fitting for the sigmoid than linear model ($p = 0.01$).

The weighted contrast designed to assess neural activity induced by the perception of unambiguous syllables highlighted the specific role of the left IPL with the left angular gyrus ($p_{s-fwe} < 0.05$ at the cluster level, see Fig.3B and Table 3A). Conversely, the perception of ambiguous speech sounds showed bilateral activations within the IFG, including the left *pars orbitalis* and right *pars triangularis* ($p_{s-fwe} < 0.05$ at the cluster level). Furthermore, processing ambiguous syllables also recruited a bilateral cluster within the superior frontal gyrus (SFG) encompassing the supplementary motor area ($p_{fwe} < 0.05$ at the cluster level, see Fig.3B and Table 3B). The analyses focusing on the perception of fine-grained acoustic features (i.e. allophonic differences) did not reveal any significant cluster passing the whole brain threshold of $p < 0.001$.

Region	BA	Peak MNI coordinates			Cluster size (<i>k</i>)	Z-value
		<i>x</i>	<i>y</i>	<i>z</i>		

(A) Unambiguous Speech Sounds - Ambiguous Speech Sounds

L Angular Gyrus ^{FWE}	BA39	-40	-84	37	74	4.37
L Parahippocampal Gyrus	BA36	-30	-40	-13	21	4.04
L Middle Frontal Gyrus	BA8	-28	18	44	20	3.84
R Parahippocampal Gyrus	BA36	32	-40	-13	24	4.46
R Inferior Temporal Gyrus	BA47	60	-54	-9	18	3.85
R Supramarginal Gyrus	BA40	62	-22	40	16	3.95
R Caudate Nucleus	-	2	0	17	11	3.87

(B) Ambiguous Speech Sounds - Unambiguous Speech Sounds

L Inferior Frontal Gyrus (<i>Pars Orbitalis</i>) ^{few}	BA47	-46	26	-3	55	4.33
L Middle Frontal Gyrus (Dorsal Premotor Cortex)	BA6	-58	2	44	16	3.36

R Superior Frontal Gyrus (Supplementary Motor Area, extending bilaterally) ^{FWE}	BA6	8	12	50	128	4.28
R Inferior Frontal Gyrus (<i>Pars Triangularis</i>) ^{FWE}	BA45	36	24	4	34	4.39

Table 3. Brain areas activated for ambiguous (A) and unambiguous syllable-embedded phonemes (B). All presented clusters contain more than 10 contiguous voxels and are below the statistics threshold $p < 0.001$, unc. Clusters passing the family-wise error correction with $p < 0.05$ at the cluster level are indicated with the mention ^{FWE}.

Behavioral results and functional network activated by semantic priming

The LMM performed on RTs (Fig. 3C) revealed a main effect of priming [$\chi^2_{(1)} = 25.78$, $p < 0.001$] and no interaction between priming and semantic category [$\chi^2_{(1)} = 0.29$, $p = 0.59$]. The RTs in the primed conditions were shorter as compared to the unprimed conditions. Planned comparisons confirmed that this effect was equivalent for the two semantic categories (Tool Primed = 945 ± 43 ms vs. Tool Unprimed = 1017 ± 43 ms, [$\chi^2_{(1)} = 21.25$, $p < 0.001$]; Animal Primed = 901 ± 38 ms vs. Animal Unprimed = 962 ± 37 ms, [$\chi^2_{(1)} = 20.04$, $p < 0.001$]). Furthermore, a main effect of the semantic category revealed that tool nouns were processed more slowly than animal nouns (Tool nouns = 981 ± 31 ms vs. Animal nouns = 931 ± 27 ms, [$\chi^2_{(1)} = 14.35$, $p < 0.001$]). The GLMM run on response accuracy did not reveal any main effect of priming nor any interaction with semantic category [$\chi^2_{s(1)} < 2.63$, $p > 0.10$]. Nonetheless, a trend was observed for the effect of semantic category: participants tended to be less accurate for tool than for animal nouns (Tool nouns = 96.3 ± 0.9 % vs. Animal nouns = 99.1 ± 0.4 %, [$\chi^2_{(1)} = 3.79$, $p = 0.051$]).

The contrast devised to identify the neural activity associated with general semantic priming, irrespective of the semantic category, resulted in a significant cluster in the left IFG encompassing both the *pars triangularis* ($p\text{-fwe} < 0.05$ at the cluster level) and *pars opercularis* ($p < 0.001$ unc., see Fig.3D and Table 3A). In a further analysis, we uncovered the regions supporting the semantic priming effect specifically for tool nouns by comparing the activity for unprimed versus primed tool nouns. The left IFG was found to be activated with two clusters in the *pars triangularis* and premotor cortex ($p\text{-fwe} < 0.05$ at the cluster level, see Fig.3D and Table 3B); the right IFG was recruited to a smaller extent ($p < 0.001$ unc.). The same analysis conducted to assess priming of animal nouns did not show any specific cluster of activity for unprimed versus primed animal nouns.

A last series of analyses aimed to highlighting the network subserving the processing of each semantic category, irrespective of the priming condition. This showed that processing of tool nouns, as compared to animal nouns, involved the bilateral IFG (i.e. *pars orbitalis*, $p\text{-fwe} < 0.05$ at the cluster level) and right SFG extending to the left hemisphere as well (i.e. supplementary motor area, $p\text{-fwe} < 0.05$ at the cluster level). In addition, we found a cluster of activity within the left OTC ($p < 0.001$ unc., see Fig.3D and Table 3C). The opposite contrast testing for activations specifically recruited for processing animal nouns, in comparison to tool nouns, did not reveal any significant cluster.

Region	BA	Peak MNI coordinates			Cluster size (<i>k</i>)	Z-value
		<i>x</i>	<i>y</i>	<i>z</i>		

(A) Unprimed nouns - Primed nouns

L Inferior Frontal Gyrus (<i>Pars Triangularis</i>) ^{FWE}	BA45	-30	30	4	54	4.30
L Inferior Frontal Gyrus (<i>Pars Opercularis</i>)	BA44	-48	20	14	26	4.02
L Superior Frontal Gyrus	BA8	-6	20	53	19	3.44
L Superior Frontal Gyrus (Supplementary Motor Area)	BA6	-10	12	57	12	3.47

(B) Unprimed Tool nouns - Primed Tool nouns

L Inferior Frontal Gyrus (<i>Pars Triangularis</i>) ^{FWE}	BA45	-30	30	4	52	4.49
L Inferior Frontal Gyrus (Ventral Premotor Cortex) ^{FWE}	BA6	-60	2	40	55	4.12
L Cerebellum Lobule VI	-	-24	-70	-26	12	3.76
L Dorsal Anterior Cingulate Cortex	BA32	-10	14	37	11	4.14

R Inferior Frontal Gyrus (<i>Pars Orbitalis</i>)	BA47	26	30	-3	30	3.96
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R Superior Frontal Gyrus	BA8	8	24	34	12	3.39
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(C) Tool nouns - Animal nouns

L Inferior Frontal Gyrus (<i>Pars Orbitalis</i>) ^{FWE}	BA47	-42	42	1	50	3.88
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L Anterior Insula	BA13	-34	20	-3	34	4.60
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L Occipitotemporal Cortex	BA37	-48	-52	-13	17	4.14
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R Superior Frontal Gyrus (Supplementary Motor Area, extending bilaterally) ^{FWE}	BA6	8	14	50	89	4.66
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R Inferior Frontal Gyrus (<i>Pars Orbitalis</i>) ^{FWE}	BA47	36	24	-6	44	4.89
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R Middle Frontal Gyrus	BA9	42	30	24	21	3.57
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R Caudate Nucleus	-	2	0	17	11	3.87
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Table 4. Brain areas activated for the main effect of semantic priming (A), the main effect of the tool semantic category (B) and semantic priming for tool nouns (C). All reported clusters contain more than 10 contiguous voxels and are below the statistics threshold $p < 0.001$, unc. Clusters passing the family-wise error correction with $p < 0.05$ at the cluster level are indicated with the mention ^{FWE}. No significant voxel was found for the main effect of the animal semantic category (i.e. Animal nouns – Tool nouns) and semantic priming for animal nouns (i.e. Animal Unprimed – Animal Primed).

Testing the existence of shared neural resources between tool use with phonology and semantics

Conjunction analyses

Given the anatomical proximity of tool-use planning and language activations (Fig. 4), we conducted conjunction analyses to directly test for their potential anatomical co-localization. The conjunctions performed between tool-use planning and each contrast of the phonological and semantic analyses did not reveal any significant overlapping cluster.

Figure 3. Behavioral and neuroimaging results for the phonological and semantic tasks. (A) Mean proportion of /ba/ responses in the phonological identification task. The dark line corresponds to the sigmoidal fitting and the gray line to the linear fitting. (B) Statistical maps thresholded at $p < 0.001$, unc., for phonological processing with speech sounds perceived unambiguously (top) and ambiguously (bottom). (C) Mean RTs for the lexical decision task in the semantic priming paradigm. The participants exhibited a facilitation in primed conditions for both tool (in purple) and animal (in orange) semantic categories. (D) Statistical maps thresholded at $p < 0.001$, unc., for semantic processing of unprimed vs. primed nouns (top), unprimed vs. primed tool nouns (middle) and tool vs. animal nouns (bottom).

Figure 4. Anatomical proximities between tool use, phonology and semantics. Left hemisphere for tool use (in red), phonology (in blue) and semantics (in green). (A) View focusing on the left IPL. (B) View focusing on the left IFG. (C) View focusing on the left OTC.

Testing the representational similarity of linguistic stimuli within the tool-use network

We conducted representational similarity analyses on three ROIs activated by tool-use planning, with known role in phonological (left IFG and left IPL) and semantic (left IFG, left IPL and left OTC) processing of language (see Table 2 in bold for the regions' coordinates); With RSA, we aimed to test whether phonology and semantics involve brain regions that are part of the tool-use network. For phonology, the model tested for neural similarity between speech sounds categorized as the same phoneme, whereas we expected dissimilarity between sounds crossing the category boundary. Testing this model on the phonological neural activity within the left IFG (mean $r = 0.08 \pm 0.06$; $p = 0.11$) and left IPL (mean $r = -0.03 \pm 0.07$; $p = 0.68$) did not reveal any significant difference against zero. Therefore, the model does not significantly explain the empirical data, indicating that the clusters of the tool-use network do not carry relevant information for phonological processing.

For the semantic task, the model assessed dissimilarity between tool and animal nouns and similarity within each semantic category for both primed and unprimed nouns. This model explained the neural activity elicited by words both within the left IFG (mean $r = 0.17 \pm 0.09$; $p = 0.04$) and left OTC (mean $r = 0.14 \pm 0.7$; $p = 0.03$). This indicates that within these tool-related cortical regions, the neural activity elicited by processing tool nouns was dissimilar from the one elicited by animal nouns. By contrast, the within category neural activity patterns were more similar: primed and unprimed tool nouns elicited similar patterns, and so did primed and unprimed animal nouns. Within the left IPL (mean $r = 0.01 \pm 0.13$; $p = 0.48$), no such effect was found suggesting this area does not represent the relations within and across each semantic category. Overall, these results indicate that neural activity within the tool use network represent relevant information for semantic processing.

Discussion

This study directly tested a co-localization of neural resources for tool-use with respectively, phonology and semantics in neurotypical adults. In line with previous studies, tool-use planning engaged the left frontoparietal areas, extending to the OTC, in addition to their homologues in the right hemisphere (Brandi et al., 2014) and the BG (Thibault et al., under review; Choi et al., 2001). Phonological processing recruited the left IPL within the angular gyrus for the perception of unambiguous speech, and the bilateral frontal areas for ambiguous speech. By contrast, the tests focusing on the perception of fine-grained acoustic features did not reveal any significant cluster of activity. These findings, coherent with previous research, indicate that the left IPL and IFG are involved in speech categorical perception. Indeed, the neural activity within left IPL is amplified for processing different phonetic categories (Raizada and Poldrack, 2007). Similarly, the left IFG and more generally the motor circuits are involved in the perception of speech sounds in noisy context (Meister et al., 2007; D'Ausilio et al., 2009). The general semantic priming network identified from the activity elicited by unprimed versus primed nouns, regardless of semantic category, shows an involvement of the left inferior and superior frontal gyri. Considering each semantic category separately within this network revealed the activation of the left IFG for semantic priming with tool nouns, whereas no specific activity occurs for priming of animal nouns. A last analysis targeting the activity elicited by semantic categories, irrespective of the priming manipulation, showed that tool nouns recruited the bilateral frontal regions and the left OTC in comparison to animal nouns, whereas the opposite contrast testing animal nouns in comparison to tool nouns did not show any significant difference. Our findings corroborate the involvement of the left IFG and left OTC in tool noun processing (Chao et al., 1999; Chao and Martin, 2000), as well as the relatively reduced activity for animal nouns compared to tool nouns (Binder et al., 2009).

The univariate conjunction analyses, employed to test for a potential co-localization of tool use activations on one side, and phonology or semantics on the other, suggest that these

processes involve relatively close but non-overlapping clusters. However, such a conjunction approach is based on the peak intensity and ignored potential differences in the spatial organization of activations. Two different stimuli can indeed elicit neural responses with a comparable intensity and yet with a significantly different spatial organization (Norman et al., 2006). Multivariate pattern analyses on the contrary allow to account for differences in these spatial patterns of brain activity. Accordingly, we then used RSA to uncover the neural similarities and dissimilarities for each linguistic function under study. This was done using ROIs selected from the tool-use network, on the basis of their expected role in phonological and semantic processing. For phonology, we tested the hypothesis that stimuli perceived as being different speech sounds should elicit more dissimilar neural patterns, whereas stimuli perceived as being the same should instead produce similar patterns of activity. Within the left IFG and left IPL, our model however did not capture the representational similarity of the neural activity elicited by speech sounds. For semantics, the model assumed the existence of dissimilarities across tool and animal categories, whereas similarities were expected for primed and unprimed nouns belonging to the same semantic category. Within the left IFG and left OTC, selected from the tool-use planning network, this model significantly captured the representational similarity for the neural activity elicited by words. This is an evidence that activity within the tool-use network contributes to the representation of semantic information.

The present findings suggest phonology and tool use are processed in separated yet close clusters, with no significant overlap. The parietal lobe is known to integrate sensory stimuli from various modalities within the same circuits, such as vision and somatosensory information (Brozzoli et al., 2012; Gentile et al., 2013). Crucially, the parietal lobe is involved in sensorimotor integration for speech (Hickok and Poeppel, 2007; Patri et al., 2020). Tool use and phonology may involve common sensory computations while remaining distinct functions, relying on different effectors and systems within the IPL (Stout and Chaminade, 2012). In line

with this interpretation, previous work indicated that the contribution of the left IPL to tool use was mainly localized within the anterior part of the SMG (Peeters et al., 2009) whereas, sensorimotor processes linked to the vocal tract were localized more posteriorly within the superior temporo-parietal region (Pa and Hickok, 2008).

The finding that semantic processing occurs within the tool-use network (i.e. left IFG and OTC) is consistent with the language embodiment theory (Barsalou, 1999; Pulvermüller, 2005). Indeed, this theoretical account suggests that semantic representations are grounded within the modality-specific systems supporting action and perception. For instance, reading a tool noun should activate the brain regions involved in using and perceiving a tool, even though no overt action is required. Several neuroimaging studies corroborated this view by showing that the conceptual representation of a tool is represented within the sensorimotor systems (Martin and Chao, 2001). However, such evidence remains indirect as it assumes that sensorimotor territories supporting tool use are the same than those involved in semantics without directly assessing the two functions in the same participants. This limitation is of particular relevance considering neuropsychological investigations reporting that patients with lesions impacting the sensorimotor circuits are not systematically impaired in language processing (Papeo et al., 2010; Papeo and Hochmann, 2012). Other data nevertheless showed that aphasic patients have difficulty to use and name tools (Fazio et al., 2009) or that apraxic patients are impaired for declarative knowledge about tools and body parts (Buxbaum and Saffran, 2002), and finally that the two deficits may coexist (Goldenberg and Randerath, 2015). These discrepancies between the existence of double dissociations versus common deficits for tool use and semantic processing might be explained by the variety of lesions and associated symptoms. In our work, we overcame the previously described limitations by performing RSA within clusters activated by tool-use and identified in those same participants who solved the

semantic task. Our findings bring new evidence that semantic processing of tool nouns occurs within the tool-related brain areas like the left IFG and left OTC.

If tool use and semantic processing of tool nouns share common neurofunctional resources, such link might be observable at the behavioral level. Recently, Thibault and colleagues demonstrated common neural activities for tool use and complex syntactic processing, resulting in reciprocal impact of one function over the other at the behavioral level (Thibault et al., under review). Similar behavioral evidence has been found for tool use and semantics. In a virtual reality context, novel tools that received a verbal label were facilitated for their use in comparison to unlabeled tools. At the neurophysiological level, in comparison to unlabeled tools, the use of a labeled tool provoked a reduction of the power within the sensorimotor beta band recorded (Foerster et al., 2020). The reverse influence of tool use on semantic processing has to our knowledge never been demonstrated, but more generally action and action-related language can reciprocally influence each other (Boulenger et al., 2006; Scorolli and Borghi, 2006; Rueschemeyer et al., 2010).

Shared neural substrates might originate from the co-evolution of tool use and language. Interestingly, primitive human endocasts from different periods revealed an expansion of the intracranial volume concomitant to a switch from basic to more complex tool-making technology estimated from tool vestiges and likely occurring 1.5 million years ago (Ponce de León et al., 2021). Crucially, from these endocasts, the authors estimated that cortical areas, such as the IFG, the posterior parietal cortex and the occipital cortex encompassing the OTC may have expanded dramatically during this period. Accordingly, evolutionary theories started to propose that neural circuits devoted to one function might have been exapted for a different purpose under specific environmental constraints, triggering neural reorganization (Dehaene and Cohen, 2007; Anderson, 2015). It has been suggested that the modification of the brain architecture induced by tool use may have facilitated the development of new neural territories,

forming a neural niche for the emergence of new cognitive abilities such as language (Iriki and Taoka, 2012). Indeed, expanding neural circuits may be *polysemic* and represent several functions that can gradually specialize and distinguish from each other, or in contrast remain represented in the same neural circuits (Iriki and Taoka, 2012). The fact that phonology and tool use are distinguishable and that semantic processing occurs within the tool-use network might result from neural recycling processes. In such way, we suggest brain regions devoted to tool use progressively subserved different functions and were able to build conceptual and semantic representations.

Finally, the co-localization of shared neural resources between tool use and semantics open new avenues for the rehabilitation field. Observation and imitation of movements improve verb production in aphasic patients (Marangolo et al., 2010). Furthermore, associating tool-use gestures with tool related semantics (i.e. explicitly verbalize tool functions) improved the condition of one out of the three patients suffering from apraxia included in a study (Stoll et al., 2020). Our findings encourage realization of studies over greater samples to assess the relevance for the generalization of such protocols.

References

- Anderson ML (2015) Précis of after Phrenology: Neural Reuse and the Interactive Brain. *Behav Brain Sci* 39.
- Aziz-Zadeh L, Wilson SM, Rizzolatti G, Iacoboni M (2006) Congruent Embodied Representations for Visually Presented Actions and Linguistic Phrases Describing Actions. *Curr Biol* 16:1818–1823.
- Baayen RH, Davidson DJ, Bates DM (2008) Memory and Language Mixed-effects modeling with crossed random effects for subjects and items. *J Mem Lang* 59:390–412.
- Barsalou LW (1999) Perceptual symbol systems. *Behav Brain Sci* 22:577–609.
- Binder JR, Desai RH, Graves WW, Conant LL (2009) Where Is the Semantic System? A Critical Review and Meta-Analysis of 120 Functional Neuroimaging Studies. *Cereb Cortex* 19:2767–2796.
- Blini E, Tilikete C, Farnè A, Hadj-Bouziane F (2018) Probing the role of the vestibular system in motivation and reward-based attention. *Cortex* 103:82–99.
- Boulenger V, Roy AC, Paulignan Y, Deprez V, Jeannerod M, Nazir TA (2006) Cross-talk between Language Processes and Overt Motor Behavior in the First 200 msec of Processing. *J Cogn Neurosci* 18:1607–1615.
- Brandi M-L, Wohlschläger A, Sorg C, Hermsdörfer J (2014) The Neural Correlates of Planning and Executing Actual Tool Use. *J Neurosci* 34:13183–13194.
- Brozzoli C, Gentile G, Ehrsson HH (2012) That's Near My Hand! Parietal and Premotor Coding of Hand-Centered Space Contributes to Localization and Self-Attribution of the Hand. *J Neurosci* 32:14573–14582.
- Brozzoli C, Roy AC, Lidborg LH, Lövdén M (2019) Language as a tool: Motor proficiency using a tool predicts individual linguistic abilities. *Front Psychol* 10:1–9.
- Buxbaum LJ, Saffran EM (2002) Knowledge of object manipulation and object function:

- dissociations in apraxic and nonapraxic subjects. *Brain Lang* 82:179–199.
- Cattaneo Z, Devlin JT, Salvini F, Vecchi T, Silvanto J (2010) The causal role of category-specific neuronal representations in the left ventral premotor cortex (PMv) in semantic processing. *Neuroimage* 49:2728–2734.
- Chao LL, Haxby J V., Martin A (1999) Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat Neurosci* 2:913–919.
- Chao LL, Martin A (2000) Representation of Manipulable Man-Made Objects in the Dorsal Stream. *Neuroimage* 12:478–484.
- Choi S, Na DL, Kang E, Lee K, Lee S, Na D (2001) Functional magnetic resonance imaging during pantomiming tool-use gestures. *Exp Brain Res* 139:311–317.
- D'Ausilio A, Pulvermüller F, Salmas P, Bufalari I, Begliomini C, Fadiga L (2009) The Motor Somatotopy of Speech Perception. *Curr Biol* 19:381–385.
- Dehaene S, Cohen L (2007) Cultural recycling of cortical maps. *Neuron* 56:384–398.
- Esteban O, Markiewicz CJ, Blair RW, Moodie CA, Ilkay Isik A, Erramuzpe A, Kent JD, Goncalves M, DuPre E, Snyder M, Oya H, Ghosh SS, Wright J, Durnez J, Poldrack RA, Gorgolewski KJ (2019) fMRIPrep: a robust preprocessing pipeline for functional MRI. *Nat Methods* 16:111–116.
- Fazio P, Cantagallo A, Craighero L, D'ausilio A, Roy AC, Pozzo T, Calzolari F, Granieri E, Fadiga L (2009) Encoding of human action in Broca's area. *Brain* 132:1980–1988.
- Foerster FR, Borghi AM, Goslin J (2020) Labels strengthen motor learning of new tools. *Cortex* 129:1–10.
- Gentile G, Guterstam A, Brozzoli C, Ehrsson HH (2013) Disintegration of Multisensory Signals from the Real Hand Reduces Default Limb Self-Attribution: An fMRI Study. *J Neurosci* 33:13350–13366.
- Goldenberg G, Randerath J (2015) *Neuropsychologia* Shared neural substrates of apraxia and

- aphasia. *Neuropsychologia* 75:40–49.
- Hickok G, Poeppel D (2007) The cortical organization of speech processing. *Nat Rev Neurosci* 8:393–402.
- Higuchi S, Chaminade T, Imamizu H, Kawato M (2009) Shared neural correlates for language and tool use in Broca's area. *Neuroreport* 20:1376–1381.
- Iriki A, Taoka M (2012) Triadic (ecological, neural, cognitive) niche construction: A scenario of human brain evolution extrapolating tool use and language from the control of reaching actions. *Philos Trans R Soc B Biol Sci* 367:10–23.
- Kriegeskorte N, Mur M, Bandettini P (2008) Representational similarity analysis - connecting the branches of systems neuroscience. *Front Syst Neurosci* 2:1–28.
- Marangolo P, Bonifazi S, Tomaiuolo F, Craighero L, Coccia M, Altoè G, Provinciali L, Cantagallo A (2010) Improving language without words: First evidence from aphasia. *Neuropsychologia* 48:3824–3833.
- Martin A, Chao LL (2001) Semantic memory and the brain: structure and processes. *Curr Opin Neurobiol* 11:194–201.
- Meister IG, Wilson SM, Deblieck C, Wu AD, Iacoboni M (2007) The Essential Role of Premotor Cortex in Speech Perception. *Curr Biol* 17:1692–1696.
- Meister IG, Wu AD, Deblieck C, Iacoboni M (2012) Early semantic and phonological effects on temporal- and muscle-specific motor resonance. *Eur J Neurosci* 36:2391–2399.
- Norman KA, Polyn SM, Detre GJ, Haxby J V (2006) Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends Cogn Sci* 10:424–430.
- Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9:97–113.
- Oosterhof NN, Connolly AC, Haxby J V (2016) CoSMoMVPA: Multi-modal multivariate pattern analysis of neuroimaging data in matlab/GNU octave. *Front Neuroinform* 10:1–

27.

- Pa J, Hickok G (2008) A parietal-temporal sensory-motor integration area for the human vocal tract: Evidence from an fMRI study of skilled musicians. *Neuropsychologia* 46:362–368.
- Papeo L, Hochmann J-R (2012) A cross-talk between brain-damage patients and infants on action and language. *Neuropsychologia* 50:1222–1234.
- Papeo L, Negri GAL, Zadini A, Rumiati RI (2010) Action performance and action-word understanding: Evidence of double dissociations in left-damaged patients. *Cogn Neuropsychol* 27:428–461.
- Patri J-F, Ostry DJ, Diard J, Schwartz J-L, Trudeau-Fisette P, Savariaux C, Perrier P (2020) Speakers are able to categorize vowels based on tongue somatosensation. *Proc Natl Acad Sci* 117:6255–6263.
- Peeters RR, Simone L, Nelissen K, Fabbri-Destro M, Vanduffel W, Rizzolatti G, Orban GA (2009) The Representation of Tool Use in Humans and Monkeys: Common and Uniquely Human Features. *J Neurosci* 29:11523–11539.
- Ponce de León MS, Bienvenu T, Marom A, Engel S, Tafforeau P, Alatorre Warren JL, Lordkipanidze D, Kurniawan I, Murti DB, Suriyanto RA, Koesbardiati T, Zollikofer CPE (2021) The primitive brain of early Homo. *Science* (80-) 372:165–171.
- Pulvermüller F (2005) Brain mechanisms linking language and action. *Nat Rev Neurosci* 6:576–582.
- Raizada RDS, Poldrack RA (2007) Selective Amplification of Stimulus Differences during Categorical Processing of Speech. *Neuron* 56:726–740.
- Rueschemeyer SA, Lindemann O, Rooij D Van, Dam W Van, Bekkering H (2010) Effects of intentional motor actions on embodied language processing. *Exp Psychol* 57:260–266.
- Schone HR, Maimon-Mor RO, Baker CI, Makin TR (2021) Expert tool users show increased

- differentiation between visual representations of hands and tools. *J Neurosci* 41:2980–2989.
- Scorolli C, Borghi AM (2006) Sentence comprehension and action: Effector specific modulation of the motor system. *Brain Res* 1130:119–124.
- Singmann H, Bolker B, Westfall J, Aust F, Ben-Shachar SM (2020) afex: Analysis of Factorial Experiments. R package version 0.27-2. <https://CRAN.R-project.org/package=afex>.
- Stoll H, de Wit MM, Middleton EL, Buxbaum LJ (2020) Treating limb apraxia via action semantics: a preliminary study. *Neuropsychol Rehabil* 0:1–18.
- Stout D, Chaminade T (2012) Stone tools, language and the brain in human evolution. *Philos Trans R Soc Lond B Biol Sci* 367:75–87.
- Thibault S, Py R, Gervasi AM, Salemm R, Koun E, Lövdén M, Boulenger V, Roy AC, Brozzoli C (under review) Tool use and language share syntactic processes and neural patterns in the basal ganglia.
- Uomini NT, Meyer GF (2013) Shared Brain Lateralization Patterns in Language and Acheulean Stone Tool Production: A Functional Transcranial Doppler Ultrasound Study. *PLoS One* 8:1–9.

Appendix

Prime	Target	Prime (translation)	Target (translation)	Condition
pieuvre	dauphin	octopus	dolphin	Animal Primed
cafard	araignée	cockroach	spider	Animal Primed
boeuf	vache	beef	cow	Animal Primed
chèvre	bouc	goat	goat	Animal Primed
pie	mouette	magpie	seagull	Animal Primed
crabe	oursin	crab	sea urchin	Animal Primed
libellule	papillon	dragonfly	butterfly	Animal Primed
lion	panthère	lion	panther	Animal Primed
cerf	biche	stag	doe	Animal Primed
rhinocéros	zèbre	rhinoceros	zebra	Animal Primed
corbeau	oie	crow	goose	Animal Primed
paon	autruche	peacock	ostrich	Animal Primed
guêpe	abeille	wasp	bee	Animal Primed
grenouille	vipère	frog	viper	Animal Primed
craie	stylo	chalk	pen	Tool Primed
javelot	raquette	javelin	racket	Tool Primed
brosse	peigne	brush	comb	Tool Primed
fouet	lasso	whip	lasso	Tool Primed
aspirateur	balai	vacuum	broom	Tool Primed
gomme	crayon	rubber	pencil	Tool Primed
équerre	compas	square	compass	Tool Primed
feutre	pinceau	felt	brush	Tool Primed
seringue	pipette	syringe	pipette	Tool Primed
décapsuleur	louche	bottle opener	ladle	Tool Primed
rame	pagaie	oar	paddle	Tool Primed
hache	machette	chopped	machete	Tool Primed

tronçonneuse	scie	chain saw	saw	Tool Primed
briquet	allumette	lighter	matche	Tool Primed
tortue	manivelle	turtle	crank	Animal Unprimed
mouche	agrafeuse	fly	stapler	Animal Unprimed
taureau	spatule	taurus	spatula	Animal Unprimed
cygne	stylet	swan	stylus	Animal Unprimed
mouton	cisaille	sheep	shears	Animal Unprimed
hippocampe	rasoir	seahorse	razoe	Animal Unprimed
coccinelle	batte	ladybug	bat	Animal Unprimed
lynx	chalumeau	lynx	blowtorch	Animal Unprimed
daim	arrosoir	deer	watering can	Animal Unprimed
âne	éplucheur	donkey	peeler	Animal Unprimed
canard	télécommande	duck	remote control	Animal Unprimed
perroquet	clef	parrot	key	Animal Unprimed
bourdon	canne	bumblebee	cane	Animal Unprimed
lézard	ponceuse	lizard	sander	Animal Unprimed
pelle	brebis	shovel	ewe	Tool Unprimed
tournevis	fourmi	screwdriver	ant	Tool Unprimed
épée	girafe	sword	giraffe	Tool Unprimed
lime	panda	lime	panda	Tool Unprimed
scalpel	puma	scalpel	puma	Tool Unprimed
pioche	koala	pickaxe	koala	Tool Unprimed
poignard	brochet	dagger	pike	Tool Unprimed
pince	écrevisse	pliers	crayfish	Tool Unprimed
hachoir	mésange	chopper	tit	Tool Unprimed
tamis	hippopotame	sieve	hippopotamus	Tool Unprimed
fourche	gorille	fork	gorilla	Tool Unprimed
aiguille	rat	needle	rat	Tool Unprimed
balayette	coq	brush	rooster	Tool Unprimed

crosse	loup	butt	wolf	Tool Unprimed
sanglier	tupou	boar	tupou	Pseudowords
aigle	telcite	eagle	telcite	Pseudowords
escargot	crapal	snail	crapal	Pseudowords
guenon	celnar	monkey	celnar	Pseudowords
hérisson	soricame	hedgehog	soricame	Pseudowords
écureuil	paceton	squirrel	paceton	Pseudowords
renard	létupien	fox	létupien	Pseudowords
grillon	fulet	cricket	fulet	Pseudowords
veau	gralut	calf	gralut	Pseudowords
crevette	permoriteur	shrimp	permoriteur	Pseudowords
huître	faurmeau	oyster	faurmeau	Pseudowords
ours	paindon	bear	paindon	Pseudowords
limace	granpoir	slug	granpoir	Pseudowords
salamandre	greplin	salamander	greplin	Pseudowords
râteau	cruine	rake	cruine	Pseudowords
marteau	ladontin	hammer	ladontin	Pseudowords
sabre	majot	saber	majot	Pseudowords
râpe	tranon	grated	tranon	Pseudowords
cutter	panton	cutter	panton	Pseudowords
massue	carporan	club	carporan	Pseudowords
canif	bimette	penknife	bimette	Pseudowords
sécateur	solaie	shears	solaie	Pseudowords
couteau	orunel	knife	orunel	Pseudowords
épuisette	rinot	net	rinot	Pseudowords
truelle	bafin	trowel	bafin	Pseudowords
perceuse	daillot	drill	daillot	Pseudowords
soufflet	pimeau	bellows	pimeau	Pseudowords
levier	riploir	lever	riploir	Pseudowords

Chapter 3

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Experimental contribution: Tool use and syntax²

² The paper presented is entitled *Tool use and language share syntactic processes and neural patterns in the basal ganglia* and is currently under revision.

Tool use and language share syntactic processes and neural patterns in the basal ganglia

Short title: Shared syntax for tool use and language

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Abstract:

Does tool use share syntactic processes with language? Acting with a tool is thought to add a hierarchical level into the motor plan. In the linguistic domain, syntax is the cognitive function handling interdependent elements. Using fMRI, we first reveal common neurofunctional substrates in the basal ganglia subserving both tool use and syntax in language. The two abilities elicit similar patterns of neural activity, indicating the existence of shared functional resources. Manual actions and verbal working memory do not contribute to this common network. In line with the existence of shared neural resources, we show bidirectional behavioral enhancement of tool use and syntactic skills in language so that training one function improves performance in the other. This reveals supramodal syntactic processes for tool use and language.

One Sentence Summary: Syntactic processes in the basal ganglia subserve both tool use and language such that training one ability boosts the other.

Dexterous tool use is a highly sophisticated skill whose sensory (1) and motor components (2) have been extensively studied across disciplines. Notably, tool use has been suggested to add a further hierarchical level to the motor plan (3–5). Interdependent elements and hierarchies are common in language, and decades of research have pointed to syntax as the cognitive function handling complex linguistic structures (6). Does tool use share syntactic processes with language? A wide range of cognitive processes exploit activity in sensorimotor regions (7, 8). This is the case for selective spatial attention (9), numerical cognition (10, 11) and, within the domain of language, phonological and semantic processes (12, 13). We posit that syntactic processes are also grounded in sensorimotor structures.

Center-embedded object relative sentences, a very well-studied syntactic model (14–16), provide a paradigmatic example of complex linguistic structures. In “*The writer that the poet admires reads the paper*”, the object relative clause introduced by the pronoun *that* is embedded in the main clause (“*The writer [Center-embedded relative clause] reads the paper*”). In such a sentence, the object of the verb of the relative clause precedes the subject (“*The writer that the poet admires [...]*”), thus altering the expected canonical subject-object order (namely, “*The poet admires the writer*”). Embedded clauses therefore split interdependent elements and add further dependencies in the sentence. However, by handling hierarchical sequential elements, syntactic processes allow us to understand such complex structures.

Neuropsychological research on acquired (17) and congenital syndromes (18, 19) as well as studies in neurotypical participants (20, 21) suggest that action and language share syntactic processes. Indeed, actions involve hierarchies of interdependent subcomponents within an entire motor sequence (22–25). Dexterous tool use, in particular, implies incorporating an external object (1). The functional combination of the body and an external object to perform an action (3) embeds a further level into the manual motor program (26). Goal-directed movements feature several subcomponents integrated in the action sequence (27), such as reaching, grasping, lifting, rotating and placing an object. This sequence provides an example of complex motor structures with several elements whose relationship needs to be subtly rearranged when the tool is embedded in the motor program (28, 29). Interestingly, an individual's tool-use dexterity in such a motor task predicts linguistic production skills in a syntactically constrained task (30). Neuroimaging investigations from the two separate domains support the behavioral link between tool use and language. Syntactic processing managing linguistic hierarchical structures relies on activity within the left inferior frontal gyrus [IIFG; (6, 14–16)] and basal ganglia [BG; (21, 31, 32)], in particular, within the striatum (33, 34).

Similarly, activity in a parieto-frontal network as well as in the BG supports skillful tool use (35–37). Brain imaging studies have therefore drawn partially overlapping neural networks for syntax (15, 21, 33) and tool use (35–38), where the BG and IIFG appear as the most likely shared neural suppliers of a common syntactic cognitive component. These lines of research have however so far diverged, and the anatomo-functional overlap between tool use and syntax remains anecdotal.

Here, we first evidenced neural overlap between tool use and syntactic processes in the basal ganglia, and representational similarity in the patterns of brain activity for the two abilities, in line with the existence of a supramodal syntactic function. We proved the specificity of these results by excluding that hand use, compared to tool use, or a verbal working memory control task, instead of syntax, contributed to the shared neural syntactic network. Multivariate classification of brain activity in the BG further revealed that syntactic patterns in language are predicted as being elicited by tool use rather than by manual action. Crucially, if tool use and language share a common syntactic function, we predict that training one modality will enhance the other. Indeed, training a specific cognitive ability can also benefit untrained tasks (39, 40) inasmuch as the trained and untrained functions share common neural resources and cognitive processes (39). We therefore exploited the mechanism of learning transfer to reveal that tool-use training, compared to manual action training, improves syntactic abilities to process linguistic structures that feature center-embedded object relatives. The reverse is also true: linguistic training with such syntactic structures improves motor performance with the tool. Such bidirectional enhancement of behavioral performance speaks in favor of a common syntactic function for tool use and language.

Anatomical overlap of tool use and syntactic activity in the basal ganglia

We first mapped the brain regions where tool use and syntactic processes overlap with fMRI. To isolate the syntactic network, 20 participants solved a task requiring to process center-embedded relative clauses (14, 15) (Experiment 1, Fig. 1A). The protocol consisted of the presentation of sentences relying on the same content words but featuring three different syntactic structures: either a coordinated (e.g., “*The writer admires the poet and reads the paper*”), subject relative (e.g., “*The writer that admires the poet reads the paper*”) or object relative clause (e.g., “*The writer that the poet admires reads the paper*”; Table 1A). Each sentence was followed by a test affirmation (e.g., “*The poet admires the writer*”; Table 1B),

which the participants had to judge as true or false with respect to the immediately preceding sentence. The participants fairly succeeded in this task (Fig. 1B) revealing, as expected, the worst sensitivity (d') scores and the longest reaction times (RTs) for the object relatives (mean \pm SEM: $d' = 1.25 \pm 0.12$; RTs = 1769 ± 97 ms) compared to both subject relatives ($d' = 1.98 \pm 0.06$; RTs = 1519 ± 76 ms; $p_s < 0.001$, Tukey post hoc) and coordinated clauses ($d' = 2.01 \pm 0.06$; RTs = 1487 ± 87 ms; $p_s < 0.001$). No difference was found between coordinated and subject relative clauses ($p_s > 0.74$). This pattern reflects the increased syntactic complexity of the object relatives with respect to the two other conditions (14). Accordingly, we assessed the functional syntactic network by contrasting brain activity elicited during the presentation of the object relatives with that elicited during the presentation of the two other sentence types. In agreement with previous studies, this window of interest targeted the processes underlying syntactic encoding of the sentence material rather than processes engaged in sentence reorganization to answer the affirmation test (15). The syntactic network consisted of activity in a parieto-frontal ensemble of cortical areas (Table S1A) as well as subcortically within the BG ($p_{s-fwe} < 0.05$ at the cluster level), encompassing the bilateral caudate nuclei, internal globus pallidus (GPi) and putamen. Frontal activity was observed within the IIFG ($p < 0.001$ unc.) in a cluster localized in Broca's area (Fig. 1C).

(A) Sentence Encoding

Coordinated Clauses	Subject Relative Clauses	Object Relative Clauses
<u>L'écrivain admire le poète</u> et écrit le papier <i>The writer admires the poet</i> and writes the paper (Canonical subject-object order)	<u>L'écrivain qui admire le poète</u> écrit le papier <i>The writer that admires the</i> <i>poet writes the paper</i> (Subject-object order compatible with the canonical order)	<u>L'écrivain que le poète admire</u> écrit le papier <i>The writer that the poet</i> <i>admires writes the paper</i> (Noncanonical subject-object order)

(B) Test Affirmation (one selected among the four)

L'écrivain admire le poète <i>The writer admires the poet</i>	Le poète admire l'écrivain <i>The poet admires the writer</i>
Le poète écrit le papier <i>The poet writes the paper</i>	L'écrivain écrit le papier <i>The writer writes the paper</i>

Table. 1. Syntactic task: comprehension of sentences in a 2-alternative forced choice (2-AFC) task. (A)

Syntactic structures presented during the sentence-encoding phase. **(B)** Test affirmation for the 2-AFC task.

To identify the overlap between the syntactic and tool-use networks, we required the same participants to use a pair of 30 cm-long pliers, or their free right hand in different trials, to move a peg from one side of a board to the other (Fig. 1D and Movies S1 and S2). We recorded their brain activity while they prepared and executed the movement with the tool or their free hand. The planning phase engages processes necessary to the organization of the components of the subsequent action (24), and is not influenced by the visual differences present during overt movement execution. We therefore isolated the activity specifically related to the preparation of movements with the tool and subtracted the activity related to preparation of manual movements and to movement execution with the tool and the hand (see Supplementary Text for contrasts defined to investigate planning and execution of free-hand actions and tool-use execution). Tool-use planning involved a network encompassing parietal and prefrontal areas (Table S1B) as well as the BG ($p_{s-fwe} < 0.05$ at the cluster level), including the bilateral caudate nuclei, putamen and GPi (Fig. 1E). A frontal region within the IIFG ($p < 0.001$ unc.) was also activated, which was located in the ventral premotor cortex (PMv), an area more posterior than the area identified in the syntactic task. The syntactic and tool-use planning networks thus anatomically overlapped within the BG, sharing significant activations of the left caudate nucleus (lCau) and bilateral GPi (Fig. 1F and Table S1C). Interestingly, even though syntax and tool-use planning both relied on the IIFG, the respective clusters of activation did not overlap (even at a lenient threshold $p < 0.005$ unc.). We employed a stringent contrast for tool-use planning (Fig. 1G-I), nonetheless we sought potential overlap between free-hand planning and syntax at the whole brain level but did not find any significant cluster of shared activation (Supplementary Text for the free-hand planning neural activity). Although syntax has been disentangled from working memory resources (15), the latter might still support the processing of complex syntactic structures. To rule out such contribution of working memory to the overlap between tool-use planning and syntactic networks, we measured brain activity in the same participants while they performed two verbal *n-back* tasks with two levels of difficulty (Fig. S1, Supplementary Text for behavioral results). As expected, working memory mainly recruited a network involving the bilateral inferior parietal lobes (angular gyri), the left middle frontal gyrus and the left caudate (Fig. S2 and Table S2). Importantly, the working memory brain map did not significantly overlap with the tool-use planning network. This functional control excludes working memory processes or unspecific difficulty as accounting for shared activations between tool-use planning and complex syntax processing.

Fig. 1. Experiment 1: Overlap of syntax and tool-use planning activity. (A) Set-up and experimental design of the syntactic task. (B) Sensitivity index (d' , left graph) and Reaction Times (RTs; right graph) for the syntactic comprehension of the three sentence structures: both the one-way repeated measures ANOVA carried out on the sensitivity (d') and the linear mixed model on RTs showed a significant main effect of Sentence (d' : $F_{(1.6,30.6)} = 40.04$; $p < 0.001$; $\eta_G^2 = 0.49$; RTs: $\chi^2_{(2)} = 25.21$, $p < 0.001$). Error bars show standard errors. *** $p < 0.001$, Tukey post hoc. (C) Statistical maps thresholded at $p < 0.001$, unc., for syntax (object relatives compared to the two other sentence types). (D) Set-up and experimental design of tool-use and free-hand motor tasks. (E) Statistical maps thresholded at $p < 0.001$, unc., for tool-use planning. (F) Joint neuronal activity for syntax and tool-use planning in the basal ganglia, thresholded at $p < 0.001$, unc. (G-I) Average brain activity level in each cluster significantly activated by both tasks. The highest activations were found for tool-use planning (blue) and object relative clauses (yellow) in the motor and syntactic tasks, respectively.

Common neurocognitive resources for tool-use planning and syntax in the basal ganglia

Does the neural overlap of activity subserving tool-use planning and syntax within the BG reflect common cognitive processes? Were this true, the same neural resources should be recruited across conditions. Accordingly, brain activities underlying tool-use planning and syntactic encoding during object relative sentences may show representational similarity in their respective spatial distribution within the overlapping clusters.

To assess this prediction, we studied the representational similarity of brain activity patterns (41) across the two motor (tool-use and free-hand planning) and the two most complex linguistic conditions (object and subject relatives). Considering the overlapping voxels revealed by the conjunction analysis ($n=41$), we tested two models, including the similarity expected between conditions of the same domain (tool use and free hand for the motor domain and object and subject relatives for the linguistic domain). Crucially, the first model tested the hypothesis of cross-domain similarity between activity patterns for tool-use planning and object relatives. The second control model instead tested for cross-domain similarity between free-hand planning and object relatives. The model assessing the representational similarity between tool-use planning and object relatives was significant (*Pearson's r* mean = 0.25 ± 0.08 ; *Fisher's z* mean = 0.29 ± 0.10 ; $t_{(19)} = 3.00$; $p = 0.007$ Bonferroni-corrected, Cohen's $d = 0.66$). In contrast, the second model testing for a similarity between free-hand planning and object relatives did not yield a good fit for the data (*Pearson's r* mean = 0.14 ± 0.09 ; *Fisher's z* mean = 0.19 ± 0.11 ; $t_{(19)} = 1.63$; $p = 0.12$ Bonferroni-corrected). To test for the specificity of the similarity between tool-use and object relative patterns, we conducted an additional control analysis. We extracted the patterns elicited by the verbal working memory tasks (*3-back* and *1-back*) on the same voxels and entered them in our models instead of the syntactic patterns. This did not reveal any significant similarity neither with tool-use nor with free-hand planning ($t_s < 1.36$; $p_s > 0.18$, Bonferroni-corrected; Supplementary Text).

We further examined whether the reported significant similarity allows a classifier trained on the motor patterns (tool use and free hand) to coherently predict those elicited by object relatives. A successful cross-domain classification would indicate that the patterns of neural activity underlying tool use and syntax in language are the same, therefore corroborating the evidence for common neural resources shared by the two abilities. We applied a classification based MultiVoxels Patterns Analysis (MVPA) on the patterns of activity extracted from the overlapping voxels identified with the conjunction analysis ($N=41$). A Support Vector Machine (SVM) classifier was trained on the motor data (tool-use planning vs. free-hand planning) and

tested cross-domain on the object relative data, with a leave-one-subject-out procedure. We assessed the accuracy of the classifier as the proportion of object relative neural patterns classified as tool-use patterns. An accuracy of 0.5 indicates that the classifier performed at chance, namely equally classifying object relative as tool-use or free-hand patterns. Crucially, an accuracy significantly above chance level means that object relative patterns were classified more as tool-use than as free-hand patterns, whereas accuracy values significantly below 0.5 indicate the opposite. Testing against a null distribution derived after 10,000 permutations, the MVPA revealed that object relative patterns were significantly classified as tool-use rather than free-hand planning patterns (accuracy = 0.87, $p = 0.003$). As a control, when tested cross-domain on the working memory neural patterns (*3-back*) within the same voxels, the accuracy of the same classifier was not significantly different from chance level (accuracy = 0.64, $p = 0.15$, Supplementary Text).

As a further step, we studied whether the similarity is maintained more locally in each individual cluster, by computing voxelwise Pearson's correlation scores between activity levels supporting tool-use planning and successful comprehension of object relatives (42). These correlation scores were compared to correlation scores found between free-hand planning and object relative processing. To this aim, we compared the difference between the two observed *Pearson's r* values to an empirical null distribution of differences obtained after 10,000 permutations. Crucially, the observed correlation between patterns for tool-use planning and object relative comprehension was significantly larger than that between free-hand planning and object relatives, both for the IGPI and rGPI (IGPI: *Pearson's r difference* = 0.61; $p = 0.03$ and rGPI: *Pearson's r difference* = 0.79; $p = 0.007$; Fig. 2A-F and Supplementary Text). The difference was not significant for the ICau (*Pearson's r difference* = -0.08; $p = 0.64$).

Overall, these findings establish that tool use and syntax rely on neural activity within common anatomical territories in the BG. The activity independently elicited by the two tasks displays similar spatial distribution, so that object relative patterns are consistently classified as being elicited by tool-use planning. This is consistent with the fact that common neural resources are recruited by the two tasks. Importantly, it has been documented that when two functions share neural resources and cognitive processes, learning transfer occurs (39): training a specific ability can therefore benefit an untrained one (39, 40). Consequently, we predict cross-domain learning transfer between tool use and syntactic skills in language.

Fig. 2. Experiment 1: Functional link between tool-use planning and syntax in the basal ganglia. (A, B and C) Distribution, after 10,000 permutations, of differences of *Pearson's r* computed for the correlations between patterns of brain activity for object relative clauses and those for motor planning of tool use and free hand separately, for the lCau (A), lGPi (B) and rGPi (C). Larger positive differences indicate stronger similarity between tool-use planning and object relative processing compared to free-hand planning and object relatives. The black line indicates the observed difference, and the red dotted line depicts the *p-value* threshold set at 0.05. (D, E and F) Spatial distribution of neural activity for tool-use planning, object relatives and free-hand planning in the basal ganglia. Each single colored square represents a single voxel for the lCau (D), lGPi (E) and rGPi (F).

Learning transfer from tool use to syntactic skills in language

Accordingly, in Experiment 2 we tested whether tool-use training improves syntactic skills in language. We employed the same syntactic task employed in Experiment 1 to measure syntactic skills in 26 naive healthy adults before and after tool-use training (Fig. 3A). The specificity of tool use was controlled for by testing a distinct group (N=26) undergoing an identical training regime but with the free hand. A third passive control group (N=26) was also included to quantify potential test-retest effects: those participants were assessed in the same syntactic task before and after watching natural documentary videos for an equivalent amount of time as the two active groups engaged in motor training. The three groups were comparable in terms of relevant sociodemographic characteristics (i.e., age, education level and handedness, Supplementary Text).

To assess the learning transfer to the syntactic task, we ensured that the participants significantly improved in their respective motor training (Fig. 3B; Supplementary Text). Then, we analyzed the impact of tool-use training, compared to both free-hand training and passive video watching, on performance in the syntactic task. We accounted for potential inter-individual differences in the initial syntactic level by including pre-test performance (d') as a covariate in a 3-way *Training* \times *Time* \times *Sentence* ANCOVA run on RTs (see Supplementary Text for the corresponding ANOVA without the continuous factor in the model). The improvement in syntax indeed depended on the type of training and the participants' initial level of syntactic performance [$F_{(2,72)}=3.99$; $p = 0.02$; $\eta_G^2 = 0.009$]. As the participants with lower scores before training are more prone to contextual improvements with task repetition (43), we specifically examined the training-dependent effects separating participants with low from those with high initial syntactic skills. To this aim, we set a d' threshold based on the performance in the pre-test session, defined as the sample median minus one standard deviation (threshold $d' > 1.38$). Participants with lower syntactic skills (tool-use group: N=8; free-hand group: N=6; video group: N=6) significantly improved with all sentence structures at post-test and independent of training (Supplementary Text). This test-retest amelioration, potentially linked to more contextual aspects of the task such as motor and response selection, may hide potential selective effects of training. Crucially, in the participants showing higher initial syntactic skills (tool-use group: N=18, free-hand group: N=20, video group: N=20), tool-use training significantly improved syntactic performance compared to both free-hand training and passive video watching (significant *Training* \times *Time* \times *Sentence* interaction of the linear mixed model (LMM): $\chi^2_{(4)} = 13.6$, $p = 0.009$; Fig. 3C). Specifically, after tool use, the participants

were significantly faster in correctly processing object relatives than before (pre-test RTs = 1892 ± 137 ms vs. post-test RTs = 1591 ± 133 ms, $p < 0.001$, Tukey post hoc). In contrast, performance for object relatives did not significantly change for the two control groups (free hand: pre-test RTs = 1994 ± 109 ms vs. post-test RTs = 1910 ± 109 ms, $p = 0.17$; video: pre-test RTs = 2051 ± 119 ms vs. post-test RTs = 1940 ± 128 ms, $p = 0.10$). Comprehension of object relatives was indistinguishable across the three groups before training ($p_s > 0.63$). A significant improvement was found for simpler syntactic structures, namely coordinated and subject relative clauses; nevertheless, these improvements were equivalent among the three groups (Fig. S3C and D, Supplementary Text).

Fig. 3. Experiments 2 and 3: Cross-domain learning transfer from tool use to syntactic skills in language.

(A) Timeline of training and syntactic pre- and post-tests. Different groups were trained either to use a tool (purple inset) or the free hand (green inset) to grab-and-enter key-shaped pegs into grooved holes, or they passively watched videos (gray inset). In Experiment 3, training difficulty was controlled with a further manual training condition (red inset) with increased sensorimotor constraints mimicking those present during tool use. (B) Motor improvement during tool-use (purple) and free-hand training (green) in Experiment 2. (C) In Experiment 2, participants with high initial syntactic skills improved for object relatives in the syntactic task after training with the tool (purple bars), but not after free-hand training (green bars) or passive video watching (gray bars). Connected dots across pre- and post-test represent individual data. (D) Motor improvement during tool-use (purple), free-hand (green) and constrained-hand training (red) in Experiment 3. (E) In Experiment 3, after tool use, the participants improved for object relatives in the syntactic task (purple bars), but not after training with the free hand (green bars) or with the hand mimicking similar sensorimotor constraints as the tool [red bars; significant *Training* \times *Time* \times *Sentence* interaction of the three-way repeated measure ANOVA (rmANOVA): $F_{(3,1,56,4)} = 2.81$; $p = 0.04$; $\eta_G^2 = 0.03$]. (F) Effect size of the improvements in Experiments 2 and 3. 2-way *Training* \times *Experiment* rmANOVA: significant main effect of *Training* ($F_{(1,60)} = 5.37$; $p = 0.02$; $\eta_G^2 = 0.082$), non-significant effect of *Experiment* ($F_{(1,60)} = 2.8$; $p = 0.11$) nor any interaction ($F_{(1,60)} = 0.51$; $p = 0.58$). *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

These results provide the first evidence that training to use a tool improves syntactic abilities in a linguistic task. This effect depended on the individuals' initial syntactic level and was found in those participants showing better syntactic skills before training. To corroborate this finding, we performed an additional experiment (Experiment 3) in which we included a sample of 39 naive participants showing high syntactic scores in the pre-test session. As an independent criterion for inclusion in this new sample of participants, we adopted the threshold of syntactic performance before training identified in Experiment 2 ($d' > 1.38$). Furthermore, to rule out the sensorimotor difficulty of the tool-use task as a factor contributing to learning transfer, we added a training condition where we reduced the degrees of freedom of free-hand movements to mimic those imposed by the tool. To this aim, we introduced sensorimotor constraints in free-hand motor training by instructing participants to cross their middle and index fingers to form a pinch (between the middle finger pad and the index nail) and to use this to grab and enter pegs into the board (Supplementary Text). Tactile feedback was furthermore hampered (Fig. 3A). These changes were meant to provide a good simulation of pliers' sensorimotor constraints and difficulty. Crucially, two groups underwent either tool-use or free-hand training as in Experiment 2 to replicate our findings in an independent sample of participants with high syntactic skills. The third group was assigned to the control training condition with the constrained hand. Syntactic skills were measured in the three groups as in the previous assessments, before and after motor training.

First, we reaffirmed that tool-use training selectively improved comprehension of object relatives [Fig. 3E; pre-test $d' = 1.59 \pm 0.11$; post-test $d' = 2.1 \pm 0.08$; $p < 0.001$, Tukey post hoc; significant *Training* \times *Time* \times *Sentence* interaction of the three-way repeated measure ANOVA (rmANOVA): $F_{(3,1,56,4)} = 2.81$; $p = 0.04$; $\eta_G^2 = 0.03$]. Second, neither free-hand (pre-test $d' = 1.59 \pm 0.14$; post-test $d' = 1.77 \pm 0.16$; $p = 0.10$) nor constrained-hand (pre-test $d' = 1.50 \pm 0.14$; post-test $d' = 1.67 \pm 0.18$; $p = 0.12$) training enhanced the performance for object relatives in a statistically significant way. After training, the tool-use group significantly outperformed both the free- ($p = 0.04$) and constrained-hand groups ($p = 0.005$) in the comprehension of object relatives. A difference between groups was observed for simpler syntactic structures (Fig. S3C and D, Supplementary Text). Furthermore, the magnitude of transfer, assessed with the effect size, was consistent with the syntactic improvement observed in Experiment 2 (Fig. 3F and Supplementary Text). Overall, these results provide further proof that tool use improves complex syntactic abilities in language. Moreover, by ruling out sensorimotor difficulties as the

driving factor, they point to the shared computational processes between tool use and processing of syntactic structures as the origin of learning transfer.

Learning transfer from syntactic training in language to tool use

In line with the previous conclusion, shared neurofunctional resources between tool use and language also predict the reversed learning transfer: training syntactic processes with complex sentences should improve tool use. In the single-blind Experiment 4, we tested this prediction by measuring tool-use performance in 48 naive healthy adults before and after syntactic training in language (Fig. 4A). Participants were randomly assigned to train with either object or subject relative clauses. Before and after syntactic training, we measured the number of pegs entered with the tool in an adapted version of the motor task devised in the previous Experiments 2 and 3. Participants underwent four pre-test and four post-test blocks of 2-minutes to assess their ability with the tool. The experimenter was blinded with respect to the type of syntactic training the participant was assigned to. The two groups were comparable in terms of relevant sociodemographic characteristics (i.e., age, education level and handedness, Supplementary Text). Given the shared syntactic processes recruited by complex linguistic structures and tool use, we expected the participants to perform better with the tool after training with object rather than with subject relatives.

Fig. 4. Experiment 4: Cross-domain learning transfer from syntax in language to tool use. (A) Timeline of syntactic training in language and motor pre- and post-tests with the tool. Different groups were tested in entering pegs as fast as possible with the tool, before and after training either to process object relative (blue) or subject relative clauses (orange). (B-C) Linguistic progress in RTs (B) and sensitivity (d') (C) during syntactic training of Experiment 4. (D) Motor performance, assessed with the number of pegs inserted with the tool equally improved in pre-test for the two groups. In post-test, only the group trained with object relatives (blue) kept improving, whereas the group trained with subject relatives (orange) did not (significant *Training* \times *Time* \times *Sentence* interaction of the LMM: $\chi^2_{(3)} = 9.88, p = 0.01$). (E) Motor improvement quantified with the slope of the regression line along the progression from the 1st to the 4th block of tool-use before (Pre) and after (Post) training with syntactic structures in language in Experiment 4. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Both groups improved in processing relative sentences during training (Fig. 4B-C). During pre-test, the two groups improved similarly in using the tool from the 1st to the 4th block. Crucially, in post-test, participants who trained with object relatives were able to enter significantly more pegs with the tool compared to those trained with subject relatives (significant *Time* \times *Block* \times *Training* interaction of the LMM $\chi^2_{(3)} = 9.88$, $p = 0.01$, Fig. 4D). Participants who trained with object relatives kept improving significantly with the tool (inserted pegs for block 4 pre-test = 12.9 ± 0.6 vs. blocks 3 post-test = 15.9 ± 0.6 and 4 post-test = 15.7 ± 0.7 , $p_s < 0.001$; and no difference compared to blocks 1 post-test = 13.0 ± 0.7 and 2 post-test = 14.3 ± 0.6 , $p_s > 0.30$; Fig. 4D). In contrast, at no point after training with subject relatives, participants' motor performance differed from the best score before training (inserted pegs for block 4 pre-test = 12.8 ± 0.8 vs. blocks 1 post-test = 12.6 ± 0.77 or 2 post-test = 13.8 ± 0.7 or 3 post-test = 13.1 ± 0.9 or 4 post-test = 14.0 ± 0.8 , $p_s > 0.54$). To better highlight the different progression of the two groups depending on their respective training, we calculated the slope of the regression line modeling individual motor performance along the blocks, before and after training separately (Supplementary Text). The slope was used to index motor improvement. A positive slope indicates that motor performance with the tool improved along the blocks, whereas a negative or horizontal slope stands for no improvement. A 2-way *Training* \times *Time* rmANOVA revealed a significant interaction [$F_{(1,46)} = 4.57$; $p = 0.03$; $\eta_G^2 = 0.05$]. The motor progression of the two groups was indistinguishable before training (subject relative group $\beta = 1.18 \pm 0.20$ vs. object relative group $\beta = 0.92 \pm 0.21$, $p = 0.91$). After training, the object relative group further improved ($\beta = 0.95 \pm 0.21$), as demonstrated by the significant difference between the observed slope and a horizontal line ($t_{(23)} = 4.47$, $p < 0.001$, Bonferroni-corrected, Cohen's $d = 0.91$) and by the comparison with the subject relative group ($\beta = 0.35 \pm 0.20$, $p = 0.03$). After training, this latter group stopped improving ($p = 0.005$ compared to before training and $t_{(23)} = 1.76$, $p = 0.18$ compared to a flat line). Altogether, the results of the behavioral experiments therefore demonstrate that the shared syntactic function between tool use and language allows for bidirectional cross-domain learning transfer.

Discussion

Our findings provide major new insights as to the neurocognitive links between tool use and syntax in language as well as to the principles underpinning cross-domain transfer. First, we showed that tool use and syntax rely on brain activity of anatomically overlapping neural

networks, particularly in striatal structures (ICau) and the GPi. Second, we found that tool-use and syntax elicit similar activity patterns, consistent with common neural processes for both tasks.

These findings point to the BG as the site of common neurocognitive resources for tool use and syntax and bolster the hypothesis of a supramodal syntactic function serving both action and language (20, 25). This is in line with the documented role of the dorsal striatum in processing complex hierarchical structures in both the motor (24) and linguistic domains (33). The dorsal striatum indeed supports a wide range of procedural learning processes across several species (44–46) and tasks (24, 47). This part of the procedural system is involved in syntactic training (47) and in the implementation of grammatical rules (21, 33). Furthermore, it acts as a parser of actions to chunk motor sequences (24, 48). Accurate and efficient tool use requires embedding an external object into the motor sequence, therefore relying more on the striatum than manual actions to parse the motor primitives (4). During dexterous tool use, hand movements integrate the functional structure of the tool in order to maintain an efficient interaction with the action target. The sensorimotor transformations imposed by the tool (28) constitute the additional level embedded to the manual motor program. Similar parsing and hierarchy handling support syntactic comprehension of center-embedded object relatives (21, 33, 34). These functional similarities are reflected by the neural overlap we revealed between tool use and syntax. It is worth noting that this overlap was found in the BG but not within the left IFG. In keeping with its documented involvement in both tool use (35) and language (15), the IIFG was recruited by both functions, yet in two separately clustered regions. This occurred more posteriorly in the PMv for tool use and more anteriorly in Broca's area for syntactic comprehension, in accordance with the cytoarchitectonic and functional specialization of IIFG for motor and linguistic processing, respectively (49, 50).

These results laid the empirical foundations for the demonstration of cross-domain learning transfer from tool use to syntactic skills in language and from linguistic syntax training to skilled tool use. Learning transfer arises provided that trained and untrained tasks rely on overlapping neural networks and shared cognitive processes (39). To date, transfer effects have been demonstrated from trained to untrained tasks belonging to the same domain: perception (51), motor (52) or cognitive control (39, 40, 43). Crucially, we extended to different cognitive domains the principle of transfer that had so far been limited to a single domain (39, 40, 51, 52). Our findings emphasize that tool use improves correct processing of object relative clauses and, reciprocally, training to process object relative clauses improves tool use. Thus, the transfer holds true even when different cognitive domains, such as action and language, are involved.

As a corollary to this principle, if trained and untrained tasks do not share common neurocognitive resources, transfer might be tempered or absent. Indeed, training with subject relative structures did not improve motor performance with the tool and free-hand training failed to induce benefits to syntax in the comprehension of complex structures. Furthermore, the benefits induced by tool use over language were not based on the mere additional sensorimotor complexity of the action executed with the tool compared to the free hand. After training with a hand configuration that involved similar sensorimotor constraints imposed by the tool, the participants did not show any advantage in processing complex syntactic structures with respect to the participants training with the free hand. Crucially, the learning transfer between tool use and syntactic processes in language occurs bidirectionally. This finding unambiguously indicates that the two abilities rely on a common cognitive component, namely a supramodal syntax. It also suggests that the neural resources underlying the shared function can be similarly mobilized by either of the two abilities to improve the other.

What drives this cross-domain transfer? Pre-activation of common resources as well as fast plasticity within shared circuitries can underlie the reciprocal boosting of behavioral performance in tool use and syntax processing in language. One possibility is that training would act as a functional prime for the subsequent task: training-dependent neuronal responses are elicited by tool use or sentence processing, thus yielding neuronal adaptation and more efficient activity (53). This in turn facilitates the subsequent behavioral performance for the untrained task relying on the same neural assemblies (54, 55). Alternatively, but not exclusively, cross-domain transfer may rely on fast plastic changes within common circuitries. Short motor training (i.e., less than 2 hours) triggers rapid functional (44) as well as local structural changes, accompanied by improvements in behavioral performance (56, 57). The untrained task may benefit from such plastic changes and recruit new resources within the shared territories. These results raise the question of whether an optimal training duration could maximize the benefits. In the theoretical framework of the expansion-renormalization hypothesis (57), a thrilling opportunity would be to take advantage of the temporal dynamics of plastic changes, for instance, by testing syntax while new neural resources are locally and temporarily available during the course of tool-use training.

Overall, our findings reignite the hypothesis of a coevolution of tool use and language (58-60). Longstanding theories have claimed a motor origin of language during evolution (25, 61). The advent and refinement of tool use may have offered the neural niche for the coevolution of new cognitive skills serving both motor and communicative aims (5, 58, 62, 63). According to this

account, the role of tool use has been twofold. On the one hand, the sophistication of tool use and tool making has put forward the need for cognitive functions to efficiently chunk, temporally parse and deal with hierarchies of sequences (60). On the other hand, tool use and tool making pose evolutionary pressure for communication, allowing better social transmission of knowledge (63). Functions responding to demands of the motor system would therefore have met communicative needs and progressively been exapted and recycled for language (62, 64). Such a coevolution scenario has involved a large brain network, from parietal (58, 60) to frontal regions (60, 65), and including the BG (66). Supporting this view, studies have shown that inoculation in mice of a human version of FOXP2, a gene involved in language sequencing, revealed neuronal plasticity within the striatum accompanied by enhanced procedural learning (67) and changes in mouse vocalizations (68). Findings on species phylogenetically closer to humans converge in supporting the existence of commonalities between tool use and early forms of communication (69, 70). For instance, lateralization of fine motor skills allowing for tool use is heritable in chimpanzees (69) and favors a common manual preference for dexterous tool use and communicative gestures (70). Here, we provide central human evidence pointing to the BG in particular as the neural niche for a supramodal syntactic function serving both action and language. In conclusion, our findings show that the motor system can be exploited to promote other cognitive functions that partly share the same neurocognitive foundations.

References

1. L. E. Miller, L. Montroni, E. Koun, R. Salemme, V. Hayward, A. Farnè, Sensing with tools extends somatosensory processing beyond the body. *Nature*. **561**, 239–242 (2018).
2. S. H. Johnson-Frey, The neural bases of complex tool use in humans. *Trends Cogn. Sci.* **8**, 71–78 (2004).
3. P. M. Greenfield, Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. *Behav. Brain Sci.* **14**, 531–551 (1991).
4. K. Pastra, Y. Aloimonos, The minimalist grammar of action. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 103–117 (2012).
5. J. Steele, P. F. Ferrari, L. Fogassi, From action to language: Comparative perspectives on primate tool use, gesture and the evolution of human language. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 4–9 (2012).
6. M. Ben-Shachar, T. Hendler, I. Kahn, D. Ben-Bashat, Y. Grodzinsky, The Neural Reality of Syntactic Transformations: Evidence from Functional Magnetic Resonance Imaging. *Psychol. Sci.* **14**, 433–440 (2003).
7. L. W. Barsalou, Grounded Cognition. *Annu. Rev. Psychol.* **59**, 617–645 (2008).
8. F. Pulvermüller, L. Fadiga, Active perception: sensorimotor circuits as a cortical basis for language. *Nat. Rev. Neurosci.* **11**, 351–360 (2010).
9. L. Craighero, L. Fadiga, G. Rizzolatti, C. Umiltà, Action for perception: A motor-visual attentional effect. *J. Exp. Psychol. Hum. Percept. Perform.* **25**, 1673–1692 (1999).
10. C. Brozzoli, M. Ishihara, S. M. Göbel, R. Salemme, Y. Rossetti, A. Farne, Touch

- perception reveals the dominance of spatial over digital representation of numbers. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 5644–5648 (2008).
11. M. H. Fischer, A. D. Castel, M. D. Dodd, J. Pratt, Perceiving numbers causes spatial shifts of attention. *Nat. Neurosci.* **6**, 555–556 (2003).
 12. O. Hauk, I. Johnsrude, F. Pulvermüller, Somatotopic Representation of Action Words in Human Motor and Premotor Cortex. *Neuron.* **41**, 301–307 (2004).
 13. S. M. Wilson, A. P. Saygin, M. I. Sereno, M. Iacoboni, Listening to speech activates motor areas involved in speech production. *Nat. Neurosci.* **7**, 701–702 (2004).
 14. M. A. Just, P. A. Carpenter, T. A. Keller, W. F. Eddy, K. R. Thulborn, Brain activation modulated by sentence comprehension. *Science.* **274**, 114–116 (1996).
 15. M. Makuuchi, J. Bahlmann, A. Anwender, A. D. Friederici, Segregating the core computational faculty of human language from working memory. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 8362–8367 (2009).
 16. A. Santi, Y. Grodzinsky, Working memory and syntax interact in Broca’s area. *Neuroimage.* **37**, 8–17 (2007).
 17. P. Fazio, A. Cantagallo, L. Craighero, A. D’ausilio, A. C. Roy, T. Pozzo, F. Calzolari, E. Granieri, L. Fadiga, Encoding of human action in Broca’s area. *Brain.* **132**, 1980–1988 (2009).
 18. A. C. Roy, A. Curie, T. Nazir, Y. Paulignan, V. des Portes, P. Fournieret, V. Deprez, Syntax at Hand: Common Syntactic Structures for Actions and Language. *PLoS One.* **8**, 1–11 (2013).
 19. F. Vargha-Khadem, K. Watkins, K. Alcock, P. Fletcher, R. Passingham, Praxic and nonverbal cognitive deficits in a large family with a genetically transmitted speech and

- language disorder. *Proc. Natl. Acad. Sci. U. S. A.* **92**, 930–933 (1995).
20. F. Pulvermüller, The syntax of action. *Trends Cogn. Sci.* **18**, 219–220 (2014).
 21. M. T. Ullman, A neurocognitive perspective on language: The declarative/procedural model. *Nat. Rev. Neurosci.* **2**, 717–726 (2001).
 22. E. Koechlin, T. Jubault, Broca’s Area and the Hierarchical Organization of Human Behavior. *Neuron.* **50**, 963–974 (2006).
 23. L. Maffongelli, E. Bartoli, D. Sammler, S. Kölsch, C. Campus, E. Olivier, L. Fadiga, A. D’Ausilio, Distinct brain signatures of content and structure violation during action observation. *Neuropsychologia.* **75**, 30–39 (2015).
 24. M. J. D. Martins, R. Bianco, D. Sammler, A. Villringer, Recursion in action : An fMRI study on the generation of new hierarchical levels in motor sequences. *Hum. Brain Mapp.* **40**, 1–16 (2019).
 25. A. C. Roy, M. A. Arbib, *The syntactic motor system* (John Benjamins Publishing Company, Amsterdam / Philadelphia, 2005).
 26. L. Cardinali, F. Frassinetti, C. Brozzoli, C. Urquizar, A. C. Roy, A. Farnè, Tool-use induces morphological updating of the body schema. *Curr. Biol.* **19**, 1157 (2009).
 27. M. Jeannerod, Visuomotor channels: Their integration in goal-directed prehension. *Hum. Mov. Sci.* **18**, 201–218 (1999).
 28. L. Cardinali, C. Brozzoli, L. Finos, A. C. Roy, A. Farnè, The rules of tool incorporation : Tool morpho-functional & sensori-motor constraints. *Cognition.* **149**, 1–5 (2016).
 29. Y. Itaguchi, K. Fukuzawa, Hand-use and tool-use in grasping control. *Exp. Brain Res.* **232**, 3613–3622 (2014).

30. C. Brozzoli, A. C. Roy, L. H. Lidborg, M. Lövdén, Language as a tool: Motor proficiency using a tool predicts individual linguistic abilities. *Front. Psychol.* **10**, 1–9 (2019).
31. M. P. Alexander, M. A. Naeser, C. L. Palumbo, Correlations of subcortical CT lesion sites and aphasia profiles. *Brain.* **110**, 961–988 (1987).
32. M. Grossman, A. Cooke, C. DeVita, C. Lee, D. Alsop, J. Detre, J. Gee, W. Chen, M. B. Stern, H. I. Hurtig, Grammatical and resource components of sentence processing in Parkinson’s disease: An fMRI study. *Neurology.* **60**, 775–781 (2003).
33. A. Moro, M. Tettamanti, D. Perani, C. Donati, S. F. Cappa, F. Fazio, Syntax and the brain: Disentangling grammar by selective anomalies. *Neuroimage.* **13**, 110–118 (2001).
34. M. Teichmann, C. Rosso, J. B. Martini, I. Bloch, P. Brugières, H. Duffau, S. Lehericy, A. C. Bachoud-Lévi, A cortical-subcortical syntax pathway linking Broca’s area and the striatum. *Hum. Brain Mapp.* **36**, 2270–2283 (2015).
35. M.-L. Brandi, A. Wohlschläger, C. Sorg, J. Hermsdörfer, The Neural Correlates of Planning and Executing Actual Tool Use. *J. Neurosci.* **34**, 13183–13194 (2014).
36. F. E. Garcea, L. J. Buxbaum, Gesturing tool use and tool transport actions modulates inferior parietal functional connectivity with the dorsal and ventral object processing pathways. *Hum. Brain Mapp.* **40**, 2867–2883 (2019).
37. S. H. Johnson-Frey, R. Newman-Norlund, S. T. Grafton, A distributed left hemisphere network active during planning of everyday tool use skills. *Cereb. Cortex.* **15**, 681–695 (2005).
38. S. Obayashi, T. Suhara, K. Kawabe, T. Okauchi, J. Maeda, Functional Brain Mapping of Monkey Tool Use. *Neuroimage.* **14**, 853–861 (2001).

39. E. Dahlin, A. S. Neely, A. Larsson, L. Bäckman, Transfer of Learning After Updating Training Mediated by the Striatum. *Science*. **320**, 1510–1512 (2008).
40. S. M. Jaeggi, M. Buschkuhl, J. Jonides, W. J. Perrig, Improving fluid intelligence with training on working memory. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 6829–6833 (2008).
41. J. Diedrichsen, N. Kriegeskorte, Representational models: A common framework for understanding encoding, pattern-component, and representational-similarity analysis. *PLoS Comput. Biol.* **13**, 1–33 (2017).
42. M. V Peelen, A. J. Wiggett, P. E. Downing, Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron*. **49**, 815–822 (2006).
43. S. M. Jaeggi, M. Buschkuhl, J. Jonides, P. Shah, Short- and long-term benefits of cognitive training. *Proc. Natl. Acad. Sci. U. S. A.* **108**, 10081–10086 (2011).
44. S. Lehericy, H. Benali, P.-F. Van De Moortele, M. Péligrini-issac, T. Waechter, K. Ugurbil, J. Doyon, Distinct basal ganglia territories are engaged in early. *Proc. Natl. Acad. Sci.* **102**, 12566–12571 (2005).
45. H. Makino, E. J. Hwang, N. G. Hedrick, T. Komiyama, Circuit Mechanisms of Sensorimotor Learning. *Neuron*. **92**, 705–721 (2016).
46. H. H. Yin, S. P. Mulcare, M. R. F. Hilário, E. Clouse, T. Holloway, M. I. Davis, A. C. Hansson, D. M. Lovinger, R. M. Costa, Dynamic reorganization of striatal circuits during the acquisition and consolidation of a skill. *Nat. Neurosci.* **12**, 333–341 (2009).
47. K. M. Tagarelli, K. F. Shattuck, P. E. Turkeltaub, M. T. Ullman, Language learning in the adult brain: A neuroanatomical meta-analysis of lexical and grammatical learning. *Neuroimage*. **193**, 178–200 (2019).

48. A. M. Graybiel, S. T. Grafton, The striatum: Where skills and habits meet. *Cold Spring Harb. Perspect. Biol.* **7**, 1–14 (2015).
49. K. Amunts, M. Lenzen, A. D. Friederici, A. Schleicher, P. Morosan, N. Palomero-Gallagher, K. Zilles, Broca's region: Novel organizational principles and Multiple Receptor Mapping. *PLoS Biol.* **8**, 1–16 (2010).
50. G. Papitto, A. D. Friederici, E. Zaccarella, The topographical organization of motor processing: An ALE meta-analysis on six action domains and the relevance of Broca's region. *Neuroimage.* **206**, 1–15 (2020).
51. D. Muret, H. R. Dinse, S. Macchione, C. Urquizar, A. Farnè, K. T. Reilly, Touch improvement at the hand transfers to the face. *Curr. Biol.* **24**, R736–R737 (2014).
52. S. Vyas, N. Even-Chen, S. D. Stavisky, S. I. Ryu, P. Nuyujukian, K. V. Shenoy, Neural Population Dynamics Underlying Motor Learning Transfer. *Neuron.* **97**, 1177–1186 (2018).
53. K. Grill-Spector, R. Henson, A. Martin, Repetition and the brain: Neural models of stimulus-specific effects. *Trends Cogn. Sci.* **10**, 14–23 (2006).
54. V. Boulenger, A. C. Roy, Y. Paulignan, V. Deprez, M. Jeannerod, T. A. Nazir, Cross-talk between Language Processes and Overt Motor Behavior in the First 200 msec of Processing. *J. Cogn. Neurosci.* **18**, 1607–1615 (2006).
55. R. N. A. Henson, Neuroimaging studies of priming. *Prog. Neurobiol.* **70**, 53–81 (2003).
56. T. Xu, X. Yu, A. J. Perlik, W. F. Tobin, J. A. Zweig, K. Tennant, T. Jones, Y. Zuo, Rapid formation and selective stabilization of synapses for enduring motor memories. *Nature.* **462**, 915–919 (2009).

57. E. Wenger, C. Brozzoli, U. Lindenberger, M. Lövdén, Expansion and Renormalization of Human Brain Structure During Skill Acquisition. *Trends Cogn. Sci.* **21**, 930–939 (2017).
58. A. Iriki, M. Taoka, Triadic (ecological, neural, cognitive) niche construction: A scenario of human brain evolution extrapolating tool use and language from the control of reaching actions. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 10–23 (2012).
59. M. S. Ponce de León, T. Bienvenu, A. Marom, S. Engel, P. Tafforeau, J. L. Alatorre Warren, D. Lordkipanidze, I. Kurniawan, D. B. Murti, R. A. Suriyanto, T. Koesbardiati, C. P. E. Zollikofer, The primitive brain of early Homo. *Science.* **372**, 165–171 (2021).
60. D. Stout, T. Chaminade, Stone tools, language and the brain in human evolution. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **367**, 75–87 (2012).
61. G. Rizzolatti, M. A. Arbib, Language within our grasp. *Trends Cogn. Sci.* **2236**, 1667–1669 (1998).
62. S. Dehaene, L. Cohen, Cultural recycling of cortical maps. *Neuron.* **56**, 384–398 (2007).
63. T. J. H. Morgan, N. T. Uomini, L. E. Rendell, L. Chouinard-Thuly, S. E. Street, H. M. Lewis, C. P. Cross, C. Evans, R. Kearney, I. De La Torre, A. Whiten, K. N. Laland, Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nat. Commun.* **6**, 4–11 (2015).
64. M. L. Anderson, Précis of after Phrenology: Neural Reuse and the Interactive Brain. *Behav. Brain Sci.* **39** (2015).
65. W. D. Hopkins, A. Meguerditchian, O. Coulon, M. Misiura, S. Pope, M. C. Mareno, S. J. Schapiro, Motor skill for tool-use is associated with asymmetries in Broca’s area and

- the motor hand area of the precentral gyrus in chimpanzees (*Pan troglodytes*). *Behav. Brain Res.* **318**, 71–81 (2017).
66. P. Lieberman, The evolution of language and thought. *J. Anthropol. Sci.* **94**, 127–146 (2016).
 67. C. Schreiweis et al. Humanized Foxp2 accelerates learning by enhancing transitions from declarative to procedural performance. *Proc. Natl. Acad. Sci. U. S. A.* **111**, 14253–14258 (2014).
 68. W. Enard et al. A Humanized Version of Foxp2 Affects Cortico-Basal Ganglia Circuits in Mice. *Cell.* **137**, 961–971 (2009).
 69. W. D. Hopkins, L. Reamer, M. C. Mareno, S. J. Schapiro, Genetic basis in motor skill and hand preference for tool use in chimpanzees (*Pan troglodytes*). *Proc. R. Soc. B Biol. Sci.* **282** (2015).
 70. W. D. Hopkins, J. L. Russell, C. Cantalupo, Neuroanatomical correlates of handedness for tool use in chimpanzees (*Pan troglodytes*): Implication for theories on the evolution of language. *Psychol. Sci.* **18**, 971–977 (2007).
 71. R. C. Oldfield, The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia.* **9**, 97–113 (1971).
 72. B. New, C. Pallier, M. Brysbaert, L. Ferrand, Lexique 2: A new French lexical database. *Behav. Res. Methods, Instruments, Comput.* **36**, 516–524 (2004).
 73. J. R. Reynolds, R. West, T. Braver, Distinct neural circuits support transient and sustained processes in prospective memory and working memory. *Cereb. Cortex.* **19**, 1208–1221 (2009).
 74. L. A. Jones, S. J. Lederman, *Human Hand Function* (Oxford Uni., 2006).

75. T. Nichols, M. Brett, J. Andersson, T. Wager, J. B. Poline, Valid conjunction inference with the minimum statistic. *Neuroimage*. **25**, 653–660 (2005).
76. N. N. Oosterhof, A. C. Connolly, J. V Haxby, CoSMoMVPA: Multi-modal multivariate pattern analysis of neuroimaging data in matlab/GNU octave. *Front. Neuroinform*. **10**, 1–27 (2016).
77. H. Singmann, B. Bolker, J. Westfall, F. Aust, S. M. Ben-Shachar, afex: Analysis of Factorial Experiments. R package version 0.27-2. <https://CRAN.R-project.org/package=afex> (2020).
78. R. H. Baayen, D. J. Davidson, D. M. Bates, Memory and Language Mixed-effects modeling with crossed random effects for subjects and items. *J. Mem. Lang.* **59**, 390–412 (2008).
79. L. L. Chao, J. V. Haxby, A. Martin, Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat. Neurosci.* **2**, 913–919 (1999).
80. C. Cavina-Pratesi, J. D. Connolly, S. Monaco, T. D. Figley, A. D. Milner, T. Schenk, J. C. Culham, Human neuroimaging reveals the subcomponents of grasping, reaching and pointing actions. *Cortex*. **98**, 128–148 (2018).

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Supplementary Materials:

Figures S1-S3; Tables S1-S3; Movies S1-S2

Supplementary Materials for

Tool use and language share syntactic processes and neural patterns in the basal ganglia

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This PDF file includes:

Materials and Methods

Supplementary Text

Figs. S1 to S3

Tables S1 to S3

Captions for Movies S1 to S2

Other Supplementary Materials for this manuscript include the following:

Movies S1 to S2

Materials and Methods

Participants

A total of 203 participants were included in the study, which consists of four different experiments. None of the participants took part in more than one experiment. All participants were healthy right-handed French native speakers with normal or corrected-to-normal vision and no known motor, linguistic or neurological disorders. They gave their written informed consent prior to experiment acquisition. All procedures were in agreement with the Helsinki declaration and approved by an ethical committee (46/17_2, OUEST IV).

Experiment 1

The fMRI acquisition in Experiment 1 included 24 participants who received a compensation of 110 euros. Four participants were excluded: two did not fulfill the a-priori-set familiarization performance requirements before any neuroimaging acquisition, one dropped out after the inclusion phase and one was removed from analyses due to substantial head movements (several runs with movements above 1.5 mm). Thus, we analyzed 20 participants with the following sociodemographic characteristics and manual preference: 10 males and 10 females; mean age \pm SD: 24 ± 4 years old; mean score on the Edinburgh handedness inventory (71): 0.93 ± 0.09 ; higher education level, namely the number of years of education after a high school degree: 3 ± 2 years.

Experiment 2

In this experiment, 85 participants were included and received a compensation of 10 euros. Six participants performed the experiment but were excluded from analysis due to performance below chance level in at least one sentence condition, and one for having incorrectly used the right hand to deliver the button press. In total, 78 participants were entered into the analyses. They had the following characteristics: 27 males and 51 females; mean age: 23 ± 3 years old; higher education level: 4 ± 1 years, mean Edinburgh score: 0.9 ± 0.12 .

Experiment 3

Experiment 3 included 46 participants who were paid 15 euros for their participation. The threshold of $d' > 1.38$ in pre-test, as identified in Experiment 2, was applied as an independent criterion for inclusion. Data from two participants were excluded due to error in sensitivity index calculation at pre-test, four other were excluded for sensitivity index below the threshold, and one other for having inverted the response keys during the task. Overall, data from 39 participants were analyzed. The group presented the following characteristics: 11 males and 28 females; mean age: 24 ± 5 years old; mean Edinburgh score: 0.87 ± 0.11 ; higher education level: 3 ± 1 years.

Experiment 4

In this experiment, 48 participants were recruited and were paid 40 euros for their participation. The group presented the following characteristics: 24 males and 24 females; mean age: 27 ± 5 years old; mean Edinburgh score: 0.88 ± 0.1 ; higher education level: 5 ± 2 years.

Tasks

Syntactic task

A two-alternative forced choice task (2-AFC) allowed to assess syntactic abilities to process sentences composed of the same content words but featuring different structures: coordinated, center-embedded subject relative, or center-embedded object relative clauses. Table 1A offers examples for each condition, and the entire material is available in Table S3. The content words included in the sentences were controlled for word frequency and number of syllables from the Lexique 3.80 database (72), as well as for the gender of the subjects and objects of the described action. Each sentence was presented using rapid serial visual presentation (RSVP) in six consecutive segments displayed in the middle of the screen for 500 ms, interspaced by a 100-ms blank screen. This presentation mode was chosen based on previous work using comprehension tasks of visually presented sentences (14, 15) to avoid idiosyncratic reading strategies and/or saccadic eye movements. After presentation of the final segment of each sentence, a test affirmation was displayed on the screen (Table 1B) until the participant answered or for a maximum of 5 s. The participants were instructed to respond as quickly and correctly as possible via a button press with their left hand as to whether the affirmation was

TRUE or FALSE with respect to the preceding sentence. The button-response association was counterbalanced across the participants.

In the fMRI Experiment 1, a total of 48 trials were presented in a randomized order during the run and consisted of the presentation of sentences featuring the three different syntactic structures in equal proportion ($N = 16$ each): coordinated, subject relative and object relative clauses. The intertrial period was jittered between 5 and 7 s. The sentences were visible through the mirror oriented towards the screen placed on the back of the scanner bore.

For behavioral Experiments 2 and 3, outside of the scanner, the total number of trials in each experiment was 72, with 24 trials per each syntactic structure. The intertrial period was jittered between 2.5 and 3.5 s, and a 1-minute rest period was added halfway through the block. The scripts controlling the presentation and recording participants' answers were programmed in *Psychtoolbox* (PTB-3) running on MATLAB (Mathworks, Natick, USA).

Verbal working memory task

In Experiment 1, to disentangle the potential contribution of working memory processes to syntactic brain activity, the participants also performed an *n-back* task with four words of equal length and frequency (Lexique 3.80). Two *1-back* and two *3-back* runs were acquired. Words were presented with a RSVP in the center of the screen for 1500 ms. The intertrial period varied between 1 s and 4 s at 1-s steps in line with effective published protocols (73). The participants were required to press a button with their left index finger if a target word appearing on the screen matched the preceding word (*1-back*) or the one presented two steps earlier (*3-back*). Each run included 76 trials with 19 targets. The word stream was made visible using the same apparatus as for the syntax task. Similar to the syntax task, the verbal working memory task scripts were programmed onto *Psychtoolbox* (PTB-3) running on MATLAB (Mathworks, Natick, USA).

fMRI tool-use task

The participants were required to use a pair of 30-cm-long pliers held with their right hand to move a peg (Fig. 1D) on a plastic board (Quercetti, Torino, Italy) between two fixed visual landmarks separated by an approximate 9-cm distance (see Movies S1 and S2). To begin a trial, the participants, in a resting position, had to wait for a pure tone signal delivered through an

MRI compatible device aimed to actively reduce MRI noise (Optoacoustics OptoACTIVE-two way noise cancellation communication system, Mazor, Israel). A single presentation of the pure tone warned the participant to prepare to move, and the double presentation of this tone presented 4 s later indicated the Go for the action. This sequence was repeated twice to pace the requested movements: grasping the peg to displace it from the first to the second location and then grasping it again to move it back to its initial position. The whole sequence (4-s planning – 4-s execution – 4-s planning – 4-s execution – 10-s rest) was repeated 15 times in a single run. If a peg fell, the participant had to indicate the missed sequence by pressing a button with the left index finger and then grab a new peg from the left side of the plastic board. The few missed trials (lower than 0.5%) were modeled separately. In a distinct run, the same task was performed with the free hand and served as a control to highlight the tool-specific neural network. The motor task device was placed in front of the participant at a reachable distance and made visible with a double mirror mounted onto the head coil. The participants' right upper arm was strapped to the trunk to limit elbow and shoulder movements. The scripts controlling the audio sequence of instructions in the scanner were delivered with Presentation software (NBS, Berkeley, USA).

Motor training

Tool-use training was similar to the tool-use task design for fMRI acquisitions. As previously described, the participants were required to insert pegs on a board using the same 30-cm-long pliers with their right hand. Training was performed with grooved, key-shaped pegs (Grooved Pegboard Test, Lafayette instruments, Model 32025²), which need to be meticulously oriented to fit the target hole. In total, four boards were placed in front of the participant with a plastic box containing the pegs located in front of the boards. The training consisted of inserting as many pegs as possible during 9 blocks of 2 minutes, interspersed with 1-minute rest. The motor performance was indexed by the total number of correctly inserted pegs. A between-subjects design across Experiments 2 and 3 tested the hypothesis that syntactic skills improved in the group of participants training with the tool compared to three control groups of participants. One control condition consisted of the same motor training but performed with the right bare hand (i.e., free-hand training) to control for unspecific effects of motor training over the untrained task (Experiments 2 and 3). The second control condition was a passive control for potential test-retest effects in the absence of any motor task. The participants assigned to this condition were required to watch soundless nature documentary videos (Experiment 2)

following the same procedure as for both tool-use and free-hand motor training, namely 9 blocks of 2-minute videos interspersed with 1-minute rest (with a gray screen).

In Experiment 3, we replicated the acquisition with tool-use and free-hand training in new samples of participants, and added a third training condition to control for the sensorimotor difficulty of tool-use training. From a sensorimotor point of view, training with the tool was more difficult than free-hand training. Indeed, the tool reduces sensory feedback while handling the pegs. In addition, the motor constraints introduced by the tool hinder the potential easing contribution of the fingers available in the free-hand condition. Proof of the difficulty is the reduced number of pegs inserted by the participants training with the tool compared with the free hand in Experiment 2. To rule out the sensorimotor difficulty of the task as a factor contributing to learning transfer, we introduced additional sensorimotor constraints in the free-hand motor training to mimic those imposed by the tool. To this end, we instructed participants to grab and enter pegs using a pinch formed by their middle and index fingers. Beside the fingers employed to carry out the grip, two further changes were applied to reduce the degrees of freedom of manual movements towards those characterizing tool use. The degrees of freedom of the hand are estimated to exceed 20 (approximately 27 (74)): 4 for each finger except for the thumb (3 for flexion/extension and 1 for abduction/adduction); 5 for the thumb; and 6 for translation and rotation of the wrist. The degrees of freedom of tool use on the other hand approximate 7: 1 for abduction/adduction of pliers and 6 for wrist translation and rotation. Participants were asked to cross their index and middle fingers (index underneath) which were strapped together at the level of the proximal phalanx with dermocompatible tape and velcro. This prevented independent flexion or extension of the fingers (-3 degrees of freedom approximately). This constraint resulted in a pliers-like configuration with the middle finger's inner side over the index finger nail, and were explicitly required to use these two fingers without the contribution of the thumb, the ring and little fingers (approximately 13 fewer degrees of freedom). Second, we hindered somatosensory feedback of participants' index and middle fingers with a layer of flat velcro between two layers of dermocompatible tape attached on each fingertip (Fig. 3A, red inset). This constrained hand condition ensured lack of direct sensory feedback, as experienced with the tool, as well as the inability to adjust peg orientation by simply slipping it between the middle and index fingers (therefore reducing the impact of the 6 degrees of freedom of flexion/extension). Accordingly, the participants had to rely more on wrist rotations to insert the pegs, with hindered sensory feedback, similar to the experience during tool use.

Motor test

The motor training was adjusted into a motor test to enable the measurement of a change in tool-use motor performance following syntactic training in Experiment 4. Participants were asked to use the tool with their right hand to enter as many pegs as possible during 4 blocks of 2 minutes, interspersed with 1-minute rest. This test was performed before and after linguistic training. The motor performance was indexed by the number of correctly inserted pegs per block.

Syntactic training

In order to evaluate the effect of linguistic training on tool use in Experiment 4, the syntax task employed in Experiments 1 to 3 was adapted into a training protocol. Training was composed of 96 trials, split in 6 blocks of 16 sentences each. Blocks were interspersed with 1-minute rest periods. Participants were allowed a maximum of 5 seconds to respond to the test affirmation presented after each sentence by pressing one of two buttons with their left hand. Once they answered, a coherent feedback appeared for 1.5 s: a green « √ » or a red « X » for correct or incorrect answers respectively. At the end of each block, the accuracy and average reaction time were displayed so that participants were made aware of their progress in performance (as in the motor training in Experiments 2 and 3). Using a single-blind procedure, participants were assigned to one of two groups: one was trained with subject relative clauses and the other with object relative clauses. Participants were reminded to try to improve their accuracy and reaction time performance at each block. Task scripts were programmed onto *Psychtoolbox* (PTB-3) running on MATLAB (Mathworks, Natick, USA).

Procedures

Experiment 1: fMRI

The experiment consisted of an inclusion session to familiarize participants with the tasks and check that the individual level of performance met the inclusion criteria. Short versions of the syntactic, verbal working memory and motor tasks were conducted. The requirements to be included in the fMRI session were at least 16 successes in the syntactic task (over 24 trials), with 4 successes for the most complex condition (object relative clauses, over 8 trials). For the

3-back task, the participants were required to correctly identify at least 3 targets out of 8 among a total of 32 trials, without performing more than 6 false alarms. For the *1-back* task, one block of 16 trials was performed, with the same requirements. This was meant to maximize the number of correct and analyzable trials in each task during the neuroimaging acquisition. The motor task for inclusion comprised two blocks of tool-use movements and two blocks of free-hand movements. In each block, the participants were instructed to insert ten pegs as quickly as possible on the two first lines of the Grooved Pegboard test. To be included in the experiment, they had to perform the two tool-use blocks in less than 5 minutes on average and the two free-hand blocks with an average of less than 1 minute. After inclusion, the participants performed two different fMRI sessions separated by two days. Each session consisted of an anatomical acquisition (T1-weighted), followed by motor (tool use and free hand) and linguistic runs in a counterbalanced order. The participants were tested in the working memory and syntactic tasks during the same session. Two additional linguistic tasks assessing phonological and semantic processing were performed in the other session; these results will be presented in a separate report. The session order was counterbalanced across participants.

Functional and anatomical MRIs were acquired with a Siemens Prisma 3T scanner (Siemens Medical systems, Erlangen, Germany) with a gradient echo EPI sequence, with TE = 30 ms and TR = 2400 ms. Volumes were acquired with 44 interleaved slices of 3-mm thickness ($3 \times 3 \times 3.3$ mm voxel size) aligned to the AC-PC plane. Overall, 171 volumes were acquired for each motor block, 305 for the syntactic task and 140 for the working memory task. T1-weighted images were acquired with a 1-mm isotropic voxel and a GeneRalized Autocalibrating Partial Parallel Acquisition (GRAPPA) acceleration factor of 2 (TE = 3.8 ms, TR = 3000 ms).

Behavioral acquisition: Experiments 2, 3 and 4

In Experiment 2, following a short familiarization with five trials, participants performed the syntactic test before and after their respective training. A first group (N=26) trained with the tool. As controls, two additional groups either trained with the free hand (N=26) or simply watched videos (N=26). The linguistic material selected in the pre-test was always different from that presented in the post-test.

In Experiment 3, three groups of 13 participants were included, and each underwent one of three different motor training: tool-use, free-hand or constrained-hand training.

In Experiment 4, 48 participants were included and equally divided into two different groups (N=24 each) with a single-blind procedure by experimenter A. Each group underwent one of two different syntactic training: with object relative clauses or subject relative clauses. Regardless of the group, before and after the syntactic training, participants performed the motor test with the tool. To avoid potential observational bias, experimenter B supervised the motor test acquisition, whereas experimenter A gave instructions for the syntactic training. Experimenter B was blind with respect to which syntactic training condition each participant had been assigned to.

Analyses

Experiment 1: fMRI analyses

Preprocessing. fMRI data were analyzed with statistical parametric mapping (SPM12; Wellcome Trust Centre for Neuroimaging). Functional data were preprocessed with a standard procedure. This consisted of spatial realignment, slice timing and coregistration of anatomical to mean functional images. Data were then spatially normalized into the MNI (Montreal Neurological Institute) stereotactic space with a resampling to 3×3×3 mm. As last step, data were spatially smoothed using a 3D Gaussian kernel with full-width at half-maximum (FWHM) of 8 mm and temporally high-pass filtered with a cutoff at 1/128 Hz.

Univariate analyses. At the first level, each participant's hemodynamic responses were modeled with a box-car function. Each motor block was designed with planning, execution, rest and, as regressors of no interest, missed trials and head movements. Both directions of the movements (back and forth) were taken into consideration. For the syntactic task, we modeled the coordinated, subject relative and object relative clauses during sentence presentation (i.e., syntactic encoding) and test affirmation separately. This last part contains participants' RTs, incorrect responses and head movements, which were entered as regressors of no interest in the model. For the working memory task, hits, false alarms, correct rejections and miss trials as well as head movements were considered. At the second level, we conducted within-subjects ANOVAs to identify the general network underlying each assessed function. We computed the interaction contrast highlighting the specific tool-use planning neural network with respect to free-hand planning and the overall execution network:

$$\text{Tool-use Planning Network} = [(\text{Tool-use}_{\text{Planning}} - \text{Free-Hand}_{\text{Planning}}) - (\text{Tool-use}_{\text{Execution}} - \text{Free-Hand}_{\text{Execution}})].$$

To assess the specific syntactic neural network, we contrasted the activity in the encoding phase for object relative clauses with that in the encoding phase for both coordinated and subject relative clauses, for correct trials only:

$$\text{Syntax Network} = [2 \text{ Object relative clauses} - (\text{Coordinated clauses} + \text{Subject relative clauses})].$$

For working memory, we computed the difference between hits in the *3-back* and *1-back* tasks:

$$\text{Working Memory Network} = \text{Hits}_{3\text{-back}} - \text{Hits}_{1\text{-back}}.$$

These contrasts were then entered into conjunction analyses (minimum statistic compared to conjunction null hypothesis, (75)), allowing to assess the anatomical overlap between the different processes: Tool-use Planning Network \cap Syntax Network, and as control, Tool-use Planning Network \cap Working Memory Network.

As further control for the specificity of the shared functional activation between tool-use planning and syntax, we computed the hand planning network as follows:

$$\text{Free-Hand Planning Network} = [(\text{Free-Hand}_{\text{Planning}} - \text{Tool-use}_{\text{Planning}}) - (\text{Free-Hand}_{\text{Execution}} - \text{Tool-use}_{\text{Execution}})],$$

and the conjunction Free-Hand Planning Network \cap Syntax Network was assessed.

To investigate the network activated during action execution, we computed both the following:

$$\text{Tool-use Execution Network} = [(\text{Tool-use}_{\text{Execution}} - \text{Free-Hand}_{\text{Execution}}) - (\text{Tool-use}_{\text{Planning}} - \text{Free-Hand}_{\text{Planning}})]$$

and

$$\text{Free-Hand Execution Network} = [(\text{Free-Hand}_{\text{Execution}} - \text{Tool-use}_{\text{Execution}}) - (\text{Free-Hand}_{\text{Planning}} - \text{Tool-use}_{\text{Planning}})]$$

as well as further studied the conjunctions Tool-use Execution Network \cap Syntax Network and Free-Hand Execution Network \cap Syntax Network.

To guarantee the reliability of the results, for each analysis, we reported each cluster at the whole brain level, containing more than 10 contiguous voxels ($> 270 \text{ mm}^3$), with a *p-value* below the 0.001 threshold uncorrected for multiple comparisons. Furthermore, each motor contrasts was submitted to an exclusive mask defined at 0.05 uncorrected for multiple comparisons aiming to rule out the contribution of the interaction second component (i.e., for Tool-use Planning Network, the contribution Hand Execution $>$ Tool Execution was masked). This mask was also used for the conjunction analyses. Clusters passing the family-wise error (FWE) correction for multiple comparisons at the cluster level were highlighted.

Multivariate analyses. We then assessed our prediction of shared cognitive processes within the overlapping territories between tool-use planning and syntax. To this aim, we tested whether the brain activity level during tool-use planning, compared to free-hand planning, presented stronger pattern similarity with brain activity levels associated with object relative clauses.

For the first series of analyses, we used the CoSMoMVPA toolbox (76) to extract, for each participant, the nonsmoothed parameter estimates (*beta*) from each voxel of the overlapping clusters for both tool-use and free-hand planning. We did the same for object and subject relative clauses. This produced for each participant four vectors of parameter estimates (i.e., one per condition), composed of all significant voxels ($n=41$) evidenced by the conjunction

analysis. We then performed a representational similarity analysis (RSA). To this aim, for each participant, the four individual vectors were entered in a 4×4 similarity matrix, where each node represented the correlation (*Pearson's r*) between the activity patterns of two conditions. Higher correlation scores indicated better similarity. The obtained matrix was symmetrical with respect to the diagonal, containing six nodes of interest, corresponding to all pairwise comparisons between non-identical conditions. The similarity matrix obtained for each individual was then compared to hypothesis-driven models aiming to predict the data. A correlation between the observed similarity matrix and the model was computed as a measure of fit of the model: the higher the correlation coefficient, the better the fit of the model. Each individual correlation score was *Fisher's* z-transformed before any statistical analysis and tested with a unilateral sample t-test against zero with a Bonferroni correction applied to correct *p-values* for multiple comparisons.

We tested two models. Both models included within-domain similarity: between the two motor conditions and between the two most complex syntactic conditions. Crucially, the two models differed regarding the tested cross-domain similarity. The first model, represented by matrix 1, tested the cross-domain similarity between tool-use planning and object relative clauses, whereas the second control model, represented by matrix 2, tested the cross-domain similarity between free-hand planning and object relative clauses.

Matrix of similarity 1:

	<i>Tp</i>	<i>Fp</i>	<i>SRC</i>	<i>ORC</i>
<i>Tp</i>	1	1	0	1
<i>Fp</i>	1	1	0	0
<i>SRC</i>	0	0	1	1
<i>ORC</i>	1	0	1	1

Matrix of similarity 2:

	<i>Tp</i>	<i>Fp</i>	<i>SRC</i>	<i>ORC</i>
<i>Tp</i>	1	1	0	0
<i>Fp</i>	1	1	0	1
<i>SRC</i>	0	0	1	1
<i>ORC</i>	0	1	1	1

Tp and *Fp* stand for tool-use planning and free-hand planning, respectively, whereas *SRC* and *ORC* indicate subject relative clauses and object relative clauses, respectively. Additionally, each node was defined by 1 or 0, with 1 representing the similarity between a pair of vectors and 0 representing a dissimilarity.

To assess the specificity of the similarity between syntax and tool-use patterns, the same analysis was also run on working memory patterns as a control. In other words, we tested for possible cross-domain similarities between *3-back* and tool-use patterns. To do so, we entered in the matrices of the models described above activity patterns elicited during *1-back* and *3-back* tasks, instead of object and subject relative patterns respectively.

We further tested whether the similarity between patterns can be exploited to accurately predict the activity elicited by complex syntactic structures from that elicited by tool-use. A classification based MultiVoxel Pattern Analysis (MVPA), employing a leave-one-subject-out procedure was run with the CoSMoMVPA toolbox. Data from the 41 significant voxels in the basal ganglia identified in the conjunction analysis was used as *features* for the classification. More specifically, a SVM classifier was trained on the nonsmoothed t-maps derived from motor activations (tool-use planning vs. baseline and free-hand planning vs. baseline) and then tested cross-domain on the activation elicited by object relatives against baseline. We normalized each *feature* employing the toolbox built-in function. At each iteration, the classifier trained on motor data from all subjects but one, iteratively left out. The classifier was then tested cross-domain on the object relatives data of all subjects (N=20 tests per iteration). This resulted in an average accuracy score for each iteration. The overall average score across all iterations was tested for significance after performing 10,000 permutations of neural patterns across subjects in order to estimate a null distribution. The *p-values* were calculated to test whether the observed difference was significantly and positively different from chance level (accuracy = 0.5). The same procedure was subsequently used with the *3-back* task to control for syntactic specificity, namely the SVM classifier was trained on the motor data and tested on the *3-back* data.

Cluster-based voxelwise correlations. We studied in more detail the similarity between patterns of activity underlying tool-use planning and object relative clauses in each cluster, by computing voxelwise correlations (42). As a control, we calculated the same voxelwise correlations also between patterns of activity underlying free-hand planning and object relative clauses, in each cluster separately. To this aim, averaged contrast estimates (*betas*) were

computed from the nonsmoothed images for each voxel for both tool-use planning and object relatives. This produced two vectors of *betas* per cluster, one for tool-use planning and one for object relatives. The correlation between the two vectors of the same cluster was assessed as a measure of the similarity of the spatial distribution of brain activity: a higher correlation coefficient indicates strong similarity. We repeated the same procedure to calculate the correlation between patterns of activity corresponding to free-hand planning and object relatives. This procedure resulted in two *Pearson's* correlation scores: one for the relationship between tool-use planning and object relative clauses and a second for the relationship between free-hand planning and object-relative clauses. For comparison, the second score was subtracted from the first one, giving an observed difference in correlations. Statistical inference was allowed by comparing the observed difference to an empirical null distribution of differences obtained after 10,000 permutations across the features of the two motor conditions. The *p-values* were calculated to test whether the observed difference was significantly positive.

Experiments 1 to 4: Behavioral data preprocessing

For the syntax and verbal working memory tasks, response times (RTs; i.e., time interval from the display of the test affirmation or target word, respectively, to participant's response) and sensitivity index (d') were measured to index performance. In the working memory task, to complement our analyses we also studied the proportion of hits and false alarms. Trials with RTs deviating from the mean ± 2.5 standard deviations were removed from analysis. This represented in total 1.48% of the trials across all experiments. Statistics on these data were run in R-studio with built-in statistical functions and the *afex* package (77). The statistical models performed for each experiment are presented below. For all analyses, *Tukey post hoc* comparisons were performed to further explore significant interactions. All results are reported as the mean \pm SEM.

Experiments 1: Behavior Statistics

For the syntactic task, we performed repeated measures ANOVAs (rmANOVA) on d' and linear mixed models (LMM) on RTs. The one-way ANOVA was performed with the within-subjects factor *Sentence* (Coordinated vs. Subject relative vs. Object relative clauses). The LMM

performed on RTs included the same within-subject factor, with *Subjects* and *Sentence* as random factors (78).

To account for differences in performance between the *1-back* and *3-back* working memory tasks, paired-sample t-tests were performed on d' , proportion of hits and proportion of false alarms. RTs were assessed through LMM analysis with *Difficulty* (*1-back* vs. *3-back*) as within-subject factor, with *Subjects* and *Difficulty* added as random factors.

Experiments 2 and 3: Statistics

To assess the progress in performance during motor training in each behavioral experiment, rmANOVAs on the number of inserted pegs were conducted with *Block* (9 blocks) as the within-subjects factor and *Training* (Tool use vs. Free hand in Experiment 2 and Tool use vs. Free hand vs. Constrained hand in Experiment 3) as the between-subjects factor. To identify performance differences between training conditions, the total number of pegs inserted across the 9 blocks were assessed: in Experiment 2 by a two-sample t-test (*Training*: tool use vs. free hand) and in Experiment 3 with a one-way rmANOVA (*Training*: tool use vs. free hand vs. constrained hand).

We accounted for possible effects of participants' initial syntactic skills on the improvement in the post-test. This was done by conducting an ANCOVA on the RTs, entering the initial syntactic performance measured by the d' as a covariate, *Sentence* and *Time* as within-subjects factors, and *Training* as a between-subjects factor. Next, syntactic performance was analyzed through a LMM on RTs with *Training* (Tool use vs. Free hand vs. Video in Experiment 2 and Tool use vs. Free hand vs. Constrained hand in Experiment 3) as the between-subjects factor and *Sentence* (Coordinated vs. Subject relative vs. Object relative clauses) and *Time* (Pre vs. Post) as within-subjects factors. *Subjects*, *Sentence* and *Time* were added to account for random effects. rmANOVA was run on d' , with *Training* (Tool use vs. Free hand vs. Video in Experiment 2 and Tool use vs. Free hand vs. Constrained hand in Experiment 3) as the between-subjects factor and *Sentence* (Coordinated vs. Subject relative vs. Object relative clauses) and *Time* (Pre vs. Post) as within-subjects factors.

To quantify the robustness of the syntactic benefits after tool-use training across Experiments 2 and 3, we finally computed the effect size of the pre-to-post-test improvement in the syntactic task (39, 43). This was done by calculating the difference between pre- and post-test

performance divided by the pooled standard deviation in the pre-test (for the entire sample of participants). The effect size in the object relative clauses condition was then analyzed in an rmANOVA with *Training* (Tool use vs. Free hand) and *Experiment* (Experiment 2 vs. 3) as between-subjects factors.

Experiment 4: Statistics

To assess the progress in performance during syntactic training, an rmANOVA on d' and a LMM on RTs were conducted. The rmANOVA was performed with *Block* (6 blocks) as the within-subjects factor and *Training* (Object relative clauses vs. Subject relative clauses) as the between-subjects factor. The LMM performed on RTs included the same within-subject factor, with *Subjects*, *Training* and *Block* as random factors.

Next, motor performance with the tool was analyzed through a LMM on the total number of inserted pegs with *Training* (Object relatives vs. Subject relatives) as the between-subjects factor and *Time* (Pre vs. Post) and *Block* (4 blocks) as within-subjects factors. *Subjects*, *Time* and *Block* were added to account for random effects.

Finally, to corroborate our results, motor performance was analyzed through an rmANOVA on the individual improvement slope (β) with *Training* (Object relatives vs. Subject relatives) as the between-subjects factors and *Time* (Pre vs. Post) as within-subjects factors. Improvement slope was obtained by performing a linear regression over the number of inserted pegs for each participant, before and after syntactic training separately. Slopes were also compared against zero with one-sample t-tests for object relatives and subject relatives separately. No difference against zero predicted no improvement (i.e. flat slope), whereas a significant difference predicted a change in performance, as indexed by a positive (i.e. increased performance) or negative (i.e. decreased performance) slope. A Bonferroni correction was applied to correct p -values for multiple comparisons.

Supplementary Text

Experiment 1

Tool and hand motor task: neural activity

To reveal the neural overlap between tool use and syntax, we mainly focused on the planning phase of the action when participants were not yet moving. This was done by comparing brain activity elicited during action planning with the tool to that elicited during preparation of the same action with the free hand. Moreover, to properly isolate motor planning activity (36), the interaction contrast controlled for activity elicited by the actual execution of the action. Regarding specific free-hand planning neural activity, the interaction contrast [Free-Hand Planning – Tool-use Planning] – [Free-Hand Execution – Tool-use Execution] revealed a cluster of activation within occipital regions [xyz (-3, 79, -1), $k = 122$, $p < 0.05$ corrected for multiple comparisons at the cluster level; xyz (-21, -79, -7), $k = 16$, $p < 0.001$; xyz (21, -76, -7), $k = 13$, $p < 0.001$]. However, closer inspection of contrast estimates did not show any activity specific to hand planning. This was confirmed by a direct comparison between free-hand planning and tool-use planning activity, which did not reveal any significant cluster of brain activation.

We also assessed brain activity elicited during action execution with the Tool-use Execution Network contrast and the Free-Hand Execution Network contrast. Four clusters in the occipital cortex displayed significant activations resulting from the Tool-use Execution Network contrast [xyz (-9, 79, 2), $k = 282$, $p < 0.05$ corrected for multiple comparisons at the cluster level; xyz (-12, -79, 17), $k = 16$, $p < 0.001$; xyz (3, -79, 26), $k = 34$; xyz (27, -76, -7), $k = 17$, $p < 0.001$]. In line with previous work (35, 79), we interpreted this cortical activity as reflecting tool category-specific activation, resulting from mere tool observation and the visual properties of tool vs. free-hand action. In contrast, executing the action with the free hand, compared with the tool, produced stronger activity in the bilateral post-central sulcus [xyz (-42, 34, 41), $k = 45$, $p < 0.001$; xyz (33, -25, 38), $k = 55$, $p < 0.001$] and the right hippocampus [xyz (36, -22, -10), $k = 25$, $p < 0.001$]. We propose that the former activation might reflect additional sensory feedback during free-hand grasping/lifting actions (80) with respect to tool actions. Importantly, irrespective of the effector, the clusters activated by action execution did not overlap with the syntax neural network.

Multivariate analyses

In the main text, we reported stronger similarity between object relatives and tool-use planning neural patterns, rather than free-hand planning neural patterns, on the 41 overlapping voxels within the basal ganglia. For the RSA, the model assessing for representational similarity between tool-use planning and *3-back* was not significant (*Pearson's r* mean = 0.16 ± 0.11 ; *Fisher's z* mean = 0.20 ± 0.15 ; $t_{(19)} = 1.36$; $p = 0.18$, Bonferroni-corrected). Similarly, testing for a similarity between free-hand planning and *3-back* did not yield a good fit for the data (*Pearson's r* mean = -0.04 ± 0.08 ; *Fisher's z* mean = -0.06 ± 0.10 ; $t_{(19)} = -0.63$; $p = 1.00$, Bonferroni-corrected). This was further corroborated by a SVM analysis using a leave-one-subject-out procedure, revealing that object relatives neural patterns were significantly classified above chance as tool use neural patterns rather than as free-hand planning. To control the specificity of these results, we performed these same two analyses using the working memory data instead of the syntactic data. This successful control converged with the results of the further control MVPA classification, where a classifier was trained on the motor patterns but tested on the *3-back* ones. The classification accuracy did not significantly differ from chance level (accuracy = 0.67, $p = 0.15$). This result indicates that the successful classification is specific for the syntactic condition. In conclusion, we can rule out the contribution of verbal working memory as well as of free-hand planning to the neuro-computational resources shared by syntactic processing and tool use.

Working memory: behavioral performance

To compare the performance between the *3-back* and *1-back* tasks, we conducted a paired-sample t-test on d' and a LMM on RTs. As expected, this showed that the *3-back* task was significantly more difficult ($d' = 2.13 \pm 0.24$ and RTs = 959 ± 32 ms) than the *1-back* task ($d' = 4.46 \pm 0.08$; $t_{(19)} = 12.48$; $p < 0.001$; Cohen's $d = 2.94$ and RTs = 821 ± 27 ms; $\chi^2_{(1)} = 15.30$, $p < 0.001$). The proportion of *hits* was 70.7 ± 4.9 % for *3-back* and 97.4 ± 0.7 % for *1-back* ($t_{(19)} = 5.9$; $p < 0.001$, Cohen's $d = 1.71$) and the proportion of *false alarms* was 9.1 ± 1.5 % for *3-back* and 0.4 ± 0.1 % for *1-back* ($t_{(19)} = 6.16$; $p < 0.001$, Cohen's $d = 1.87$).

Working memory: neural activity

The working memory neural network was assessed with the contrast Hits_{3-back} – Hits_{1-back}. This showed activations within the left middle frontal gyrus, the right superior frontal gyrus, the left caudate nucleus and bilateral activations within the inferior parietal lobules (see Table S2 for all details). This attentional network is consistent with that previously reported for working memory processes (39, 72). Importantly, nothing significantly survived to the conjunction with tool-use activations. Therefore, working memory does not contribute to the common network for tool-use planning and syntax.

Experiment 2

Motor training

We first tested the efficacy of both tool-use and free-hand training by quantifying individual motor improvement with the number of correctly inserted pegs in each training block (2-way *Training* \times *Block* rmANOVA: significant interaction [$F_{(5,2,261.5)} = 5.35$; $p < 0.001$; $\eta_G^2 = 0.016$]). The participants improved from the first to the last block, both with the tool (Block 1 = 9 ± 1 pegs vs. Block 9 = 15 ± 1 pegs; $p < 0.001$, Tukey post hoc) and the free hand (Block 1 = 47 ± 1 pegs vs. Block 9 = 58 ± 2 pegs; $p < 0.001$, Tukey post hoc). Furthermore, as expected, the participants training with the tool inserted fewer pegs than those training with the hand, overall (tool use = 112 ± 6 pegs vs. free hand = 492 ± 13 pegs; $t_{(35.5)} = 26.04$; $p < 0.001$, Cohen's $d = 7.22$), as well as in each of the nine blocks separately ($p_s < 0.001$, Tukey post hoc).

Syntactic improvement: Main effects and interaction effects on RTs and d'

The LMM on RTs in the participants showing high initial syntactic skills revealed main effects of the factors *Time* ($\chi^2_{(1)} = 30.81$, $p < 0.001$) and *Sentence* [$\chi^2_{(2)} = 101.92$, $p < 0.001$]. RTs were longer for object relative clauses than for subject relative clauses which in turn showed longer RTs compared to coordinated clauses. This overall reflects increasing difficulty for more complex syntactic structures.

As reported in the main text, the significant *Training* \times *Time* \times *Sentence* interaction revealed a selective improvement in correctly processing object relative clauses after tool-use training compared to free-hand training and video watching. Tukey post hoc tests also showed, irrespective of the training condition, a significant reduction in RTs in post-test compared to pre-test for coordinated clauses (tool use: pre-test RTs = 1397 ± 104 ms vs. post-test RTs = 1233 ± 114 ms; free-hand: pre-test RTs = 1564 ± 83 ms vs. post-test RTs = 1354 ± 92 ms; video: pre-test RTs = 1682 ± 100 ms vs. post-test RTs = 1450 ± 87 ms; $p_s < 0.05$), as well as for subject relative clauses (tool use: pre-test RTs = 1564 ± 122 ms vs. post-test RTs = 1310 ± 126 ms; free hand: pre-test RTs = 1717 ± 91 ms vs. post-test RTs = 1473 ± 88 ms; video: pre-test RTs = 1831 ± 105 ms vs. post-test RTs = 1584 ± 113 ms; $p_s < 0.001$). This might reflect unspecific test-retest effects since RT reductions were also observed after watching videos. A significant *Time* \times *Sentence* interaction was also found [$\chi^2_{(2)} = 6.53$, $p = 0.03$]. All post hoc results were significant, with a tendency for object relatives to improve less than the two other

sentence structures and for a reduction in the difference between subject relatives and coordinated clauses in post-test. No other main effects nor interactions were significant [$\chi^2_s < 4.07, p_s > 0.13$]. The 3-way rmANOVA on d' only showed main effects of *Time* [$F_{(1,55)} = 10.22; p = 0.002; \eta_G^2 = 0.023$] and *Sentence* [$F_{(1.4,74.4)} = 69.56; p < 0.001; \eta_G^2 = 0.268$]. In agreement with the results on RTs, sensitivity increased in post-test relative to pre-test and was lower for object relative clauses than for coordinated and subject relative clauses. No other main effects nor interactions were found to be significant [$F_s < 2.59; p_s > 0.06$].

Syntactic improvement: Main effects and interaction effects on RTs and d' for participants with low initial syntactic skills

The LMM on RTs in the participants showing low initial syntactic skills revealed main effects of the factors *Time* [$\chi^2_{(1)} = 13.65, p < 0.001$] and *Sentence* [$\chi^2_{(2)} = 43.95, p < 0.001$]. RTs were shorter in post-test than in pre-test and longer for object relative clauses than for subject relative clauses which in turn showed longer RTs compared to coordinated clauses. This reflected the increasing difficulty for more complex syntactic structures. No other main effects nor interactions were significant [$\chi^2_s < 7.92, p_s > 0.09$]. The 3-way rmANOVA on d' showed main effects of *Time* [$F_{(1,17)} = 42.3; p < 0.001; \eta_G^2 = 0.282$] and *Sentence* [$F_{(1.8,30.8)} = 80.41; p < 0.001; \eta_G^2 = 0.59$]. In line with the results on RTs, sensitivity increased in post-test relative to pre-test and was lower for object relative clauses than for coordinated and subject relative clauses. No other main effects nor interactions were found to be significant [$F_s < 2.24; p_s > 0.13$].

Syntactic improvement: Main effects and interaction effects on RTs and d' for the whole sample of participants

The LMM on global RTs, independent of initial syntactic skills, confirmed the results described above. It revealed main effects of the factors *Time* [$\chi^2_{(1)} = 43.49, p < 0.001$] and *Sentence* [$\chi^2_{(2)} = 136.13, p < 0.001$]. Shorter RTs were found in the post-test than in the pre-test. RTs were also longer for object relative clauses than for coordinated and subject relative clauses, the latter showing longer RTs compared to coordinated clauses. The interaction between the two factors was also significant [$\chi^2_{(2)} = 6.53, p = 0.03$]. All post hoc results were significant, with a tendency for object relatives to improve less than the two other sentence types. No other main effects nor interactions were significant [$\chi^2_s < 4.53, p_s > 0.23$]. The 3-way rmANOVA on d' only showed

main effects of *Time* [$F_{(1,75)} = 31.56$; $p < 0.001$; $\eta_G^2 = 0.05$] and *Sentence* [$F_{(1.4,101.5)} = 104.62$; $p < 0.001$; $\eta_G^2 = 0.27$]. In agreement with the results on RTs, sensitivity increased in the post-test relative to the pre-test and was lower for object relative clauses than for coordinated and subject relative clauses. No other main effects nor interactions were significant [$F_s < 2.2$; $p_s > 0.12$].

Experiment 3

Motor training

The participants improved [*Training* \times *Block* interaction: $F_{(9.9,178.6)} = 3.6$; $p < 0.001$; $\eta_G^2 = 0.039$] during tool-use training (Block 1 = 7 ± 1 pegs vs. Block 9 = 14 ± 1 pegs; $p < 0.001$, Tukey post hoc), constrained-hand training (Block 1 = 4 ± 1 pegs vs. Block 9 = 11 ± 1 pegs; $p < 0.001$, Tukey post hoc), as well as during free-hand training (Block 1 = 43 ± 3 pegs vs. Block 9 = 58 ± 2 pegs; $p < 0.001$, Tukey post hoc). We checked whether increased sensorimotor difficulty with the constrained hand yielded poorer motor performance than free-hand training and equivalent performance with tool-use training. A one-way rmANOVA performed on the total number of inserted pegs revealed an effect of *Training* [$F_{(2,36)} = 324.9$ $p < 0.001$; $\eta_G^2 = 0.948$]. As expected, Tukey post hoc showed that the participants training with the constrained hand inserted significantly fewer pegs (84 ± 5) than the participants training with the free hand (486 ± 20 pegs; $p < 0.001$). Importantly, the number of pegs inserted by the constrained hand group did not differ from the number of pegs inserted by the tool-use group (106 ± 6 pegs, $p = 0.44$). This held true even when considering each block separately [2-way *Training* \times *Block* rmANOVA, significant interaction: $F_{(9.9,178.6)} = 3.6$; $p < 0.001$; $\eta_G^2 = 0.039$]. Participants inserted significantly fewer pegs with the constrained than the free hand ($p_s < 0.001$). Crucially, the participants training with the constrained hand and those with the tool inserted a comparable number of pegs throughout the nine blocks ($p_s > 0.33$). The motor performance thus validated the choice of the constrained hand to assess the potential contribution of sensorimotor difficulty to the cross-domain benefit.

Syntactic improvement: Main effects and interaction effects on RTs and d'

The LMM on RTs showed main effects of *Time* [$\chi^2_{(1)} = 38.7$, $p < 0.001$], *Sentence* [$\chi^2_{(2)} = 75.26$, $p < 0.001$] and *Training* [$\chi^2_{(2)} = 9.4$, $p < 0.009$] whereas no interactions were found [$\chi^2_s < 8.17$; $p_s > 0.08$]. The Time and Sentence main effects reflected similar modulations as found in the previous Experiment 2. The main effect of *Training* was due to significantly slower RTs for the constrained hand group compared to the free hand group ($p = 0.03$).

The rmANOVA on d' also revealed main effects of *Time* [$F_{(1,36)} = 12.8$; $p = 0.001$; $\eta_G^2 = 0.047$] and *Sentence* [$F_{(1.4,59.2)} = 61.36$; $p < 0.001$; $\eta_G^2 = 0.388$]. These effects accounted for identical modulations as reported in Experiment 2. The significant *Training* \times *Time* \times *Sentence*

interaction discussed in the main text highlighted a selective improvement in processing object relative clauses after tool-use training compared to both free- and constrained-hand training. No such effect was found for coordinated clauses (tool-use pre-test $d' = 2.37 \pm 0.03$ vs. post-test $d' = 2.33 \pm 0.06$; free-hand pre-test $d' = 2.25 \pm 0.06$ vs. post-test $d' = 2.29 \pm 0.06$; constrained-hand pre-test $d' = 2.27 \pm 0.05$ vs. post-test $d' = 2.32 \pm 0.08$; $p_s > 0.67$). Similarly for subject relative clauses, no significant improvement was observed after tool-use and free-hand training (tool-use pre-test $d' = 2.32 \pm 0.05$ vs. post-test $d' = 2.31 \pm 0.05$; free-hand pre-test $d' = 2.10 \pm 0.05$ vs. post-test $d' = 2.27 \pm 0.07$; $p_s > 0.11$). Participants training with the constrained hand showed a significant improvement in this condition (pre-test $d' = 1.99 \pm 0.09$ vs. post-test $d' = 2.25 \pm 0.09$; $p = 0.02$). However, the pre-test ability in processing subject relatives within the constrained hand group was significantly lower in comparison to the tool groups ($p = 0.04$), possibly explaining the differential progression from pre- to post-test. Additionally, a *Time* \times *Sentence* interaction emerged [$F_{(1.6, 56.4)} = 5.36$; $p = 0.01$; $\eta^2 = 0.027$], explained by a significant improvement in post-test, irrespective of training, in processing object and subject relative compared to coordinated clauses. No other main effects nor interactions were found to be significant [$F_s < 2.76$; $p_s > 0.07$].

Experiment 4

Syntactic training

We first tested the efficacy of both object relative and subject relative training by quantifying individual syntactic improvement with RTs and d' in each of the six training blocks. As expected, RTs in object relative group were longer (1944 ± 52 ms) than those in the subject relative group (1380 ± 53 ms; two-way *Training* \times *Block* rmANOVA: significant main effect of *Training* [$\chi^2_{(1)} = 16.00, p < 0.001$]). Importantly, both groups improved similarly from the first to the last block of training (significant main effect of *Block* [$\chi^2_{(5)} = 84.64, p < 0.001$]; no significant interaction of *Block* with *Training* [$\chi^2_{(5)} = 4.16, p = 0.52$]).

The analysis on the d' confirmed these results (2-way *Training* \times *Block* rmANOVA: main effect of *Training* [$F_{(1,46)} = 12.09; p = 0.001; \eta_G^2 = 0.148$] and of *Block* [$F_{(3,9,180.1)} = 25.69; p < 0.001; \eta_G^2 = 0.159$]). Participants in the object relative group showed lower d' (1.27 ± 0.07) than participants in subject relative group ($d' = 1.79 \pm 0.04$), reflecting more difficult processing of object relatives. Participants in both groups improved along the training. Moreover, the significant interaction between *Block* and *Training* ($[F_{(3,9,180.1)} = 3.35; p = 0.01; \eta_G^2 = 0.024]$) indicated a difference in performance (d') over blocks between the groups (object relative group: Block 1 = 0.60 ± 0.18 vs. Block 6 = $1.64 \pm 0.16, p < 0.001$; subject relative group: Block 1 = 1.47 ± 0.12 vs. Block 6 = $1.98 \pm 0.07, p < 0.001$). Tukey post hoc tests showed that the intergroup difference reduced along training, being significant from the 1st to the 4th blocks ($p_s < 0.03$) and still remaining close to significant for the 5th and 6th blocks (non-significant $p_s < 0.09$). None of the two groups performed at ceiling at the end of training. This was confirmed by a one-sample t-test performed on the data for the 6th block against the perfect performance ($d' = 2.17$ reflected 8 hits and 8 correct rejections out of 16 trials), both for the group training with object relatives [$t_{(23)} = 3.43; p = 0.004$, Bonferroni-corrected Cohen's $d = 0.70$] and the one training with subject relatives [$t_{(23)} = 2.68; p = 0.02$, Bonferroni-corrected, Cohen's $d = 0.55$].

These results confirm the behavioral differences described in the three previous experiments in processing object relatives compared to subject relatives. Furthermore, both groups of participants similarly benefited from their respective training, improving their performance in processing syntactic structures.

Tool-use improvement

The LMM on the number of inserted pegs showed main effects of *Time* [Pre vs. Post; $\chi^2_{(1)} = 64.35$, $p < 0.001$] and *Block* [1 vs. 2 vs. 3 vs. 4; $\chi^2_{(3)} = 47.08$, $p < 0.001$]. Participants significantly improved in using the tool after the syntactic training (inserted pegs in pre-test = 11.3 ± 0.3 vs. post-test = 14.0 ± 0.3 , $p < 0.001$) and they significantly improved regardless of the pre- and post-test along the four block ($p_s < 0.001$).

Quantification of effect size across Experiments 2 and 3

We further quantified the robustness of the cross-domain transfer from tool use to syntax by analyzing the effect size of the syntactic improvement (39, 43) following different training (tool use vs. free hand) across the two experiments (Experiments 2 vs. 3). We found that the benefits in syntactic comprehension of object relative clauses after tool-use as compared to free-hand training are consistent and of equivalent magnitude across experiments [Fig. 3F; 2-way *Training* \times *Experiment* rmANOVA: significant main effect of *Training* ($F_{(1,60)} = 5.37$; $p = 0.02$; $\eta_G^2 = 0.082$), nonsignificant effect of *Experiment* ($F_{(1,60)} = 2.8$; $p = 0.11$) nor any interaction ($F_{(1,60)} = 0.51$; $p = 0.58$)].

Initial syntactic skills for Experiments 2 and 3

To ensure that the improvement in post-test did not pertain to different syntactic skills before training, we controlled for pre-test syntactic performance between the training groups of Experiments 2 and 3. In the description of these experiments in the main text, we reported significant *Training* \times *Time* \times *Sentence* interactions, and Tukey post hoc tests did not show any difference in pre-test performance between groups for object relatives ($p_s > 0.63$) nor for coordinated ($p_s > 0.09$). In experiment 3 a significant difference appeared for subject relative clauses between tool-use and constrained-hand groups ($p = 0.04$), whereas all the remaining comparisons remain non-significant ($p_s > 0.18$). To ensure that the groups were homogeneous, we conducted additional analyses on d' and RTs, only considering pre-test performance with the three syntactic structures.

For d' , a 2-way rmANOVA including *Training* as between-subjects and *Sentence* as within-subjects factors was performed for Experiments 2 and 3 separately. This did not reveal any main effect of *Training* nor any interaction [$F_s < 2.32$; $p_s > 0.11$]. RTs were modeled with a LMM including the same factors as well as *Subjects* and *Sentence* as random effects. This analysis revealed a main effect of *Training* [$\chi^2_s > 6.17$; $p_s < 0.04$] for both Experiments 2 and 3, however post-hoc tests did not show difference between groups, with the smallest p -value ($p = 0.09$) found for a planned comparison between free-hand and constrained-hand groups in Experiment 3. Furthermore, the *Training* \times *Condition* interaction [$\chi^2_s < 3.54$; $p_s > 0.47$] was not significant. In summary, these analyses showed that the specific improvement in object relatives after tool-use training cannot be attributed to differences in pre-test performance.

Sociodemographic information

To rule out any effect of participant sociodemographic information (age, education level and handedness) on training, we compared this information between training groups in Experiments 2 and 3 via a series of one-way ANOVAs.

In Experiment 2, the three groups of participants with high initial syntactic skills were comparable in terms of age (tool use: 23 ± 3 years old, free hand: 23 ± 3 years old and video: 22 ± 2 years old, $F_{(2,55)} = 1.89$; $p = 0.16$), education level (tool use: 4 ± 2 years, free hand: 4 ± 1 years and video: 3 ± 1 years, $F_{(2,55)} = 1.58$; $p = 0.21$), and handedness (tool use: 0.85 ± 0.13 , free hand: 0.91 ± 0.11 and video: 0.92 ± 0.11 , $F_{(2,55)} = 1.80$; $p = 0.17$).

The same was observed in Experiment 3 for education level (tool use: 4 ± 1 years, free hand: 3 ± 2 years and constrained hand: 4 ± 2 years, $F_{(2,36)} = 1.19$; $p = 0.31$), and handedness (tool use: 0.88 ± 0.12 , free hand: 0.87 ± 0.14 and constrained hand: 0.88 ± 0.12 , $F_{(2,36)} = 0.39$; $p = 0.68$). A significant main effect of age [$F_{(2,36)} = 3.94$; $p = 0.02$; $\eta^2 = 0.180$] was found, indicating the average age of the constrained hand group (27 ± 6 years old) significantly differed from the free hand group (22 ± 3 years, $p = 0.02$). No difference was observed between the tool-use group (24 ± 5 years) and any of the two other groups ($p_s > 0.25$).

In Experiment 4, we tested for potential differences in sociodemographic characteristics (age, education level and handedness) between the two training groups (object relatives vs. subject relatives) via a series of two-sample t-tests. The two groups of participants were comparable in terms of age (object relatives: 27 ± 6 years old and subject relatives: 27 ± 5 years old, $t_{(46)} = 0.06$; $p = 0.95$); education level (object relatives: 4 ± 2 years and subject relatives: 5 ± 3 years, $t_{(46)} = 0.86$; $p = 0.39$); and handedness (object relatives: 0.89 ± 0.11 and subject relatives: 0.88 ± 0.10 , $t_{(46)} = 0.28$; $p = 0.78$).

Fig. S1. Experiment 1: *n-back* behavioral performance. (A) Mean sensitivity index (d'). (B) Mean Reaction Times (RTs) for the *1-back* and *3-back* tasks. Analyses revealed a memory load effect in the *3-back* condition compared to the *1-back* condition, with reduced sensitivity index (d') and longer RTs. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Fig. S2. Experiment 1: The working memory network. Statistical maps thresholded at $p < 0.001$, unc., for verbal working memory (*3-back* vs. *1-back*).

Fig. S3. Experiments 2 and 3: Lack of training group differences for subject relative and coordinated clause comprehension. In Experiment 2 (top panel), (A) for subject relative clauses and (B) coordinated clauses, no group difference was found on RTs. All training groups showed significantly shorter RTs in post-test with respect to pre-test. In Experiment 3 (bottom panel) (C) for subject relative clauses and (D) coordinated clauses, no group

difference was found on d' . Performance did not significantly vary between the pre- and post-test. Each dot linking pre-test to a post-test dot represents an individual participant. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Region	BA	Peak MNI coordinate s			Cluster size (<i>k</i>)	Z-value
		<i>x</i>	<i>y</i>	<i>z</i>		
(A) Syntax Network: 2 Object relative clauses – (Subject relative clauses + Coordinated clauses)						
L Striatum (cluster extending to Globus Pallidus) ^{FWE}	-	-18	14	-1	179	4.54
L Inferior Frontal Gyrus ¹	BA45	-42	29	5	28	4.05
L Angular Gyrus	BA39	-42	-52	32	14	3.69
R Striatum (cluster extending to Globus Pallidus) ^{FWE}	-	15	11	-1	177	4.32
R Angular Gyrus	BA39	51	-49	26	30	3.94

(B) Tool-use Planning Network: (Tool-use Planning – Free-Hand Planning) - (Tool-use Execution – Free-Hand Execution)

L Postcentral Gyrus (extending to Supramarginal Gyrus) ^{FWE}	BA1, 2, 3, 40	-63	-19	29	147	4.25
L Globus Pallidus (extending to Caudate) ^{FWE}	-	-6	-4	-10	124	4.83
L Inferior Frontal Gyrus ²	BA44	-60	11	26	37	3.99
L Occipitotemporal Cortex	BA19	-51	-73	-10	31	3.69
L Supramarginal Gyrus	BA40	-33	-37	38	26	3.64
L Putamen	-	-33	-13	-7	14	3.62
R Striatum (cluster extending to Globus Pallidus) ^{FWE}	-	33	-16	-7	750	5.34
		30	-1	17	11	3.66
R Supramarginal Gyrus ^{FWE}	BA40	36	-34	44	196	4.54
R Postcentral Gyrus (extending to Supramarginal Gyrus)	BA1, 2, 3, 40	57	-19	35	52	4.11
R Occipitotemporal Cortex	BA37	48	-55	-13	37	3.63
R Superior Temporal Gyrus	BA22	66	-19	-1	17	3.61
R Ventral Premotor Cortex	BA6	60	8	26	14	3.48

(C) Conjunction Syntax Network \cap Tool-use Planning Network

L Globus Pallidus	-	-12	5	-4	14	3.48
L Caudate Nucleus	-	-21	20	2	13	3.54
R Globus Pallidus	-	12	-1	2	14	3.66

Table S1. Brain areas activated for syntax (A), tool-use planning (B) and their conjunction (C). All presented clusters contain more than 10 contiguous voxels and are below the statistics threshold $p < 0.001$, unc. Clusters passing the family-wise error correction with $p < 0.05$ at the cluster level are indicated with the mention ^{FWE}. ¹*Pars triangularis*; ²*Pars opercularis*.

Region	BA	Peak MNI coordinates			Cluster size (<i>k</i>)	Z-value
		<i>x</i>	<i>y</i>	<i>z</i>		

Working Memory Network = Hits_{3-back} – Hits_{1-back}

L Angular Gyrus ^{FWE}	BA39	-30	-67	32	1931	5.61
L Middle Frontal Gyrus ^{FWE}	BA6	-24	14	47	673	5.78
L Dorsolateral Prefrontal Cortex ^{FWE}	BA46	-48	35	17	314	4.40
L Inferior Temporal Gyrus ^{FWE}	BA20	-48	-58	-10	156	4.11
L Caudate Nucleus ^{FWE}	-	-15	17	-7	182	4.49
L Anterior Lingual Gyrus ^{FWE}	BA19	-30	-46	-7	61	3.93
L Midbrain ^{FWE}	-	-9	-28	-7	53	4.13
L Anterior Prefrontal Cortex	BA10	-18	59	14	42	4.87
L Precentral Gyrus	BA4	-51	-7	35	40	4.29
L Middle Temporal Gyrus	BA21	-60	-10	-10	29	4.26
L Posterior Lingual Gyrus	BA18	-12	-76	-10	11	3.81

R Superior Frontal Gyrus ^{FWE}	BA6	24	-1	53	522	5.78
R Angular Gyrus ^{FWE}	BA39	39	-76	29	326	4.77
R Medial Orbitofrontal Cortex (extending bilaterally) ^{FWE}	BA11	9	32	-13	177	4.00
R Posterior Lingual Gyrus ^{FWE}	BA18	15	-76	-7	98	3.92
R Caudate Nucleus	-	18	17	5	47	4.47
R Anterior Lingual Gyrus	BA19	27	-43	-7	43	3.93
R Cerebellum Crus I	-	36	-70	-31	41	4.02
R Cerebellum Lobule IX	-	9	-55	-49	25	4.54
R Cerebellum Lobule VIIb	-	30	-70	-46	22	3.92
R Precentral Gyrus	BA4	51	-4	32	12	3.41

Table S2. Brain areas activated for working memory. All presented clusters contain more than 10 contiguous voxels and are below the statistics threshold $p < 0.001$, unc. Clusters passing the family-wise error correction with $p < 0.05$ at the cluster level are indicated with the mention ^{FWE}.

Coordinated clauses	Subject relative clauses	Object relative clauses
L'adversaire contente le marin et refait la partie	L'adversaire qui contente le marin refait la partie	L'adversaire que le marin contente refait la partie
L'amiral délivre l'alcoolique et piétine le drapeau	L'amiral qui délivre l'alcoolique piétine le drapeau	L'amiral que l'alcoolique délivre piétine le drapeau
L'architecte nourrit la copine et prépare le dîner	L'architecte qui nourrit la copine prépare le dîner	L'architecte que la copine nourrit prépare le dîner
L'artisan surprend le fermier et dévore le dessert	L'artisan qui surprend le fermier dévore le dessert	L'artisan que le fermier surprend dévore le dessert
L'assistante appelle l'employé et nettoie la cuisine	L'assistante qui appelle l'employé nettoie la cuisine	L'assistante que l'employé appelle nettoie la cuisine
L'écrivain admire le poète et écrit le papier	L'écrivain qui admire le poète écrit le papier	L'écrivain que le poète admire écrit le papier
L'espagnol envie la danseuse et adore le spectacle	L'espagnol qui envie la danseuse adore le spectacle	L'espagnol que la danseuse envie adore le spectacle
L'étudiante renseigne le chômeur et révise la leçon	L'étudiante qui renseigne le chômeur révise la leçon	L'étudiante que le chômeur renseigne révise la leçon
L'inspecteur attend la maîtresse et réclame le silence	L'inspecteur qui attend la maîtresse réclame le silence	L'inspecteur que la maîtresse attend réclame le silence
L'inventeur revoit l'acheteur et entoure le dessin	L'inventeur qui revoit l'acheteur entoure le dessin	L'inventeur que l'acheteur revoit entoure le dessin
L'officier attache la complice et arrache le couteau	L'officier qui attache la complice arrache le couteau	L'officier que la complice attache arrache le couteau
La belle-mère détend la fiancée et arrange les cheveux	La belle-mère qui détend la fiancée arrange les cheveux	La belle-mère que la fiancée détend arrange les cheveux
La belle-soeur avise le doyen et prévoit le séjour	La belle-soeur qui avise le doyen prévoit le séjour	La belle-soeur que le doyen avise prévoit le séjour
La bergère visite le pêcheur et dessine la colline	La bergère qui visite le pêcheur dessine la colline	La bergère que le pêcheur visite dessine la colline
La bourgeoise console la gardienne et mentionne le crédit	La bourgeoise qui console la gardienne mentionne le crédit	La bourgeoise que la gardienne console mentionne le crédit
La caissière accueille le portier et fournit la tenue	La caissière qui accueille le portier fournit la tenue	La caissière que le portier accueille fournit la tenue
La championne enchante le plongeur et réchauffe le plateau	La championne qui enchante le plongeur réchauffe le plateau	La championne que le plongeur enchante réchauffe le plateau

La chanteuse supporte la vedette et respecte le contrat	La chanteuse qui supporte la vedette respecte le contrat	La chanteuse que la vedette supporte respecte le contrat
La cliente arrête le vendeur et apporte le manteau	La cliente qui arrête le vendeur apporte le manteau	La cliente que le vendeur arrête apporte le manteau
La compagne soutient le cadet et repasse le rideau	La compagne qui soutient le cadet repasse le rideau	La compagne que le cadet soutient repasse le rideau
La comtesse installe la servante et demande le paquet	La comtesse qui installe la servante demande le paquet	La comtesse que la servante installe demande le paquet
La concierge salue le vieillard et surveille le jardin	La concierge qui salue le vieillard surveille le jardin	La concierge que le vieillard salue surveille le jardin
La cousine habille la grand-mère et descend les étages	La cousine qui habille la grand-mère descend les étages	La cousine que la grand-mère habille descend les étages
La fleuriste arrose la coiffeuse et échange la monnaie	La fleuriste qui arrose la coiffeuse échange la monnaie	La fleuriste que la coiffeuse arrose échange la monnaie
La française aborde l'étrangère et traduit la facture	La française qui aborde l'étrangère traduit la facture	La française que l'étrangère aborde traduit la facture
La juriste défend la stagiaire et contemple le palais	La juriste qui défend la stagiaire contemple le palais	La juriste que la stagiaire défend contemple le palais
La légiste connaît l'infirmière et regarde la télé	La légiste qui connaît l'infirmière regarde la télé	La légiste que l'infirmière connaît regarde la télé
La libraire espionne le mendiant et balaie le trottoir	La libraire qui espionne le mendiant balaie le trottoir	La libraire que le mendiant espionne balaie le trottoir
La maman conseille le tailleur et rejoint la maison	La maman qui conseille le tailleur rejoint la maison	La maman que le tailleur conseille rejoint la maison
La marchande informe la chinoise et affiche le panneau	La marchande qui informe la chinoise affiche le panneau	La marchande que la chinoise informe affiche le panneau
La marraine endort la belle-fille et active le réveil	La marraine qui endort la belle-fille active le réveil	La marraine que la belle-fille endort active le réveil
La masseuse contraint le coureur et étend la serviette	La masseuse qui contraint le coureur étend la serviette	La masseuse que le coureur contraint étend la serviette
La médium inspire l'amoureux et mérite le tableau	La médium qui inspire l'amoureux mérite le tableau	La médium que l'amoureux inspire mérite le tableau
La menteuse ignore la coupable et évite le regard	La menteuse qui ignore la coupable évite le regard	La menteuse que la coupable ignore évite le regard

La notaire distrair l'analyste et efface les empreintes	La notaire qui distrair l'analyste efface les empreintes	La notaire que l'analyste distrair efface les empreintes
La patronne dérange le malade et accorde la semaine	La patronne qui dérange le malade accorde la semaine	La patronne que le malade dérange accorde la semaine
La pédiatre critique l'apprenti et remplit le carnet	La pédiatre qui critique l'apprenti remplit le carnet	La pédiatre que l'apprenti critique remplit le carnet
La pianiste embrasse la mariée et augmente la musique	La pianiste qui embrasse la mariée augmente la musique	La pianiste que la mariée embrasse augmente la musique
La recrue flatte la joueuse et remporte la victoire	La recrue qui flatte la joueuse remporte la victoire	La recrue que la joueuse flatte remporte la victoire
La sage-femme tolère la hippie et dispose le fauteuil	La sage-femme qui tolère la hippie dispose le fauteuil	La sage-femme que la hippie tolère dispose le fauteuil
La sauvage retient le bonhomme et comprend le problème	La sauvage qui retient le bonhomme comprend le problème	La sauvage que le bonhomme retient comprend le problème
La serveuse amuse le mari et oublie le café	La serveuse qui amuse le mari oublie le café	La serveuse que le mari amuse oublie le café
La sorcière attire le chasseur et déchire la chemise	La sorcière qui attire le chasseur déchire la chemise	La sorcière que le chasseur attire déchire la chemise
La témoin réveille la victime et démarre la voiture	La témoin qui réveille la victime démarre la voiture	La témoin que la victime réveille démarre la voiture
La voisine observe l'inconnue et soulève la fenêtre	La voisine qui observe l'inconnue soulève la fenêtre	La voisine que l'inconnue observe soulève la fenêtre
La voleuse détient le pompiste et déclenche le moteur	La voleuse qui détient le pompiste déclenche le moteur	La voleuse que le pompiste détient déclenche le moteur
La voyante soulage la gitane et récite le poème	La voyante qui soulage la gitane récite le poème	La voyante que la gitane soulage récite le poème
Le bandit occupe la comptable et emporte le journal	Le bandit qui occupe la comptable emporte le journal	Le bandit que la comptable occupe emporte le journal
Le barbier imite le dandy et incline le miroir	Le barbier qui imite le dandy incline le miroir	Le barbier que le dandy imite incline le miroir
Le batteur accable la mascotte et essuie l'instrument	Le batteur qui accable la mascotte essuie l'instrument	Le batteur que la mascotte accable essuie l'instrument
Le boucher provoque la nourrice et avale le gâteau	Le boucher qui provoque la nourrice avale le gâteau	Le boucher que la nourrice provoque avale le gâteau

Le boxeur suspecte le vainqueur et repousse la menace	Le boxeur qui suspecte le vainqueur repousse la menace	Le boxeur que le vainqueur suspecte repousse la menace
Le chauffeur excuse le parent et allume la radio	Le chauffeur qui excuse le parent allume la radio	Le chauffeur que le parent excuse allume la radio
Le chercheur corrige la chimiste et rassemble les données	Le chercheur qui corrige la chimiste rassemble les données	Le chercheur que la chimiste corrige rassemble les données
Le comique implique l'interprète et proclame l'ouverture	Le comique qui implique l'interprète proclame l'ouverture	Le comique que l'interprète implique proclame l'ouverture
Le curieux caresse la diva et conserve le collier	Le curieux qui caresse la diva conserve le collier	Le curieux que la diva caresse conserve le collier
Le docteur recherche la patiente et achète le cadeau	Le docteur qui recherche la patiente achète le cadeau	Le docteur que la patiente recherche achète le cadeau
Le garçon entend la gamine et éteint la lumière	Le garçon qui entend la gamine éteint la lumière	Le garçon que la gamine entend éteint la lumière
Le gendarme bouscule l'innocente et referme la cellule	Le gendarme qui bouscule l'innocente referme la cellule	Le gendarme que l'innocente bouscule referme la cellule
Le génie inscrit l'ingénieur et finit le travail	Le génie qui inscrit l'ingénieur finit le travail	Le génie que l'ingénieur inscrit finit le travail
Le gérant affronte le maçon et recouvre la piscine	Le gérant qui affronte le maçon recouvre la piscine	Le gérant que le maçon affronte recouvre la piscine
Le glacier fascine la touriste et décrit les parfums	Le glacier qui fascine la touriste décrit les parfums	Le glacier que la touriste fascine décrit les parfums
Le grand-père cherche l'italien et regrette le mensonge	Le grand-père qui cherche l'italien regrette le mensonge	Le grand-père que l'italien cherche regrette le mensonge
Le héros libère la déesse et répète la chanson	Le héros qui libère la déesse répète la chanson	Le héros que la déesse libère répète la chanson
Le lecteur consulte l'éditeur et illustre le roman	Le lecteur qui consulte l'éditeur illustre le roman	Le lecteur que l'éditeur consulte illustre le roman
Le livreur encaisse l'irlandais et renverse le tiroir	Le livreur qui encaisse l'irlandais renverse le tiroir	Le livreur que l'irlandais encaisse renverse le tiroir
Le ministre emmène l'avocate et apprend le discours	Le ministre qui emmène l'avocate apprend le discours	Le ministre que l'avocate emmène apprend le discours
Le papa retrouve le bébé et attrape la bouteille	Le papa qui retrouve le bébé attrape la bouteille	Le papa que le bébé retrouve attrape la bouteille

Le parrain reprend le neveu et refuse le portable	Le parrain qui reprend le neveu refuse le portable	Le parrain que le neveu reprend refuse le portable
Le pilote reçoit le monsieur et amène les affaires	Le pilote qui reçoit le monsieur amène les affaires	Le pilote que le monsieur reçoit amène les affaires
Le pompier secourt l'allemande et abîme le briquet	Le pompier qui secourt l'allemande abîme le briquet	Le pompier que l'allemande secourt abîme le briquet
Le savant exclut le critique et gaspille la peinture	Le savant qui exclut le critique gaspille la peinture	Le savant que le critique exclut gaspille la peinture
Le sculpteur rembourse le plombier et emballe les jouets	Le sculpteur qui rembourse le plombier emballe les jouets	Le sculpteur que le plombier rembourse emballe les jouets
Le seigneur rassure la princesse et réduit la douleur	Le seigneur qui rassure la princesse réduit la douleur	Le seigneur que la princesse rassure réduit la douleur
Le sergent écoute le voyou et détruit le dossier	Le sergent qui écoute le voyou détruit le dossier	Le sergent que le voyou écoute détruit le dossier
Le soldat poursuit le bourreau et protège le trésor	Le soldat qui poursuit le bourreau protège le trésor	Le soldat que le bourreau poursuit protège le trésor
Le souverain séduit la duchesse et honore le royaume	Le souverain qui séduit la duchesse honore le royaume	Le souverain que la duchesse séduit honore le royaume
Le traiteur relance le commis et cuisine la commande	Le traiteur qui relance le commis cuisine la commande	Le traiteur que le commis relance cuisine la commande
Le valet remplace le baron et présente le salon	Le valet qui remplace le baron présente le salon	Le valet que le baron remplace présente le salon
Le vigile intrigue la fidèle et décharge le carton	Le vigile qui intrigue la fidèle décharge le carton	Le vigile que la fidèle intrigue décharge le carton

Table S3. Linguistic material used in the syntactic task (in French). Depending on participants, sentences defined by two animated agents and one inanimate object were presented with each of the three syntactic structures: coordinated clauses (left column), subject relative clauses (middle column) and object relative clauses (right column).

Movie S1. Tool-use Task

Video available at <https://osf.io/sgb4d/>

Movie S2. Free-hand Task

Video available at <https://osf.io/sgb4d/>

Chapter 4

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General Discussion

Summary of the main results

In the first study, we reported and discussed the degree of functional co-localization between tool use on one side and semantics or phonology on the other. The multivariate approach we employed, the RSA, showed that the activations elicited by the phonological task within the left IPL and IFG, regions that are were activated by the use of the tool, failed to significantly represent the stimuli of the linguistic task (Fig. 21 in blue). Conversely, the neural activity elicited by semantic processing within the regions activated by tool use, allowed to represent the semantic category of words used in the linguistic task. The RSA revealed that the dissimilarities in the activity patterns were significantly represented within the left OTC and IFG (Fig. 21 in red). In the second study, we uncovered the neural overlap between tool use and complex syntactic processing (Fig. 21 in green). Importantly, this neural overlap was not explained by any activity related to the increased role of working memory for complex syntactic structure, nor by the activity related to the control of a manual action. Indeed, the working memory network did not overlap with the tool use network, as the free-hand planning network did not with the complex syntax network. In addition to the functional co-localization, via a series of multivariate analyses, we revealed the similar spatial distribution of neural activity within the BG for tool use and complex syntactic processing, so that those voxels presenting a high level of activity for tool use were more activated by processing complex syntactic structures too. Behaviorally, this neural relation resulted in a bidirectional cross-domain learning transfer, where training with a tool, but not the free-hand, improved the performance in complex syntactic processing; similarly, training complex syntax resulted in the improvement of the tool-use ability.

Overall, our results support our prediction that tool use and language share neural resources, in particular for semantics and syntax. Furthermore, the functional relevance of these shared resources is reflected by bidirectional cross-domain learning transfer between tool use and language, as we documented for syntax. This general discussion will consider our findings with respect to previous work in the field of embodied cognition supporting the claim that phonological, semantic and syntactic processing of language is grounded within the sensorimotor network. Our findings will be also discussed with respect to theories suggesting a coevolution of tool use and language. Then, we will discuss the learning transfer and its potential underlying mechanisms that might open new perspectives for learning of a novel language or rehabilitating impaired motor and language functions. In a last section, we will

defend the hypothesis that our findings reveal the BG manage a supramodal hierarchical function subserving the motor and language domains.

Figure 21: Summary of the neuroimaging results regarding the existence of a shared network between tool use and language. Green ticks indicate areas where neural resources are shared between tool use and language, whereas red crosses indicate areas where no evidence for shared neural resources was found in our work. For phonology (in blue), we did not find shared neural substrates with tool use in the left IFG and left IPL. For semantics (in red) shared neural resources within tool use were observed in the left IFG and left OTC but not in the left IPL. For syntax (in green) shared neural resources were found in the BG but not in the left IFG.

The co-localization of neural resources

One main question tested across our two studies relies on the hypothesis that several brain regions whose activity supports tool use are also recruited for language processing. With our contribution we provide empirical evidence for a co-localization of the neural resources between the two abilities, suggested by previous theoretical work (Greenfield, 1991; Stout & Chaminade, 2012). In the present section, we discuss our results with respect to the expected co-localization of tool use and, respectively, phonology, semantics and syntax.

1. Tool use and phonology

Because of their documented involvement in tool use (e.g. Brandi et al., 2014) and phonological processes (e.g. Raizada and Poldrack, 2007), we reasoned that the left IFG and IPL could represent the hubs for the co-localization of neural resources supporting the two abilities. Both the left IFG and IPL are involved in sensorimotor computations in the motor and language domains. For instance, the parietal cortex participates in the remapping of the surrounding space when a tool is used (Iriki et al., 1996) and supports the discrimination of speech sounds (Raizada & Poldrack, 2007). The tasks we devised to study tool use and phonology indeed recruited these areas, even though not within the same clusters. We found that the phonological processes activated the angular gyrus localized more posteriorly with respect to the portion of SMG activated by the tool use task. In the frontal areas, phonology mainly recruited the *pars orbitalis*, whereas tool use induced activation within the ventral portion of the precentral sulcus. The activations of anatomical different, although contiguous, territories are reflected by the RSA approach: the neural activity patterns elicited by the phonological task within areas activated by tool use did not allow to decode the phonological

category of the stimuli (i.e. /ba/ or /da/). Even though using a tool requires the integration and discrimination of refined perceptual features, this process likely relies on separated neural resources than those recruited by phonology for speech perception. This observation is consistent with previous predictions that the SMG and especially the aSMG is specifically involved in the association of hand actions with the functional use of the tool (Peeters et al., 2009). This latter area has been suggested to be outside of the linguistic network (see Peeters et al., 2009; Stout and Chaminade, 2012).

2. Tool use and semantics

Conversely to phonology, the RSA approach we employed for semantics suggests the existence of shared neural resources between this language component and tool use. Tool use activated the left IFG and OTC, two regions whose activity contributes to the semantic distinction between tool and animal nouns. The encoding of such semantic relationship within areas of the tool use network supports the existence of shared neural resources between tool use and semantic processing. Despite a meta-analysis suggested independent neural circuits for tool use and tool naming (Ishibashi et al., 2016), our findings are consistent with previous convergent neuroimaging results showing that the left IFG and OTC are recruited for semantic processing involving tool representations (Cattaneo et al., 2010; Chao et al., 1999; Perani et al., 1999), as well as for tool use (Brandi et al., 2014). Although acquired in different studies and participants, these previous data indirectly suggested that similar neural resources could be at stake for the motor and language domains. Our findings are in agreement with the grounded cognition theory suggesting that the semantic concepts are not amodal but rather grounded onto the systems dedicated to perception and action (Barsalou, 1999, 2008; Pulvermüller, 2005; Pulvermüller & Fadiga, 2010). Along this line, the concept of tool should evoke activity within the sensorimotor circuits involved in tool actions (i.e. left IFG) and perception of tool motion (i.e. OTC). The co-localization of semantics and tool use highlighted by our analysis might potentially rely on the fact that tool nouns have been employed. Indeed, previous neuropsychological studies have pointed towards the existence of shared neural resources between action and action concepts (Arévalo et al., 2007; Kemmerer et al., 2012). Crucially, even if some studies failed to evidence a causal link between tool-use impairments and tool conceptual knowledge with the existence of double dissociations (Papeo et al., 2010; Rumiati et al., 2001), positive evidence also comes from patients with aphasia who are impaired in both tool naming and tool pantomime (Fazio et al., 2009). Crucially, lesion-symptom mapping analyses revealed overlapping neural representations between language and pantomimes

impairments in patients with left hemisphere lesions (Goldenberg & Randerath, 2015). Finally, another study reported that patients impaired in naming tool nouns were also impaired for imitating meaningful (e.g. hammering) but not meaningless (i.e. finger tapping) actions (Mengotti et al., 2013). This latter study suggests language-action association or dissociation observed in neuropsychological studies might depend on the degree of common conceptual features between action and language.

3. Tool use and syntax

We revealed the existence of shared neural resources between tool use and syntactic processing within the BG. Furthermore, by a series of multivariate analyses conducted on the BG, we demonstrated that the spatial organization of the activations elicited by tool use in comparison to manual actions was more similar to the one elicited by the syntactic task. In our view, these findings reflect the implementation of complex hierarchies within the BG. On one hand, the involvement of this subcortical structure has been demonstrated for syntactic violation detection (Moro et al., 2001), grammar learning (Tagarelli et al., 2019) and complex syntactic processing (Teichmann et al., 2015). On the other hand, preparing or executing an action sequence hierarchically organized recruits the BG (Martins, Bianco, et al., 2019; Wymbs et al., 2012). Most importantly, tool use or tool pantomime have been reported to recruit the BG (Choi et al., 2001; Garcea & Buxbaum, 2019; Johnson-Frey et al., 2005; Obayashi et al., 2001) whose role has been linked to the increased difficulty of the action sequence. This difficulty is likely explained by the further hierarchical level the use of a tool implies in comparison to manual actions (Greenfield, 1991; Pastra & Aloimonos, 2012). By doing a parallel with an embedded syntactic structure for language, the tool action can be described as follows *[move your hand [grasp a tool [grasp a peg and insert the peg] release the tool] move back your hand]*, whereas the free-hand action will present one level less, so that the sequence can be described as follows *[move your hand [grasp a peg and insert the peg] move back your hand]*. In our opinion, these results reflect the existence of closely linked neural networks that are localized within the BG or even the existence of common neural resources recruited by the two functions. If the second hypothesis holds true, this would suggest a set of neurons are devoted to processing hierarchies across different domains, such as the motor and language domains. To date, the available fMRI techniques do not allow to determine whether the neural resources activated within overlapping clusters are truly the same neuronal populations or interleaved subpopulations involving distinct subnetworks. The main limitation comes from the spatial resolution given by the voxel size used in functional sequences in MRI, usually going from 2 to 3 mm³. A voxel of this size

contains a large number of neurons and synapses, preventing the possibility to identify whether the exact same neuronal populations are activated by tasks pertaining to different domains. Multivariate analysis approaches in fMRI can help to circumvent these limitations by considering the spatial organization of the activations rather than their differences in signal magnitude. By exploiting the advantage given by multivariate approaches to the fMRI analyses, we showed that complex syntax and tool use do not simply overlap within the BG. More than that, we revealed that the spatial organization of the neural activation elicited by the two tasks is similar. However, developing techniques with better spatial but also temporal resolutions will be critical in the future to tackle these questions.

Hierarchical processing is also supported by the left IFG for both complex syntax (Walenski et al., 2019) and action with (Choi et al., 2001) and without a tool (Koechlin & Jubault, 2006). As a consequence, scholars suggested that shared neural resources within this area provide a supramodal syntactic/hierarchical function (Fiebach & Schubotz, 2006; Fitch & Martins, 2014; Greenfield, 1991; Roy & Arbib, 2005; Stout & Chaminade, 2012; Tettamanti & Weniger, 2006). In our experiments, the complex syntax task and tool-use planning indeed involved the left IFG, however their respective clusters of activity did not overlap in this region. The cluster elicited by complex syntax in the left *pars triangularis* was localized more anteriorly than the tool-use planning cluster in the precentral sulcus bordering the left *pars opercularis*. These findings are in line with previous neuroimaging meta-analyses (Clos et al., 2013; Papitto et al., 2020), showing the motor system recruits territories of the left IFG that are distinct from those involved in language. One possibility is that different domains are represented separately within the left IFG and do not share neural resources (Fedorenko et al., 2012). Nonetheless, even though these regions are anatomically distinct, this does not prevent they might nurture a strong functional link. Interestingly, a functional interrelation between the BG and the left IFG has been evidenced previously for linguistic processing (Booth et al., 2007). Indeed, functional connectivity analyses (i.e. dynamic causal modelling) revealed unidirectional connections from the putamen to the left IFG in a phonological rhyming judgment task. Furthermore, for syntax, a white matter tract (called Broca-striatum tract) between the BG and left IFG has been proposed to take part in complex syntactic processing (Teichmann et al., 2015). Given the role of the subcortico-frontal connections for motor control (Graybiel et al., 1994), we can speculate this pathway also subserves the realization of hierarchical actions. Therefore, hierarchical processing in the motor domain may emerge from the shared neural resources within the BG before projecting on the portions of the IFG just

posteriorly to the projections for complex syntax. In others words the BG might deal with hierarchical processing across two different domains, whereas further processing refinements might be performed in the specific clusters for action and language.

4. Functional consequences of the co-localization

What does this co-localization imply? Functions sharing neural resources can be interdependent, so to have the potential of reciprocally impacting each other. Indeed, our behavioral investigations revealed the bidirectional cross-domain learning transfer between tool use and complex syntax. In other words, training to use a tool improves complex syntax processing, whereas actions without a tool do not. Reciprocally, training in processing complex syntactic structures in language improves tool use abilities. We did not test this reciprocal interdependence for tool use and semantics. Nonetheless, a recent study tested the effect of labelling new tools on their functional use (Foerster et al., 2020). In a virtual reality environment, the participants were submitted to novel tools that either received a verbal labeled or not. Then, they learnt to use these tools and in a last experimental run they were asked to properly use or simply move them. Crucially, the tools that had been labelled at the beginning of the experiment were more rapidly and correctly used than the unlabeled tools. Furthermore, labelling had no facilitation effect when the participants were asked to simply move the tool (i.e. no functional use). The EEG recordings indicated this behavioral effect was accompanied by a reduction of power within the sensorimotor beta frequency band. Indeed, about 340 ms after the appearance of a virtual tool, using a labelled tool elicited a beta-band signal decrease within the centro-parieto-occipital areas. The authors interpreted this neurophysiological modulation as an augmented learning of body states related to tool use via the activation of a lexical representation. Overall, this study and our findings invite to test in more details the reciprocal benefits between tool use and semantics.

Semantics and syntax are grounded within the tool-use sensorimotor network

In the manuscript introduction, we discussed the large amount of evidence in favor of grounded phonology and semantic processes of language within the sensorimotor system. In line with these findings, we revealed shared neural resources between tool use and semantics within the left IFG and OTC in neurotypical adults. In a first section we aim to discuss our findings for semantics with respect to previous evidence. By contrast, to date there is no strong support about the anchoring of syntax to the sensorimotor circuits. At best the existing evidence to this regard suggests common computations between language and action, albeit it is mainly related to the detection of structural errors during observation of motor sequences. Our finding goes beyond this and revealed neural similarities between tool use and complex syntactic processing within the BG. In a second section, we will propose that syntax is an embodied function similarly as phonology and semantics are.

1. Semantics is grounded within the tool action system

The involvement of sensorimotor regions in language processing is now widely accepted, especially for phonology and semantics. For instance, phonology relies on the motor territories involved in speech production (D'Ausilio et al., 2009; Pulvermüller et al., 2006; Roy et al., 2008; Wilson et al., 2004). Reading action verbs activates the motor and premotor areas according to a somatotopic gradient (Hauk et al., 2004). Thus we tested the hypothesis that phonology and semantics might be grounded within a sensorimotor network specific to tool use. Indeed tool use and phonological processing both require the integration and discrimination of fine-grained sensory information, in particular from the visual, tactile and proprioceptive modalities for tool use (Bahmad et al., 2020; Cardinali et al., 2016; Miller et al., 2018; Pazen et al., 2020), and in the auditory and somatosensory modality for phonology (Hickok & Poeppel, 2007; Pa & Hickok, 2008; Raizada & Poldrack, 2007). The left IPL and IFG likely play a role of interface between multisensory perception and motor plans for both language and tool use. However, our current findings suggest that sensory integration for tool use and speech rely on distinct neural circuits of the left IPL and IFG.

For semantics, previous evidence suggests animal and tool nouns respectively involve shape recognition areas within the medial and lateral fusiform gyrus, on one side, and motion

perception areas within the pSTG and pMTG (Chao et al., 1999) on the other. Furthermore, the left frontoparietal areas responded strongly when tool pictures were observed or named with respect to the neural activity elicited by animal, face and object pictures (Chao & Martin, 2000). Nonetheless, these studies did not test whether the same territories were recruited when using a tool, leaving the possibility that tool use and semantics are represented in close but distinct neural regions, as suggested by a meta-analysis of neuroimaging studies focusing on tool naming, recognition and use (Ishibashi et al., 2016). By directly testing the neural bases of tool use and semantics in the same group of participants, our findings showed overlapping neural representations between the two functions.

The debate is still ongoing regarding the reason and the nature of the sensorimotor activations for language processes (Cayol et al., 2020; Cayol & Nazir, 2020). Some criticisms arise from the fact that the sensorimotor activations might not be necessary for language. They could just result from post-conceptual mental imagery processes (Machery, 2007; Mahon & Caramazza, 2008) or top-down factors in giving attention to specific stimuli aspects (Papeo & Hochmann, 2012). To rule out the possibility of voluntary post-conceptual visuomotor representations, studies would have to prove that the sensorimotor involvement in semantic processing is implicit and rapid (Kiefer et al., 2008). Our study aimed to control for these aspects. Indeed, we employed an implicit task where access to semantic category was not explicit because participants had to perform a lexical decision task instead of semantic categorization. Finally, our fMRI models aimed to regress out the period of time where the post-conceptual processing may occur by modeling the stimuli onset separately from the response period. Despite these precautions, fMRI does not allow to reveal the time-course of the neural responses because of its relatively low temporal resolution. However, most of the EEG/MEG experiments performed previously found that the involvement of the sensorimotor circuits in semantics occurred early (within 200-250 ms) after stimulus onset (Boulenger, Silber, et al., 2008; Hoenig et al., 2008; Kiefer et al., 2008; Pulvermüller, Shtyrov, et al., 2005). Such timing of activation suggests that the language-related motor activity cannot correspond to post-conceptual mental imagery processes. In light of these studies, overall, our findings are evidence for the contribution of tool-use sensorimotor areas to semantic processing.

2. The grounded syntax

Does syntax in language also involve the sensorimotor hierarchical neural circuits? The proposal of grounded syntax into the sensorimotor network emerged more recently than for phonology and semantics (Pulvermüller, 2010; Pulvermüller & Fadiga, 2010). In this regard, researchers have proposed that action is syntactically organized (Pulvermüller, 2014; Roy & Arbib, 2005). A brain region in particular, the left IFG, has been suggested to work as a supramodal hierarchical processor across several domains (Fadiga et al., 2006; Fiebach & Schubotz, 2006; Fitch & Martins, 2014; Tettamanti & Weniger, 2006).

Preliminary investigations aiming to uncover the potential existence of a grounded syntax mainly focused on the observation of motor sequences (Maffongelli et al., 2015; Sitnikova et al., 2003, 2008). These sequences presented a structural error, corresponding to the inversion between sub-movements of an entire motor sequence (e.g. put the pasta in a pan before the water). The analysis of the electrophysiological response to the error detection revealed a P600 evoked response, consistent with the response elicited by the detection of structural errors in sentences. Patients with a non-fluent aphasia resulting from a lesion to the left IFG furthermore presented difficulties, as compared to controls, in reordering sequences depicting human actions, whereas performance for reordering physical events sequences remained intact (Fazio et al., 2009). However, these findings did not indicate whether performing the action is supported by similar neural computations than language. A first attempt to uncover syntactic aspects of action execution focused on children suffering SLI/DLD, whose ability to produce syntactically complex structure is impaired (Roy et al., 2013). In addition to these language deficits, these children manifested structural motor anomalies with respect to typically-developing (TD) children. In this kinematic study, children had to grasp and move a bottle, whose weight (i.e. heavy or light) was either known or unknown before the movement. Conversely to TD children, SLI children were unable to anticipate the moving phase from the reaching phase when the bottle weight was known. Since this contribution, too few attempts have been made to unravel syntactic aspects in the action domain. Yet, the neural bases supporting such processes remain largely unknown. The lack of neuroimaging investigations in this area may be explained by the difficulty to implement complex action sequences in a fMRI scanner.

Indeed, an extremely simplified version of action sequence has been mainly employed as an optimal task to uncover the neural bases of hierarchical processing within the motor system: tapping sequences with fingers, such as on a keyboard. Tapping with a single finger is

the lowest level of the motor sequence. More complex levels can be obtained by adding fingers to the sequence to be tapped. In such a way, several different sequences can be learnt and then associated into a superordinate motor sequence (see Koechlin and Jubault, 2006). The superordinate motor sequence consists of low-level chunks integrated into a higher-level sequence. Specific rules guide the order of the chunks and the long-distance dependencies. For instance, let us imagine three sequences of finger tapping, such as sequence α = CABA, β = ACBC and γ = CBAB, where each letter corresponds to a given key. These three lower-level sequences can be chunked into different superordinate sequences, such as $\alpha\beta\gamma$ or $\gamma\alpha\beta$. At the behavioral level, execution of a superordinate sequence increases the response time between key presses representing the chunking transition from one low-level sequence to another (Koechlin & Jubault, 2006). Performing superordinate sequences involves the bilateral IFG (Koechlin & Jubault, 2006) and the BG (Wymbs et al., 2012). One recent study extended these findings, by asking participants to perform a motor task which follows a recursive rule (Martins, Bianco, et al., 2019). Recursion is the property of a function, defined recursive when it can be applied to its own result (i.e. namely *recursively*). It is a characteristic of language, specifically of certain syntactic rules allowing to embed the clauses one into the other, infinitely. Performing a motor sequence under a recursive rule recruits the BG but not the left IFG (Martins, Bianco, et al., 2019). Overall, these studies suggest the hierarchical rule-governed actions are handled by the left IFG and/or BG.

Albeit finger tapping is a well-controlled paradigm to study motor hierarchical processing, this remains far from the reality of motor behavior characterizing our daily life. Thus, to study whether complex syntax processing is grounded into sensorimotor processes, we think tool use is the most ecological task. Indeed, the tool is an external object to control and to embed between the hand and the distant object to handle (Greenfield, 1991). Our findings suggest the structural organization of tool-use action displays similarities with a complex syntactic structure in language. Indeed, both complex syntax and tool use recruit the BG and reciprocally impact each other at the behavioral level. Therefore, this supports the idea that more complex syntactic structures for language are grounded within the neural territories processing complex hierarchical structure for action. These results clearly invite to reconsider the specificity of language syntax suggested by some scholars (Hauser et al., 2002; Moro, 2014; Tettamanti & Moro, 2012). The idea that syntax is embodied has been thoroughly challenged in the past, mainly defending the putative uniqueness of human syntax and its specificity for the language domain. This criticism mostly originates from the hypothesis that syntactic

complexity for language is unique and distinct from other cognitive functions supporting hierarchical implementations. In this line, the potential similarities existing with the motor domain have been dismissed as being, at best, a metaphor but not a reality (Moro, 2014). However, our data, together with the above-mentioned indirect evidence, show that it is difficult to argue that syntax is represented in amodal neural structures: hierarchies irrespectively of the motor or linguistic domain involve a pool of common functional resources.

The role of human brain evolution

The brain architecture is the result of the long human evolution history. Thus, if tool use and language are represented within the same set of brain regions or conversely represented in close but distinct neural territories, it is most likely the product of the brain evolution history. Language and tool use are two functions highly developed in humans in comparison to other living species. These human specific cognitive refinements have likely originated from their interrelations during the evolution of the brain, resulting in the sharing of neural resources. In this section, we aim to discuss our findings with respect to theoretical accounts of human evolution.

1. The role of evolution in the current organization of tool use and language networks

Our studies revealed distinct but anatomically close clusters for tool use and phonology within the left IFG and IPL. Semantics and tool use on the contrary appear co-localized within the left IFG and OTC. Finally, tool use and syntax are co-localized within the BG, whereas separated but close clusters are activated by the two abilities within the IFG. This anatomical organization has to be considered with respect to the brain evolution history. Among the evolutionary mechanisms, exaptation is probably one of the most critical for the emergence of novel traits (Gould & Vrba, 1982). Exaptation can be defined as an evolutionary process consisting of an adaptive shift in the function of a trait already existing but serving a different purpose. For instance, such mechanism has likely contributed in *Archaeopteryx* to the reuse of feathers in order to fly, whereas their original function was likely for thermoregulation purposes (Gould & Vrba, 1982). More recently, such exaptation process has been proposed to occur within the brain (Anderson, 2016; Dehaene & Cohen, 2007; Iriki & Taoka, 2012; Kolodny &

Edelman, 2018). To characterize exaptation at the neural level, the authors talk about neural reuse. Indeed, a set of cognitive functions may have emerged, during human evolution, from the reuse of ancient biological mechanisms subserving a different role. For cognitive functions whom the appearance is too recent, neural reuse has been proposed as a mechanism supporting their emergence. For instance, it has been suggested that the ability to read, consisting in recognition of word forms, has emerged thanks to neural reuse of circuits devoted to recognition of object shapes (Dehaene & Cohen, 2007). Neural reuse has also likely supported the emergence of other cognitive functions such as language and tool use (Anderson, 2016; Dehaene & Cohen, 2007; Iriki & Taoka, 2012; Kolodny & Edelman, 2018).

Thus, neural reuse might explain why different functions share similar neural circuits and also suggests that functions implemented in different brain regions could have evolved separately and on different time frames. The ability to discriminate meaningful sounds, as implied in phonological processing, likely emerged before the appearance of tool-use behaviors in humans. Indeed, living species, such as the swamp sparrows are able to categorically perceive song notes presenting a continuous variation (Lachlan & Nowicki, 2015), but no record exists regarding their ability to use tools. Hence, this seemingly trait for categorical perception between humans and birds suggests human phonology and tool use may have evolved on different time frames and consequently in distinct neural circuits. However, the human phonological ability might have also undergone specific refinements along our evolution, so that the phonological ability of modern humans might be different from the one of our ancestors. While the human brain kept increasing, the phonological function could have been refined thanks to the contribution of emerging neural territories. Interestingly, investigations of human skull fossils show dramatic increase of the cranial volume across time. Most importantly, the increase of cranial volume is contingent with a transition in stone tool making technology (i.e. from Oldowan to Acheulean technology), also corresponding to a switch in terms of technological complexity, and occurring about 1.5 Mya (Ponce de León et al., 2021). Because these expansions mainly occurred at the level of the occipital, inferior frontal and posterior parietal bones, the authors suggest it might be strongly related to the emergence of language in humans. Indeed, the inferior frontal and inferior parietal areas are critical for language in modern humans and especially for phonology.

The emergence of more complex tool-making behaviors has reshaped our brain and we can hypothesize that some expanded brain regions have progressively served different purposes than their original ones. For instance, it has been suggested that tool-use progressively increased

the cortical surface of the inferior parietal areas, forming a new neural niche for emergent cognitive functions such as language (Iriki & Taoka, 2012). Hence, phonology may be represented at proximity of the tool-use network because it reused and exapted the neural circuits originally dedicated to tool use. This hypothesis is in part consistent with meta-analyses of neuroimaging investigations evidencing close but distinct clusters for action and language within the left IFG (Clos et al., 2013; Papitto et al., 2020). This line of results suggests that the motor processes rely on the posterior frontal territories whereas language relies on anterior frontal regions. Further meta-analytic investigations might be necessary to uncover such relations in the left IPL, where anterior territories should be devoted to tool use and separated from posterior ones critical for language (see Peeters et al., 2009; Stout and Chaminade, 2012).

The existence of shared neural resources found between semantics and tool use might also result from neural reuse. Primitive forms of semantics may have emerged before tool use. Indeed, a non-tool-user species like the Siberian jay is able to produce referential calls indicating the presence of different predators (Gill & Bierema, 2013). Hence, these referential calls can be considered as a primitive semantic function, helping to characterize the type of threat in order to help the congeners to select the most adequate coping behavior. In hominids, the ability to recognize and represent an object at the conceptual level may have facilitated the emergence of sensorimotor representations for their use. Reciprocally, we can speculate, this object became *tool* and was associated to strengthened conceptual representations (Weisberg et al., 2007). In the course of this gradual evolution process tool use and their associated conceptual representations may have co-evolved in neural system subserving both action and semantics. The role of the left IFG and left OTC we found for both tool use and semantics can be consistent with neural reuse processes occurring during the co-evolution trajectory of these two functions.

Finally, regarding the link between tool use and syntax, neural recycling processes could explain the neural organization of the involved regions. Critically shared neural resources are found within the BG and distinct but close clusters in the left IFG for the two functions. Syntax has been suggested to be a human specific function (Hauser et al., 2002). However, the human specificity of syntax has been questioned since evidence showed combinatorial aspects are also present in animal vocalizations (Sainburg et al., 2019). Nonetheless, relatively to animals, the human superiority for syntactic processing is still well admitted, allowing human language to be a unique form of communication system within the animal reign (Zaccarella & Friederici, 2017). On another aspect it has been proposed that the increasing complexity of the human tool-

use behaviors has been mirrored by the increasing complexity of the communication forms (Ambrose, 2001; Morgan et al., 2015; Ponce de León et al., 2021). In other words, language and tool use might be so developed in humans because the two processes influenced each other. The role of combinatorial hierarchical processes may have been crucial for this co-evolution. Both the BG and left IFG might be involved in this reciprocal influence. Given that we found shared neural resources between tool use and complex syntax within the BG, we might hypothesize that the two functions reciprocally took advantage of these neural structures over the course of human evolution. In the primitive human brain, the BG might be involved in low-level combinatorial processes before being further refined for the hierarchical processing of more complex structures for action (i.e. tool use) and language (i.e. combinatorial syntax). Regarding the separated clusters observed in the left IFG, we previously suggested these clusters are devoted to contribute to the hierarchical processing performed at the level of the BG. Hence, it is possible that during human evolution the left IFG allowed general hierarchical processing before progressively specializing into two clusters dedicated to a given domain. Interestingly, at the ontogenetic level a progressive specialization of the left IFG has been proposed: the left IFG would process hierarchies for the motor and language domains within the same neural circuits that become progressively specialized from the age of two (Greenfield, 1991).

Does neural reuse imply that the new function replaced the original one or can the former simply reuse the neural circuits without impacting the latter? Hence, one possibility, in accordance with the neural recycling hypothesis, is that exaptation may result in destructive processes for the original function. The hypothesis of destructive processes have been tested with the reading ability (van Paridon et al., 2021). Both literate and illiterate participants were tested on their ability to recognize faces and objects. Indeed, the visual word form area (VWFA) specifically involved in reading has likely exapted the neural circuits devoted to visual recognition (Dehaene & Cohen, 2007). Crucially literate participants were better at recognizing faces, suggesting that the reading ability improve rather than weaken the recognition mechanisms (van Paridon et al., 2021). In light of to these findings, we propose the interpretation that functions co-evolving together also foster each other, so for instance tool use may have nurtured the emergence of higher complexity in linguistic syntax and vice versa during the evolution.

2. The motor origin of language

Human language origin is a fascinating debate and among various possible scenarios, one proposes a gestural origin of language. Support in favor of this the gestural hypothesis comes from non-human primates' studies. Indeed, non-human primates use gestures for communication purpose (Meguerditchian et al., 2010, 2013). Crucially, communication gestures in non-human primates are preferentially performed with the right hand while other actions (i.e. food grasping) are not lateralized (Meguerditchian et al., 2010, 2013). This suggests a left-hemisphere lateralization for communication gestures in non-human primates, paralleling the left-hemisphere preference for verbal language in humans. The existence of protolanguage (i.e. primitive forms of communications) in primates may have the basis for the evolution of a vocal language in modern humans. Accordingly, the gestural theory of language emergence also proposes humans language may have gradually evolved from manual to vocal communications (Corballis, 2003). The hand motor control, beyond its involvement for action realization is also involved in action observation and comprehension (see *mirror neurons* theory, Rizzolatti et al., 1996). Such system for action realization and comprehension may also be present in the mouth motor control area that borders the hand area (Rizzolatti & Arbib, 1998). One possibility is that human brain gradually switch to the comprehension of manual gestures towards the comprehension of vocal gestures and the associated sounds produced by the vocal tract. The role of tool use within this gradual evolution cannot be ruled out. Indeed, findings suggest that cultural transmission of stone tool making is highly dependent on language but not imitation. This indicates that protolanguage forms may have been a prerequisite towards a transition for more complex stone tool making technology (Morgan et al., 2015).

The co-localization and learning transfer

The bidirectional cross-domain learning transfer observed between tool use and complex syntactic processing is likely related to the modulation of the co-localized neural resources. The following section will discuss the neural modulations involved by the learning tasks. With respect to previous evidence, we speculate that both neural plasticity and pre-activation occurred within the shared neural resources and explained the learning transfer.

1. Plasticity and transfer

Learning is the process of acquiring new knowledge, behaviors or skills. As a consequence, during learning, the task performance increases until a plateau where the progression becomes slower (see Dayan and Cohen, 2011; Wolpert et al., 2011 for the principles of sensorimotor learning). As a consequence of learning, the brain structure is modified, notably thanks to plasticity phenomena. A seminal study conducted in humans found that the grey matter volume increased for participants trained to juggle (Draganski et al., 2004). The temporal dynamic of plasticity during learning respected the expansion-renormalization model: an expansion phase up to a peak of plasticity followed by a renormalization phase (Wenger et al., 2016, 2017). This dynamic occurs for training lasting several weeks, which was not the case with the training tasks we employed that lasted for less than 30 minutes. However, the duration of the task does not prevent the occurrence of plasticity processes. Indeed, brain plasticity takes place in the early stages of training as demonstrated by studies in humans (Sagi et al., 2012) or in animals (Xu et al., 2009), where participants trained during about one to two hours. Furthermore, the functional activity accompanying training was found modulated in the early stages of training when the behavioral improvements were greater (Berlot et al., 2020). Thus, plastic changes as a consequence of short training are compatible with the tasks we employed in this thesis.

During sensorimotor learning, the fMRI investigations have reported that neural activity increases or decreases in specific brain regions along the learning time course (for a review, see Dayan and Cohen, 2011). These modulations of the hemodynamic response have been interpreted as the requirement to recruit more neural resources or rather to economize them for learning a new task. Thus functional modulations are likely explained by structural changes measured in influential sMRI studies that describe changes in the grey or white matter structure (Draganski et al., 2004; Wenger et al., 2016, 2017). However, sMRI does not offer sufficient

spatial resolution to identify which cellular or molecular compartment is invested by the plastic changes. Describing these phenomena is critical to understand on which cellular grounds the learning transfer revealed by our investigations might be based. Most of the evidence regarding the reorganization of neural tissues during learning comes from animal or human postmortem studies. Neurogenesis is rare in the adult brain and mostly occurs in the hippocampus (Ehninger & Kempermann, 2008) and the olfactory bulb (Huart et al., 2013). It has also recently been suggested to occur within the BG as well (Ernst et al., 2014). Nonetheless, the structural modulations recorded thanks to sMRI have been found outside of these regions, suggesting that the measures involved must capture other kinds of changes than neurogenesis. Indeed, in the neural tissues, axon collaterals emerge, dendrites proliferate and dendritic spines appear in order to receive synaptic connections. The plastic changes are not only restricted to neurons but also involve the glial cells, so that oligodendrocytes create the myelin sheath surrounding the axons hence facilitating signal transmission. Furthermore, other glial cells, such as microglia and astrocytes undergo modulations along the learning process. All these cellular and molecular transformations are likely resulting in the modulations of the non-invasive sMRI measures (Fig. 22; for reviews and opinions, see Wenger et al., 2017 and Zatorre et al., 2012).

Figure 22: The neural plasticity dynamics. A) Changes in behavioral performance over the time course of motor learning. B) Grey matter changes accompanying the behavioral performance and following an expansion and a renormalization phase. C) Potential neurogenesis mechanisms accompanying the learning. D) Potential synaptic changes mechanisms accompanying the learning. E) Potential glial changes mechanisms accompanying learning. From Wenger et al., 2017.

The aforementioned cellular changes participate in the performance improvement observed at the behavioral level, even though the relation between neural and behavioral changes is not totally deciphered (Wenger et al., 2017). Hence, we can speculate that the tool-use and complex syntax learning tasks we employed have likely induced plasticity in the brain and more particularly within the shared neural resources between the two functions localized in the BG. Previous studies uncovered changes within the BG at the structural level after pen manipulation (Wenger et al., 2016) and at the functional level for learning a novel language with tasks tackling the grammar (Tagarelli et al., 2019). Thus, with respect to our findings of a bidirectional learning transfer, we hypothesize that the neural resources have been mobilized within the BG after tool-use and complex syntax learning and have benefited to the untrained function. This is one of the exciting hypotheses derived from our work that future fMRI and sMRI investigations will have to test.

2. Pre-activation and transfer

Alternatively to neural plasticity, the pre-activation of the shared neural resources could explain the cross-domain learning transfer. Indeed, pre-activation of neural resources that are consecutively recruited for another process is characterized by a behavioral facilitation. This facilitation is called the priming effect and for instance is known for semantic processing as we discussed throughout the manuscript. As a reminder, when a word is preceded by another from the same semantic category (e.g. *nurse* – *doctor*), a behavioral facilitation occurs and is characterized by faster responses when performing a lexical decision task in comparison to pairs of semantically unrelated words (e.g. *nurse* – *dog*). The behavioral priming effect is explained by the consecutive recruitment of the same neural resources (Henson, 2003). Indeed, words from the same semantic categories are represented within specific neural networks (Carota et al., 2017). Both tool use and complex syntax activate the BG neural tissues, hence training one function could have pre-activated the neural resources subsequently recruited by the other function during the post-test. This idea might be challenged by the view that priming effect usually occurs within short time windows that were not manipulated during our experiments. Indeed, going back to the lexical decision task in the semantic priming paradigm, the time interval between the two words presented is about a couple of milliseconds. Conversely, the time interval between training and the post-test tasks was in the order of several minutes (i.e. time for switching from the training to the test task and time to perform the task). Nonetheless, a study revealed the neural adaptation effect is observable for stimuli separated by 20 to 30 s, suggesting the priming effect can last longer than milliseconds (Rangarajan et al., 2020).

To summarize, we speculate the bidirectional learning transfer between tool use and syntax is explained by neural plasticity and pre-activation processes. Noteworthy, these two possibilities are not exclusive alternatives and they might co-occur. In other words, the plastic changes occurring during learning might participate in the functional reorganization and pre-activation of the neural resources. We did not test this behavioral impact for semantics and phonology. Regarding phonology, given that no shared neural resources were found, it is unlikely the two functions will impact each other. Nonetheless, given that tool use and speech perception both require discrimination of fine-grained sensory inputs and regions involved in these processes are anatomically close within the left IPL and IFG, we cannot totally rule out a potential reciprocal impact through local connections for instance. Regarding semantics, behaviorally it has been found that complex manual training improved conceptual-semantic

processing of action verbs evoking manual actions which had been performed during training (Locatelli et al., 2012). Furthermore, training on various cognitive tasks involving action verbs revealed brain structural changes within the sensorimotor areas (Ghio et al., 2018). This reciprocal impact suggests the existence of a cross-talk between action verbs and actual actions (Boulenger et al., 2006; Boulenger, Silber, et al., 2008). To the best of our knowledge, the effect of tool use learning over semantics or semantic learning over tool use has never been studied in neurotypical adults. As we mentioned, the closest existing evidence showed novel tools assigned to a specific label were facilitated for their use in comparison to unlabeled tools (Foerster et al., 2020). Furthermore, this effect was accompanied by a decrease of the power in the sensorimotor beta-band. This neural modulation might be interpreted as pre-activation of the neural resources shared between tool concepts and tool use. Overall, testing all these opportunities on neurotypical adults will be of particular interest for designing new learning or rehabilitation protocols.

Taking advantage of the neural plasticity

In the previous section, we defended the position that bidirectional learning transfer between tool use and language might arise from neural plasticity induced by learning. We discussed a large set of evidence regarding the effect of learning on brain structure and function. One influential account in the field of learning-induced neural plasticity has been the expansion-renormalization model (Wenger et al., 2017). The next section aims to discuss how a better understanding of this dynamic might help to develop new learning and rehabilitation protocols aiming to exploit neural plasticity mechanisms.

1. Exploiting plasticity

To learn a new task, specific brain regions will mobilize new resources; a peak of plasticity is then reached, corresponding to the maximum expansion of the grey matter volume; in a final phase there is a renormalization (Wenger et al., 2017). This neural dynamic accompanies the behavioral progresses, so that in the early stages of the training, i.e. during the expansion phase, the performance improves. As soon as a plateau of performance is reached and the rate of improvement becomes slower, it suggests the most optimal pathways have been set, corresponding to the renormalization phase. Noteworthy, this idea is still a hypothesis, since no causal relation between performance increase and brain structure evolution has been demonstrated so far (Wenger et al., 2017). The specific duration of the expansion-renormalization process likely depends on several factors ranging from the number of repetitions performed, the motivation of the trainee, the quality of the training, the novelty of the task and many others. In a study conducted in young adults performing a daily training of 30 to 60 minutes, the peak of plasticity occurred after 4 weeks of training. On the seventh week the grey matter structure was renormalized (Wenger et al., 2016). Conversely, in a study where monkeys were trained to extensively use a tool for two weeks, the authors revealed a peak of plasticity from the end of the first training week roughly corresponding to the reach of the performance plateau (Quallo et al., 2009). Albeit these timeline discrepancies, these results suggest that different trainings follow the expected expansion-renormalization phenomena.

We can hypothesize that the peak of plasticity could be particularly beneficial for learning transfer because at this specific period, the maximum of neural resources are available. Thus, if this phenomenon takes place in the neural resources shared by co-localized functions, the learning-induced plasticity for one function should benefit to the untrained one. Considering

tool use and complex syntax, this can be turned into the question of whether syntactic comprehension will further benefit from the peak of plasticity in comparison to the training of less than 30 minutes used in our experiments. Furthermore, it opens the opportunities to boost learning of a novel language and facilitate the recovery of impaired language abilities.

2. Boosting language learning thanks to the tool

One exciting topic to explore is whether this interdependence between tool use and language could facilitate learning of a new language. Learning a new language is particularly crucial in our interconnected world and diverse learning strategies are required to develop innovative and playful learning protocols. Does the tool-induced plasticity can facilitate new language learning? Based on our results in a native language, we might expect that tool use learning will boost both semantics and syntax when learning a second language. A study focusing on foreign language learning for three months, where participants had to learn up to 500 new words each week, revealed an increase of the cortical thickness within the left IFG (Mårtensson et al., 2012). Given that we found shared neural resources between tool use and semantics in the left IFG, we might expect that plasticity induced within this area by the means of tool use could also boost the ability to learn new words in an unknown language.

Interestingly, motor learning is mostly represented in two phases with a fast and then a slow evolution of the motor performance (Dayan & Cohen, 2011). The slow phase coincides with the reach of the plateau performance, where the performance improvements become slower. This plateau of performance is likely related to the selection of preferential neural pathways subserving the skilled ability (Wenger et al., 2017). Now, let us consider a participant learning a new language and starting to reach a performance plateau (e.g. slow progression to acquire new vocabulary or grammatical rules). At this moment, tool-use learning could boost foreign language learning thanks to the plasticity induced by motor training, offering the possibility to test new neural pathways within the neural resources shared by tool-use and language processing. Tool use can be a way to induce plasticity that in turn can be beneficial to learn a new language. Overall, we think the range of possibilities to explore is large regarding the *reuse* of the novel neural resources triggered by the plasticity. These possibilities might involve different functions and go well beyond the link between language and tool use.

3. Rehabilitating a function by training the other

Boosting learning for neurotypical individuals is exciting but exploiting the plasticity induced by learning to rehabilitate impaired functions in patients is likely an even more fascinating possibility. Tool use and language respectively involve large interconnected networks, such as the left frontoparietal network for tool use and left frontotemporal network for language. These functions can be severely impaired if a part of these networks is damaged. Let us consider a patient with a lesion localized onto the left IFG, presenting a non-fluent aphasia with impairments for processing complex syntactic structures (Caramazza & Zurif, 1976). The extent of each lesion is specific for each patient and can affect a large set of brain regions or be much localized. Considering a non-fluent aphasia patient with a lesion onto the left IFG, intact BG and presenting no evident motor impairments, we could expect to improve the patient's syntactic abilities by inducing plasticity within the BG thanks to tool-use training. This would in turn benefit to hierarchical processing not only in the motor domain but, most critically also in the language domain. The plasticity induced by motor training might facilitate a reallocation of the neural resources from damaged to intact neural resources. This notion of functional reallocation of neural resources is already supported by evidence in infarct rodents (Jones, 2017) and also in humans suffering neurodegenerative disease (Grady et al., 2003). Future investigations are required to test whether aphasia patients could benefit from tool-use learning and slightly improve their functional condition in language. Furthermore, we can also hypothesize the reverse would hold true. Indeed, patients with apraxia might benefit from language learning involving either syntactic or semantic processing in order to improve their ability to use a tool. However, we have to recognize this line of research might be complex given that lesions are very different from one patient to another and are sometimes spreading onto a large set of brain regions and consequently affecting multiple functions ranging from motor control to language. Yet, some evidence invite to consider the development of such protocols. Indeed, imitation and observation of actions improve action verbs recovery in aphasics (Marangolo et al., 2010), while verbalizing the function of a tool may help to improve the condition of apraxics (Stoll et al., 2020).

The supramodal hierarchical function

Our findings for a bidirectional learning transfer between tool use and complex syntax suggest that co-localized functions maintain strengthened links. Nonetheless, complex syntax and tool use do not simply overlap within the BG but also present a similar fine-grained spatial organization of the activations. In other words, within the overlapping BG network, a voxel activated at a given intensity for complex syntax will likely activate at a similar intensity for tool use but not free hand. This neural similarity might correspond to the similarity of the processes managed within the BG. Indeed, both tool use and complex syntax require to handle complex hierarchical sequences. Given this statement, we might rather consider that a supramodal hierarchical or syntactic function shared between the motor and language domains is represented within the BG, instead of a simple co-localization of two distinct functions. In this section, we will present the reasons why tool use can be considered as syntactic. Then we will discuss the contribution of different brain regions to supramodal hierarchical processing.

1. The syntactic use of a tool

Can we consider a motor action is syntactically organized just as a sentence is? Can we claim that tool use is syntactically more complex than a free-hand action? The hypothesis of a hierarchical motor system emerged early and rejected the possibility that motor behaviors only resulted from a serial association of isolated motor acts (Lashley, 1951 and for a discussion about Lashley's work, see Fitch & Martins, 2014; Rosenbaum et al., 2007). Furthermore, one of the propositions is that tool use implies a different hierarchical complexity in comparison to free-hand actions (Greenfield, 1991). Indeed a sequence of actions with the bare hand can require to *combine* the hand with an object to grasp. Conversely, using a tool adds an additional combinatorial level, because the hand has to be combined with the tool, themselves combine with the object to handle. These combinatorial aspects for a motor action have been proposed to parallel the combinatorial aspects of language where words are assembled to form a sentence (Greenfield, 1991; Roy & Arbib, 2005). More recently, the combinatorial aspect of actions involving manipulation of tools has been discussed and emerged to the proposition that our motor acts are ruled by a motor syntax (Pastra & Aloimonos, 2012; Pulvermüller, 2014; Roy et al., 2013). Conversely to tool use, the constrained hand condition in our findings did not reveal any benefit for syntactic processing. Yet, this condition yielded equivalent motor performance compared to tool use and was designed with the purpose of mimicking the use of pliers. Thus,

our findings clearly revealed that tool use involves different mechanisms in comparison to an action performed with the constrained hand. Earlier, we proposed that the simple fact of handling a tool adds a further hierarchical level into the manual motor plan, that might parallel the embedding of a relative clause within a main clause in language (e.g. *The writer [that the poet admires] writes the paper*). Another possibility is that using a tool allows to implement a recursive rule. As previously mentioned, recursion is a property of language allowing for instance to embed an infinite number of relative clauses within a sentence (e.g. *The writer [that the poet admires [that the singer congratulates]] writes the paper*.). Recursion might be also present in actions (Vicari & Adenzato, 2014). For instance, let us take the example of a woodworker that can use for his work a wood chisel and mallet individually for different purposes. However for specific purposes, the woodworker will have to associate the wood chisel with the mallet. This association can be considered as recursive because the woodworker is modifying a wood board thanks to an action set associating his hand action over a mallet and this action in turn over a wood chisel. In language, an object relative clause interrupts the classical subject-object canonical order. Indeed in the following sentence *The writer [that the poet admires] writes the paper*; *the writer* has a double function because he is the subject of the main clause *The writer writes the paper* but also the object of the relative clause *The poet admires [the writer]*. This structure interrupts the classic subject-object canonical order and increases the long-distance dependency between the *writer* and the *poet* with respect to the relative clause. Regarding tool use it is possible that tools like reverse pliers interrupt the *canonical* aspect of an action. Indeed to grasp an object with a classic tool would require to open and then close the hand, whereas reverse pliers require to close the hand to open the tool and then open the hand to close the tool. Such kinematic organization can be considered as an interruption of the *canonical* organization of a manual goal directed movement. Finally, similarly to *the writer* in the object relative example, the tool has a double function in the motor sequence. Indeed, the tool is *object* of the manual action (i.e. the hand handles the tool) and also *subject* of the main action goal (i.e. the tool with the hand handle the object). Noteworthy, we do not defend that these processes for the motor domain strictly parallel those in language. Instead we tried to identify which commonalities in the cognitive mechanisms might account for the behavioral link and shared neural resources we found between tool use and syntax. These proximities of hierarchical processing between the two domains may represent the implementation of a supramodal hierarchical function.

2. Supramodal hierarchical processing in the brain

Well before our findings, supramodal hierarchical processing has been discussed by numerous opinion papers and suggested to occur within the left IFG across different domains such as language, action and music (Fiebach & Schubotz, 2006; Fitch & Martins, 2014; Greenfield, 1991; Tettamanti & Weniger, 2006). Given that our findings revealed functionally distinct clusters in the left IFG for both complex syntax and tool use, we cannot support this hypothesis. Furthermore previous neuroimaging meta-analyses (Clos et al., 2013; Papitto et al., 2020) found language and action are represented in different anatomical regions within the left IFG. This observation is also consistent with a fMRI study revealing that, within the left IFG, language processing occurs separately from domain general processing (Fedorenko et al., 2012). Finally, a recent review discussed the role of the left IFG for language and other functions involving hierarchical processing such as music, mathematics and even the theory of mind (Friederici, 2020). The paper conclusions suggest that processing hierarchies across various domains involves distinct neural hubs.

A supramodal hierarchical function might be represented somewhere else than the left IFG. Given our findings, we think the BG are a critical neural hub for hierarchical processing across the motor and language domains. To the best of our knowledge, the role of the BG in hierarchical processing has mainly been suggested for language and action, but further investigations might be required to test whether different domains such as music (Asano et al., 2021) or even mathematics might be represented within the BG. Furthermore, supramodal hierarchical processing might be supported by the posterior temporal regions. Indeed, the left pMTG and regions at its vicinity (i.e. left pSTG, left pSTS and left angular gyrus) are recruited by complex syntax (Matchin & Hickok, 2020; Pyllkkänen, 2019; Walenski et al., 2019). Interestingly lesions to the pMTG impaired processing of hierarchical structures in the vision domain (i.e. fractals; Martins, Krause, et al., 2019). In the motor domain, this region has been found active in the perception of tool motion (Beauchamp & Martin, 2007). Given we did not find shared neural resources between tool use and complex syntax within this area, it rather suggests the hierarchical structure of the movement is not encoded there. Overall, these results suggest the hierarchical processing function is not restricted to a specific neural hub. The BG support a supramodal hierarchical function shared between the motor and language domains. The left IFG is also involved in hierarchical processing in the motor and language domains but the two domains recruited distinct clusters. We can speculate that the role of these latter is

domain-specific and aims to refine the domain-general processing performed downstream within the basal ganglia.

General conclusion

The two experimental contributions presented in this manuscript confirm the existence of shared neural resources between tool use and language. While no shared neural substrates were found between phonology and tool use, we provided evidence that semantic processing takes place within the left IFG and left OTC also recruited by tool use. Complex syntax and tool use furthermore both recruited the BG, whereas the two functions recruited close but anatomically distinct clusters within the left IFG. These findings result in a bidirectional cross-domain learning transfer from tool use to complex syntax and reciprocally from complex syntax to tool use. These findings invite to refine the language embodiment theory, by considering that not only phonology and semantics are grounded but also syntax. The co-localization of neural resources and the presence of anatomically close clusters between tool use and language can be explained by theoretical accounts on human evolution suggesting co-evolution and neural recycling processes between tool use and language. We also discussed that the processes allowing the bi-directional crossdomain phenomena might take advantage of the learning-induced neural plasticity or the pre-activation occurring within the shared neural resources. The possibility to take advantage of such plasticity offers fascinating opportunities to design ecological and playful learning and rehabilitation protocols taking advantage of the tool to improve language abilities.

References

- Agostoni, E., Coletti, A., Orlando, G., & Tredici, G. (1983). Apraxia in deep cerebral lesions. *Neurosurgery, and Psychiatry*, 46, 804–808. <https://doi.org/10.1136/jnnp.46.9.804>
- Alexander, M. P., Naeser, M. A., & Palumbo, C. L. (1987). Correlations of subcortical CT lesion sites and aphasia profiles. *Brain*, 110(4), 961–988. <https://doi.org/10.1093/brain/110.4.961>
- Ambrose, S. H. (2001). Paleolithic technology and human evolution. *Science*, 291(5509), 1748–1753. <https://doi.org/10.1126/science.1059487>
- Anderson, M. L. (2016). Précis of after Phrenology: Neural Reuse and the Interactive Brain. *Behavioral and Brain Sciences*, 39(e120), 1–45. <https://doi.org/10.1017/S0140525X15000631>
- Arévalo, A., Perani, D., Cappa, S. F., Butler, A., Bates, E., & Dronkers, N. (2007). Action and object processing in aphasia: From nouns and verbs to the effect of manipulability. *Brain and Language*, 100, 79–94. <https://doi.org/10.1016/j.bandl.2006.06.012>
- Asano, R., Boeckx, C., & Seifert, U. (2021). Hierarchical control as a shared neurocognitive mechanism for language and music. *Cognition*, 216, 1–16. <https://doi.org/10.1016/j.cognition.2021.104847>
- Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., & Iacoboni, M. (2006). Congruent Embodied Representations for Visually Presented Actions and Linguistic Phrases Describing Actions. *Current Biology*, 16(18), 1818–1823. <https://doi.org/10.1016/j.cub.2006.07.060>
- Bahmad, S., Miller, L. E., Pham, M. T., Moreau, R., Salemme, R., Koun, E., Farnè, A., & Roy, A. C. (2020). Online proprioception feeds plasticity of arm representation following tool-use in healthy aging. *Scientific Reports* |, 10(17275), 1–9. <https://doi.org/10.1038/s41598-020-74455-5>
- Bak, T. H., & Chandran, S. (2012). Viewpoint What wires together dies together: Verbs, actions and neurodegeneration in motor neuron disease. *Cortex*, 48, 936–944. <https://doi.org/10.1016/j.cortex.2011.07.008>
- Bak, T. H., & Hodges, J. R. (2001). Motor neurone disease, dementia and aphasia: coincidence, co-occurrence or continuum? Introductory Remarks on Terminology. *Journal of Neurology*, 248(4), 260–270. <https://doi.org/10.1007/s004150170199>
- Bak, T. H., & Hodges, J. R. (2004). The effects of motor neurone disease on language: Further evidence. *Brain and Language*, 89, 354–361. [https://doi.org/10.1016/S0093-934X\(03\)00357-2](https://doi.org/10.1016/S0093-934X(03)00357-2)
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, 22(4), 577–609. <https://doi.org/10.1017/S0140525X99002149>
- Barsalou, L. W. (2008). Grounded Cognition. *Annual Review of Psychology*, 59(1), 617–645. <https://doi.org/10.1146/annurev.psych.59.103006.093639>
- Basso, A., Casati, G., & Vignolo, L. A. (1977). Phonemic Identification Defect in Aphasia. *Cortex*, 13(1), 85–95.

[https://doi.org/10.1016/S0010-9452\(77\)80057-9](https://doi.org/10.1016/S0010-9452(77)80057-9)

- Beauchamp, M. S., & Martin, A. (2007). Grounding object concepts in perception and action: Evidence from fMRI studies of tools. *Cortex*, 43(3), 461–468. [https://doi.org/10.1016/S0010-9452\(08\)70470-2](https://doi.org/10.1016/S0010-9452(08)70470-2)
- Beck, B. B. (1980). *Animal Tool Behavior: The Use and Manufacture of Tools by Animals*. Garland STPM Publisher.
- Beilock, S. L. (2009). Grounding cognition in action: expertise, comprehension, and judgment. *Progress in Brain Research*, 174, 3–11. [https://doi.org/10.1016/S0079-6123\(09\)01301-6](https://doi.org/10.1016/S0079-6123(09)01301-6)
- Beilock, S. L., Lyons, I. M., Mattarella-Micke, A., Nusbaum, H. C., & Small, S. L. (2008). Sports experience changes the neural processing of action language. *Proceedings of the National Academy of Sciences of the United States of America*, 105(36), 13269–13273. <https://doi.org/10.1073/pnas.0803424105>
- Ben-Shachar, M., Hendler, T., Kahn, I., Ben-Bashat, D., & Grodzinsky, Y. (2003). The Neural Reality of Syntactic Transformations: Evidence from Functional Magnetic Resonance Imaging. *Psychological Science*, 14(5), 433–440. <https://doi.org/10.1111/1467-9280.01459>
- Berlot, E., Popp, N. J., & Diedrichsen, J. (2020). A critical re-evaluation of fMRI signatures of motor sequence learning. *ELife*, 9(e55241), 1–24. <https://doi.org/10.7554/eLife.55241>
- 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. *Cerebral Cortex*, 19, 2767–2796. <https://doi.org/10.1093/cercor/bhp055>
- Binder, J. R., Mckiernan, K. A., Parsons, M. E., Westbury, C. F., Possing, E. T., Kaufman, J. N., & Buchanan, L. (2003). Neural Correlates of Lexical Access during Visual Word Recognition. *Journal of Cognitive Neuroscience*, 15(3), 372–393. <https://doi.org/10.1162/089892903321593108>
- Bishop, D. V. M. (2017). Why is it so hard to reach agreement on terminology? The case of developmental language disorder (DLD). *International Journal of Language & Communication Disorders*, 52(6), 671–680. <https://doi.org/10.1111/1460-6984.12335>
- Blumstein, S. E., Baker, E., & Goodglass, H. (1977). Phonological factors in auditory comprehension in aphasia. *Neuropsychologia*, 15(1), 19–30. [https://doi.org/10.1016/0028-3932\(77\)90111-7](https://doi.org/10.1016/0028-3932(77)90111-7).
- Booth, J. R., Wood, L., Lu, D., Houk, J. C., & Bitan, T. (2007). The role of the basal ganglia and cerebellum in language processing. *Brain Research*, 1133, 136–144. <https://doi.org/10.1016/j.brainres.2006.11.074>
- Borghi, A. M., Gianelli, C., & Scorolli, C. (2010). Sentence comprehension: effectors and goals, self and others. An overview of experiments and implications for robotics. *Frontiers in Neurorobotics*, 4(3), 1–8. <https://doi.org/10.3389/fnbot.2010.00003>
- Boronat, C. B., Buxbaum, L. J., Coslett, B. H., Tang, K., Saffran, E. M., Kimberg, D. Y., & Detre, J. A. (2005). Distinctions between manipulation and function knowledge of objects: evidence from functional magnetic resonance imaging. *Cognitive Brain Research*, 23, 361–373.

<https://doi.org/10.1016/j.cogbrainres.2004.11.001>

- Boulenger, V., Hauk, O., & Pulvermüller, F. (2009). Grasping Ideas with the Motor System: Semantic Somatotopy in Idiom Comprehension. *Cerebral Cortex*, 19(8), 1905–1914. <https://doi.org/10.1093/cercor/bhn217>
- Boulenger, V., Martel, M., Bouvet, C., Finos, L., Krzonowski, J., Farnè, A., & Roy, A. C. (2020). Feeling better: Tactile verbs speed up tactile detection. *Brain and Cognition*, 142, 1–10. <https://doi.org/10.1016/j.bandc.2020.105582>
- Boulenger, V., Mechtouff, L., Thobois, S., Broussolle, E., Jeannerod, M., & Nazir, T. A. (2008). Word processing in Parkinson's disease is impaired for action verbs but not for concrete nouns. *Neuropsychologia*, 46(2), 743–756. <https://doi.org/10.1016/j.neuropsychologia.2007.10.007>
- 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. *Journal of Cognitive Neuroscience*, 18(10), 1607–1615. <https://doi.org/10.1162/jocn.2006.18.10.1607>
- Boulenger, V., Silber, B. Y., Roy, A. C., Paulignan, Y., Jeannerod, M., & Nazir, T. A. (2008). Subliminal display of action words interferes with motor planning: A combined EEG and kinematic study. *Journal of Physiology Paris*, 102, 130–136. <https://doi.org/10.1016/j.jphysparis.2008.03.015>
- Brandi, M.-L., Wohlschläger, A., Sorg, C., & Hermsdörfer, J. (2014). The Neural Correlates of Planning and Executing Actual Tool Use. *The Journal of Neuroscience*, 34(39), 13183–13194. <https://doi.org/10.1523/JNEUROSCI.0597-14.2014>
- Broca, P. (1861). Perte de la parole: ramollissement chronique et destruction partielle du lobe antérieur gauche du cerveau. *Bulletin de La Société Française d'anthropologie*, 235–238.
- Brozzoli, C., Gentile, G., & Ehrsson, H. H. (2012). That's Near My Hand! Parietal and Premotor Coding of Hand-Centered Space Contributes to Localization and Self-Attribution of the Hand. *Journal of Neuroscience*, 32(42), 14573–14582. <https://doi.org/10.1523/JNEUROSCI.2660-12.2012>
- Brozzoli, C., Gentile, G., Petkova, V. I., & Ehrsson, H. H. (2011). fMRI Adaptation Reveals a Cortical Mechanism for the Coding of Space Near the Hand. *Journal of Neuroscience*, 31(24), 9023–9031. <https://doi.org/10.1523/JNEUROSCI.1172-11.2011>
- Brozzoli, C., Roy, A. C., Lidborg, L. H., & Lövdén, M. (2019). Language as a tool: Motor proficiency using a tool predicts individual linguistic abilities. *Frontiers in Psychology*, 10(1639), 1–9. <https://doi.org/10.3389/fpsyg.2019.01639>
- Buxbaum, L. J. (2001). Ideomotor apraxia: A call to action. *Neurocase*, 7(6), 445–458. <https://doi.org/10.1076/neur.7.6.445.16223>
- Buxbaum, L. J. (2017). Learning, remembering, and predicting how to use tools: Distributed neurocognitive mechanisms: Comment on Osiurak and Badets (2016). *Psychological Review*, 124(3), 346–360. <https://doi.org/10.1037/rev0000051>

- Buxbaum, L. J., & Saffran, E. M. (2002). Knowledge of object manipulation and object function: dissociations in apraxic and nonapraxic subjects. *Brain and Language*, 82(2), 179–199. [https://doi.org/10.1016/s0093-934x\(02\)00014-7](https://doi.org/10.1016/s0093-934x(02)00014-7)
- Caplan, D., Gow, D., & Makris, N. (1995). Analysis of lesions by MRI in stroke patients with acoustic-phonetic processing deficits. *Neurology*, 45(2), 293–298. <https://doi.org/10.1212/WNL.45.2.293>
- Caplan, D., & Waters, G. S. (1999). Verbal working memory and sentence comprehension. *Behavioral and Brain Sciences*, 22, 77–126. <https://doi.org/10.1017/s0140525x99291789>
- Caramazza, A., & Zurif, E. B. (1976). Dissociation of algorithmic and heuristic processes in language comprehension: Evidence from aphasia. *Brain and Language*, 3(4), 572–582. [https://doi.org/10.1016/0093-934X\(76\)90048-1](https://doi.org/10.1016/0093-934X(76)90048-1)
- Cardinali, L., Brozzoli, C., Finos, L., Roy, A. C., & Farnè, A. (2016). The rules of tool incorporation : Tool morpho-functional & sensori-motor constraints. *Cognition*, 149, 1–5. <https://doi.org/10.1016/j.cognition.2016.01.001>
- Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A. C., & Farnè, A. (2009). Tool-use induces morphological updating of the body schema. *Current Biology*, 19(13), 1157. <https://doi.org/10.1016/j.cub.2009.06.048>
- Carota, F., Kriegeskorte, N., Nili, H., & Pulvermüller, F. (2017). Representational Similarity Mapping of Distributional Semantics in Left Inferior Frontal, Middle Temporal, and Motor Cortex. *Cerebral Cortex*, 27(1), 294–309. <https://doi.org/10.1093/cercor/bhw379>
- Casado, P., Martin-Loeches, M., Leon, I., Hernandez-Gutierrez, D., Espuny, J., Munoz, F., Jimenez-Ortega, L., Fondevilla, S., & de Vega, M. (2018). When syntax meets action : Brain potential evidence of overlapping between language and motor sequencing. *Cortex*, 100, 40–51. <https://doi.org/10.1016/j.cortex.2017.11.002>
- Cattaneo, Z., Devlin, J. T., Salvini, F., Vecchi, T., & Silvanto, J. (2010). The causal role of category-specific neuronal representations in the left ventral premotor cortex (PMv) in semantic processing. *NeuroImage*, 49(3), 2728–2734. <https://doi.org/10.1016/j.neuroimage.2009.10.048>
- Cayol, Z., & Nazir, T. A. (2020). Why Language Processing Recruits Modality Specific Brain Regions: It Is Not About Understanding Words, but About Modelling Situations. *Journal of Cognition*, 3(1), 1–23. <https://doi.org/10.5334/joc.124>
- Cayol, Z., Rotival, C., Paulignan, Y., & Nazir, T. A. (2020). “Embodied” language processing: Mental motor imagery aptitude predicts word-definition skill for high but not for low imageable words in adolescents. *Brain and Cognition*, 145(105628), 1–10. <https://doi.org/10.1016/j.bandc.2020.105628>
- Chang, E. F., Rieger, J. W., Johnson, K., Berger, M. S., Barbaro, N. M., & Knight, R. T. (2010). Categorical speech representation in human superior temporal gyrus. *Nature Neuroscience*, 13(11), 1428–1432. <https://doi.org/10.1038/nn.2641>
- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving

- and knowing about objects. *Nature Neuroscience*, 2(10), 913–919. <https://doi.org/10.1038/13217>
- Chao, L. L., & Martin, A. (2000). Representation of Manipulable Man-Made Objects in the Dorsal Stream. *NeuroImage*, 12, 478–484. <https://doi.org/10.1006/nimg.2000.0635>
- Chevillet, M. A., Jiang, X., Rauschecker, J. P., & Riesenhuber, M. (2013). Automatic Phoneme Category Selectivity in the Dorsal Auditory Stream. *Journal of Neuroscience*, 33(12), 5208–5215. <https://doi.org/10.1523/JNEUROSCI.1870-12.2013>
- Choi, S., Na, D. L., Kang, E., Lee, K., Lee, S., & Na, D. (2001). Functional magnetic resonance imaging during pantomiming tool-use gestures. *Experimental Brain Research*, 139(4), 311–317. <https://doi.org/10.1007/s002210100777>
- Chouinard, P. A., & Goodale, M. A. (2010). Category-specific neural processing for naming pictures of animals and naming pictures of tools: An ALE meta-analysis. *Neuropsychologia*, 48(2), 409–418. <https://doi.org/10.1016/j.neuropsychologia.2009.09.032>
- Chumbley, J. I., Balota, D. A., Clifton, C., Myers, J. L., Neely, J. H., & Rayner, K. (1984). A word's meaning affects the decision in lexical decision. *Memory & Cognition*, 12(6), 590–606. <https://doi.org/10.3758/bf03213348>.
- Clos, M., Amunts, K., Laird, A. R., Fox, P. T., & Eickhoff, S. B. (2013). Tackling the multifunctional nature of Broca's region meta-analytically: Co-activation-based parcellation of area 44. *NeuroImage*, 83, 174–188. <https://doi.org/10.1016/j.neuroimage.2013.06.041>
- Colby, C. L., & Duhamel, J.-R. (1991). Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. *Neuropsychologia*, 29(6), 517–537. [https://doi.org/10.1016/0028-3932\(91\)90008-v](https://doi.org/10.1016/0028-3932(91)90008-v).
- Copland, D. A., de Zubicaray, G. I., McMahon, K., & Eastburn, M. (2007). Neural correlates of semantic priming for ambiguous words: An event-related fMRI study. *Brain Research*, 1131(1), 163–172. <https://doi.org/10.1016/j.brainres.2006.11.016>
- Corballis, M. C. (2003). From mouth to hand: Gesture, speech, and the evolution of right-handedness. *Behavioral and Brain Sciences*, 26(2), 199–208. <https://doi.org/10.1017/S0140525X03000062>
- Culham, J. C., & Valyear, K. F. (2006). Human parietal cortex in action. *Current Opinion in Neurobiology*, 16(2), 205–212. <https://doi.org/10.1016/j.conb.2006.03.005>
- D'ausilio, A., Bufalari, I., Salmas, P., & Fadiga, L. (2012). The role of the motor system in discriminating normal and degraded speech sounds. *Cortex*, 48, 882–887. <https://doi.org/10.1016/j.cortex.2011.05.017>
- D'Ausilio, A., Pulvermüller, F., Salmas, P., Bufalari, I., Begliomini, C., & Fadiga, L. (2009). The Motor Somatotopy of Speech Perception. *Current Biology*, 19(5), 381–385. <https://doi.org/10.1016/j.cub.2009.01.017>
- Damasio, H., & Damasio, A. (1980). The anatomical basis of conduction aphasia. *Brain*, 103, 337–350. <https://doi.org/10.1159/000412318>

- Darwin, C. (1871). *The descent of the man and selection in relation to sex*. Princeton University Press.
- Davare, M., Kraskov, A., Rothwell, J. C., & Lemon, R. N. (2011). Interactions between areas of the cortical grasping network. *Current Opinion in Neurobiology*, 21(4), 565–570. <https://doi.org/10.1016/j.conb.2011.05.021>
- Dayan, E., & Cohen, L. G. (2011). Neuroplasticity subserving motor skill learning. *Neuron*, 72(3), 443–454. <https://doi.org/10.1016/j.neuron.2011.10.008>
- De Vincenzi, M., Job, R., Matteo, R. Di, Angrilli, A., Penolazzi, B., Ciccarelli, L., & Vespignani, F. (2003). Differences in the perception and time course of syntactic and semantic violations. *Brain and Language*, 85, 280–296. [https://doi.org/10.1016/S0093-934X\(03\)00055-5](https://doi.org/10.1016/S0093-934X(03)00055-5)
- Dee, H., Benton, A., & Van Allen, M. (1970). Apraxia in relation to hemispheric locus of lesion and aphasia. *Transactions of the American Neurological Association*, 95, 147–150. <https://pubmed.ncbi.nlm.nih.gov/4105576/>
- Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron*, 56(2), 384–398. <https://doi.org/10.1016/j.neuron.2007.10.004>
- Desai, R. H., Binder, J. R., Conant, L. L., & Seidenberg, M. S. (2010). Activation of Sensory-Motor Areas in Sentence Comprehension. *Cerebral Cortex*, 20, 468–478. <https://doi.org/10.1093/cercor/bhp115>
- Diedrichsen, J., & Kriegeskorte, N. (2017). Representational models: A common framework for understanding encoding, pattern-component, and representational-similarity analysis. *PLoS Computational Biology*, 13(4), 1–33. <https://doi.org/10.1371/journal.pcbi.1005508>
- Diedrichsen, J., & Zotow, E. (2015). Surface-Based Display of Volume-Averaged Cerebellar Imaging Data. *PLoS ONE*, 10(7), 1–18. <https://doi.org/10.1371/journal.pone.0133402>
- Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U., & Arne, M. (2004). Neuroplasticity: changes in grey matter induced by training. *Nature*, 427(6972), 311–312. <https://doi.org/10.1038/427311a>
- Dressing, A., Martin, M., Beume, L.-A., Kuemmerer, D., Urbach, H., Kaller, C. P., Weiller, C., & Rijntjes, M. (2020). The correlation between apraxia and neglect in the right hemisphere: A voxel-based lesion-symptom mapping study in 138 acute stroke patients. *Cortex*, 132, 166–179. <https://doi.org/10.1016/j.cortex.2020.07.017>
- Dronkers, N. F., Plaisant, O., Iba-Zizen, M. T., & Cabanis, E. A. (2007). Paul Broca's historic cases: high resolution MR imaging of the brains of Leborgne and Lelong. *Brain*, 130, 1432–1441. <https://doi.org/10.1093/brain/awm042>
- Ehninger, D., & Kempermann, G. (2008). Neurogenesis in the adult hippocampus. *Cell and Tissue Research*, 331, 243–250. <https://doi.org/10.1007/s00441-007-0478-3>
- Ernst, A., Alkass, K., Bernard, S., Salehpour, M., Perl, S., Tisdale, J., Possnert, G., Druid, H., & Frisén, J. (2014). Neurogenesis in the striatum of the adult human brain. *Cell*, 156(5), 1072–1083.

<https://doi.org/10.1016/j.cell.2014.01.044>

- Fadiga, L., Craighero, L., Buccino, G., & Rizzolatti, G. (2002). Speech listening specifically modulates the excitability of tongue muscles: a TMS study. *European Journal of Neuroscience*, 15(2), 399–402. <https://doi.org/10.1046/j.0953-816x.2001.01874.x>.
- Fadiga, L., Craighero, L., & Roy, A. C. (2006). Broca's Region: A speech Area? In Y. Grodzinsky & K. Amunts (Eds.), *Broca's region*. Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780195177640.003.0009>
- 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(7), 1980–1988. <https://doi.org/10.1093/brain/awp118>
- Fedorenko, E., Duncan, J., & Kanwisher, N. (2012). Language-selective and domain-general regions lie side by side within Broca's area. *Current Biology*, 22(21), 2059–2062. <https://doi.org/10.1016/j.cub.2012.09.011>
- Fernandino, L., Conant, L. L., Binder, J. R., Blindauer, K., Hiner, B., Spangler, K., & Desai, R. H. (2012). Parkinson's disease disrupts both automatic and controlled processing of action verbs. *Brain and Language*, 127, 65–74. <https://doi.org/10.1016/j.bandl.2012.07.008>
- Fiebach, C. J., & Schubotz, R. I. (2006). Dynamic anticipatory processing of hierarchical sequential events: a common role for Broca's area and ventral premotor cortex across domains? *Cortex*, 42(4), 499–502. [https://doi.org/10.1016/s0010-9452\(08\)70386-1](https://doi.org/10.1016/s0010-9452(08)70386-1).
- Filimon, F. (2010). Human cortical control of hand movements: Parietofrontal networks for reaching, grasping, and pointing. *Neuroscientist*, 16(4), 388–407. <https://doi.org/10.1177/1073858410375468>
- Fischer, M. H., & Zwaan, R. A. (2008). Embodied language: A review of the role of the motor system in language comprehension. *Quarterly Journal of Experimental Psychology*, 61(6), 825–850. <https://doi.org/10.1080/17470210701623605>
- Fitch, W. T., & Martins, M. D. (2014). Hierarchical processing in music, language, and action: Lashley revisited. *Annals of the New York Academy of Sciences*, 1316(1), 87–104. <https://doi.org/10.1111/nyas.12406>
- Fodor, J. (1975). *The Language of Thoughts*. Harvard University Press.
- Foerster, F. R., Borghi, A. M., & Goslin, J. (2020). Labels strengthen motor learning of new tools. *Cortex*, 129, 1–10. <https://doi.org/10.1016/j.cortex.2020.04.006>
- Friederici, A. D. (2020). Hierarchy processing in human neurobiology: How specific is it? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1789), 1–9. <https://doi.org/10.1098/rstb.2018.0391>
- Friederici, A. D., & Kotz, S. A. (2003). The brain basis of syntactic processes: functional imaging and lesion studies. *NeuroImage*, 20, S8–S17. <https://doi.org/10.1016/j.neuroimage.2003.09.003>
- Friederici, A. D., Rüschemeyer, S. A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and

- superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cerebral Cortex*, 13(2), 170–177. <https://doi.org/10.1093/cercor/13.2.170>
- Fritz-Laylin, L. K. (2020). The evolution of animal cell motility. *Current Biology*, 30(10), R477–R482. <https://doi.org/10.1016/j.cub.2020.03.026>.
- Gallivan, J. P., Adam McLean, D., Valyear, K. F., & Culham, J. C. (2013). Decoding the neural mechanisms of human tool use. *ELife*, 2013(2), 1–29. <https://doi.org/10.7554/eLife.00425>
- Garcea, F. E., & Buxbaum, L. J. (2019). Gesturing tool use and tool transport actions modulates inferior parietal functional connectivity with the dorsal and ventral object processing pathways. *Human Brain Mapping*, 40(10), 2867–2883. <https://doi.org/10.1002/hbm.24565>
- Gentile, G., Guterstam, A., Brozzoli, C., & Ehrsson, H. H. (2013). Disintegration of Multisensory Signals from the Real Hand Reduces Default Limb Self-Attribution: An fMRI Study. *Journal of Neuroscience*, 33(33), 13350–13366. <https://doi.org/10.1523/JNEUROSCI.1363-13.2013>
- Gentilucci, M., Roy, A. C., & Stefanini, S. (2004). Grasping an object naturally or with a tool: are these tasks guided by a common motor representation? *Exp Brain Res*, 157, 496–506. <https://doi.org/10.1007/s00221-004-1863-8>
- Gerschlagel, W., Siebner, H. R., & Rothwell, J. C. (2001). Decreased corticospinal excitability after subthreshold 1 Hz rTMS over lateral premotor cortex. *Neurology*, 57(3), 449–455. <https://doi.org/10.1212/WNL.57.3.449>
- Geschwind, N. (1965). Disconnexion syndromes in animals and man. *Brain*, 88(2), 237–294.
- Geschwind, N. (1970). The Organization of Language and the Brain. *Science*, 170(3961), 940–944. <https://doi.org/10.1093/acprof:oso/9780195177640.003.0026>
- Ghio, M., Locatelli, M., Tettamanti, A., Perani, D., Gatti, R., & Tettamanti, M. (2018). Cognitive training with action-related verbs induces neural plasticity in the action representation system as assessed by gray matter brain morphometry. *Neuropsychologia*, 114, 186–194. <https://doi.org/10.1016/j.neuropsychologia.2018.04.036>
- Gianelli, C., Farnè, A., Salemme, R., Jeannerod, M., & Roy, A. C. (2011). The Agent is Right: When Motor Embodied Cognition is Space-Dependent. *PloS One*, 6(9), 1–8. <https://doi.org/10.1371/journal.pone.0025036>
- Gill, S. A., & Bierema, A. M. K. (2013). On the Meaning of Alarm Calls: A Review of Functional Reference in Avian Alarm Calling. *Ethology*, 119(6), 449–461. <https://doi.org/10.1111/eth.12097>
- Ginex, V., Gilardone, G., Viganò, M., Monti, A., Judica, E., Passaro, I., Gilardone, M., Vanacore, N., & Corbo, M. (2020). Interaction Between Recovery of Motor and Language Abilities After Stroke. *Archives of Physical Medicine and Rehabilitation*, 101(8), 1367–1376. <https://doi.org/10.1016/j.apmr.2020.04.010>
- Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic Bulletin & Review*, 9(3), 558–565. <https://doi.org/10.3758/bf03196313>

- Glenberg, A. M., Sato, M., & Cattaneo, L. (2008). Use-induced motor plasticity affects the processing of abstract and concrete language. *Current Biology*, 18(7), R290–R291. <https://doi.org/10.1016/j.cub.2008.02.036>.
- Goldberg, R. F., Perfetti, C. A., & Schneider, W. (2006a). Brief Communications Perceptual Knowledge Retrieval Activates Sensory Brain Regions. *The Journal of Neuroscience*, 26(18), 4917–4921. <https://doi.org/10.1523/JNEUROSCI.5389-05.2006>
- Goldberg, R. F., Perfetti, C. A., & Schneider, W. (2006b). Distinct and common cortical activations for multimodal semantic categories. *Cognitive, Affective and Behavioral Neuroscience*, 6(3), 214–222. <https://doi.org/10.3758/cabn.6.3.214>.
- Goldenberg, G. (1996). Defective imitation of gestures in patients with damage in the left or right hemispheres. *Journal of Neurology, Neurosurgery, and Psychiatry*, 61(7), 176–180. <https://doi.org/10.1136/jnnp.61.2.176>
- Goldenberg, G. (1999). Matching and imitation of hand and finger postures in patients with damage in the left or right hemispheres. *Neuropsychologia*, 37(5), 559–566. [https://doi.org/10.1016/s0028-3932\(98\)00111-0](https://doi.org/10.1016/s0028-3932(98)00111-0).
- Goldenberg, G. (2003). Apraxia and beyond: Life and work of Hugo Liepmann. *Cortex*, 39(3), 509–524. [https://doi.org/10.1016/S0010-9452\(08\)70261-2](https://doi.org/10.1016/S0010-9452(08)70261-2)
- Goldenberg, G., Hartmann, K., & Schlott, I. (2003). Defective pantomime of object use in left brain damage: apraxia or asymbolia? *Neuropsychologia*, 41, 1565–1573. [https://doi.org/10.1016/S0028-3932\(03\)00120-9](https://doi.org/10.1016/S0028-3932(03)00120-9)
- Goldenberg, G., & Randerath, J. (2015). Neuropsychologia Shared neural substrates of apraxia and aphasia. *Neuropsychologia*, 75, 40–49. <https://doi.org/10.1016/j.neuropsychologia.2015.05.017>
- González, J., Barros-Loscertales, A., Pulvermüller, F., Meseguer, V., Sanjuán, A., Belloch, V., & Avila, C. (2006). Reading cinnamon activates olfactory brain regions. *NeuroImage*, 32, 906–912. <https://doi.org/10.1016/j.neuroimage.2006.03.037>
- Goodale, A. M., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–25. [https://doi.org/10.1016/0166-2236\(92\)90344-8](https://doi.org/10.1016/0166-2236(92)90344-8).
- Gould, S. J., & Vrba, E. S. (1982). Exaptation a missing term in the science of form. *Paleobiology*, 8(1), 4–15. <https://doi.org/10.1017/S0094837300004310>
- Grady, C. L., McIntosh, A. R., Beig, S., Keightley, M. L., Burian, H., & Black, S. E. (2003). Evidence from Functional Neuroimaging of a Compensatory Prefrontal Network in Alzheimer's Disease. *Journal of Neuroscience*, 23(3), 896–993. <https://doi.org/10.1523/JNEUROSCI.23-03-00986.2003>.
- Grafton, S. T. (2010). The cognitive neuroscience of prehension: Recent developments. *Experimental Brain Research*, 204(4), 475–491. <https://doi.org/10.1007/s00221-010-2315-2>
- Graybiel, A. M. (1998). The Basal Ganglia and Chunking of Action Repertoires. *Neurobiology of Learning and Memory*, 70, 119–136. <https://doi.org/10.1038/s41380-018-0199-x>
- Graybiel, A. M., Aosaki, T., Flaherty, A. W., & Kimura, M. (1994). The basal ganglia and motor control. *Science*, 265(5180), 1826–1830. <https://doi.org/10.1155/NP.2003.107>

- Greenfield, P. M. (1991). Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. *Behavioral and Brain Sciences*, 14(4), 531–551. <https://doi.org/10.1017/S0140525X00071235>
- Grossman, M., Anderson, C., Khan, B. A., Avants, B. B., Elman, L., & Mccluskey, L. (2008). Impaired action knowledge in amyotrophic lateral sclerosis. *Neurology*, 71(18), 1396–1401. <https://doi.org/10.1212/01.wnl.0000319701.50168.8c>.
- Hagoort, P., & Swaab, T. (2013). MUC (Memory, Unification, Control) and beyond. *Frontiers in Psy*, 4(416), 1–13. <https://doi.org/10.3389/fpsyg.2013.00416>
- Hahne, A., & Jescheniak, J. D. (2001). What's left if the Jabberwock gets the semantics? An ERP investigation into semantic and syntactic processes during auditory sentence comprehension. *Cognitive Brain Research*, 11(2), 199–212. [https://doi.org/10.1016/s0926-6410\(00\)00071-9](https://doi.org/10.1016/s0926-6410(00)00071-9).
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic Representation of Action Words in Human Motor and Premotor Cortex. *Neuron*, 41(2), 301–307. [https://doi.org/10.1016/S0896-6273\(03\)00838-9](https://doi.org/10.1016/S0896-6273(03)00838-9)
- Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The Faculty of Language: What Is It, Who Has It, and How Did It Evolve? *Science*, 298(2002), 1569–1579. <https://doi.org/10.1126/science.298.5598.1569>
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal corten. *Science*, 293(2425–2430), 87–96. <https://doi.org/10.4324/9780203496190>
- Henson, R. N. A. (2003). Neuroimaging studies of priming. *Progress in Neurobiology*, 70(1), 53–81. [https://doi.org/10.1016/S0301-0082\(03\)00086-8](https://doi.org/10.1016/S0301-0082(03)00086-8)
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, 8(5), 393–402. <https://doi.org/10.1038/nrn2113>
- Higuchi, S., Chaminade, T., Imamizu, H., & Kawato, M. (2009). Shared neural correlates for language and tool use in Broca's area. *NeuroReport*, 20(15), 1376–1381. <https://doi.org/10.1097/WNR.0b013e3283315570>
- Hoenig, K., Sim, E.-J., Bochev, V., Herrnberger, B., & Kiefer, M. (2008). Conceptual Flexibility in the Human Brain: Dynamic Recruitment of Semantic Maps from Visual, Motor, and Motion-related Areas. *Journal of Cognitive Neuroscience*, 20(10), 1799–1814. <https://doi.org/10.1162/jocn.2008.20123>.
- Holt, L. E., & Beilock, S. L. (2006). Expertise and its embodiment: Examining the impact of sensorimotor skill expertise on the representation of action related text. *Journal Psychonomic Bulletin & Review*, 13(4), 694–701. <https://doi.org/10.3758/bf03193983>.
- Huart, C., Rombaux, P., & Hummel, T. (2013). Plasticity of the Human Olfactory System: The Olfactory Bulb. *Molecules*, 18(9), 11586–11600. <https://doi.org/10.3390/molecules180911586>
- Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, 379(6562), 249–251. <https://doi.org/10.1038/379249a0>

- Iacoboni, M. (2008). The role of premotor cortex in speech perception: Evidence from fMRI and rTMS. *Journal of Physiology Paris*, 102, 31–34. <https://doi.org/10.1016/j.jphysparis.2008.03.003>
- Imamizu, H., Kuroda, T., Miyauchi, S., Yoshioka, T., & Kawato, M. (2003). Modular organization of internal models of tools in the human cerebellum. *Proceedings of the National Academy of Sciences of the United States of America*, 100(9), 5461–5466. <https://doi.org/10.1073/pnas.0835746100>
- Imamizu, H., Miyauchi, S., Tamada, T., Sasaki, Y., Ryouzuke, T., Pütz, B., Yoshioka, T., & Kawato, M. (2000). Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature*, 403(6766), 192–195. <https://doi.org/10.1038/35003194>.
- Iriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *NeuroReport*, 7(14), 2325–2330. <https://doi.org/10.1097/00001756-199610020-00010>
- Iriki, A., & Taoka, M. (2012). Triadic (ecological, neural, cognitive) niche construction: A scenario of human brain evolution extrapolating tool use and language from the control of reaching actions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1585), 10–23. <https://doi.org/10.1098/rstb.2011.0190>
- Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences of the United States of America*, 96(16), 9379–9384. <https://doi.org/10.1073/pnas.96.16.9379>.
- Ishibashi, R., Pobric, G., Saito, S., Ralph, M. A., & Lambon, R. (2016). The neural network for tool-related cognition: An activation likelihood estimation meta-analysis of 70 neuroimaging contrasts. *Cognitive Neuropsychology*, 33(3–4), 241–256. <https://doi.org/10.1080/02643294.2016.1188798>
- Ishibashi, R., Ralph Lambon, M. A., Saito, S., & Pobric, G. (2011). Different roles of lateral anterior temporal lobe and inferior parietal lobule in coding function and manipulation tool knowledge: Evidence from an rTMS study. *Neuropsychologia*, 49(5), 1128–1135. <https://doi.org/10.1016/j.neuropsychologia.2011.01.004>
- Itaguchi, Y., & Fukuzawa, K. (2014). Hand-use and tool-use in grasping control. *Experimental Brain Research*, 232(11), 3613–3622. <https://doi.org/10.1007/s00221-014-4053-3>
- Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, 17(2), 187–202. <https://doi.org/10.1017/S0140525X00034026>
- Jeannerod, M. (1995). Mental imagery in the motor context. *Neuropsychologia*, 33(11), 1419–1432. [https://doi.org/10.1016/0028-3932\(95\)00073-c](https://doi.org/10.1016/0028-3932(95)00073-c).
- Jeannerod, M. (1999). Visuomotor channels: Their integration in goal-directed prehension. *Human Movement Science*, 18(2–3), 201–218. [https://doi.org/10.1016/S0167-9457\(99\)00008-1](https://doi.org/10.1016/S0167-9457(99)00008-1)
- Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends in Neurosciences*, 18(7), 314–320. [https://doi.org/10.1016/0166-2236\(95\)93921-J](https://doi.org/10.1016/0166-2236(95)93921-J)

- Jirak, D., Menz, M. M., Buccino, G., Borghi, A. M., & Binkofski, F. (2010). Grasping language-A short story on embodiment. *Consciousness and Cognition*, 19, 711–720. <https://doi.org/10.1016/j.concog.2010.06.020>
- Johari, K., Walenski, M., Reifegerste, J., Ashrafi, F., Behroozmand, R., Daemi, M., & Ullman, M. T. (2019). A dissociation between syntactic and lexical processing in Parkinson's disease. *Journal of Neurolinguistics*, 51, 221–235. <https://doi.org/10.1016/j.jneuroling.2019.03.004>
- Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends in Cognitive Sciences*, 8(2), 71–78. <https://doi.org/10.1016/j.tics.2003.12.002>
- Johnson-Frey, S. H., Newman-Norlund, R., & Grafton, S. T. (2005). A distributed left hemisphere network active during planning of everyday tool use skills. *Cerebral Cortex*, 15(6), 681–695. <https://doi.org/10.1093/cercor/bhh169>
- Jones, T. A. (2017). Motor compensation and its effects on neural reorganization after stroke. *Nature Neuroscience Review*, 18, 267–280. <https://doi.org/10.1038/nrn.2017.26>
- Just, M. A., & Carpenter, P. A. (1993). The intensity dimension of thought: pupillometric indices of sentence processing. *Canadian Journal of Experimental Psychology = Revue Canadienne de Psychologie Expérimentale*, 47(2), 310–339. <https://doi.org/10.1037/h0078820>
- Just, M. A., Carpenter, P. A., Keller, T. A., Eddy, W. F., & Thulborn, K. R. (1996). Brain activation modulated by sentence comprehension. *Science*, 274, 114–116. <https://doi.org/10.1126/science.274.5284.114>
- Kaan, E., Harris, A., Gibson, E., & Holcomb, P. (2000). The P600 as an index of syntactic integration difficulty. *Language and Cognitive Processes*, 15(2), 159–201. <https://doi.org/10.1080/016909600386084>
- Kaan, E., & Swaab, T. Y. (2003). Repair, Revision, and Complexity in Syntactic Analysis: An Electrophysiological Differentiation. *Journal of Cognitive Neuroscience*, 15(1), 98–110. <https://doi.org/10.1162/089892903321107855>.
- Kalénine, S., & Buxbaum, L. J. (2016). Thematic knowledge, artifact concepts, and the left posterior temporal lobe: Where action and object semantics converge. *Cortex*, 82, 164–178. <https://doi.org/10.1016/j.cortex.2016.06.008>
- Kemmerer, D., Rudrauf, D., Manzel, K., & Tranel, D. (2012). Behavioral patterns and lesion sites associated with impaired processing of lexical and conceptual knowledge of actions. *Cortex*, 48, 826–848. <https://doi.org/10.1016/j.cortex.2010.11.001>
- Kertesz, A., & Hooper, P. (1982). Praxis and language: the extent and variety of apraxia in aphasia. *Neuropsychologia*, 20(3), 275–286. [https://doi.org/10.1016/0028-3932\(82\)90102-6](https://doi.org/10.1016/0028-3932(82)90102-6)
- Kiefer, M., Sim, E.-J., Herrnberger, B., Grothe, J., & Hoenig, K. (2008). The Sound of Concepts: Four Markers for a Link between Auditory and Conceptual Brain Systems. *Journal of Neuroscience*, 28(47), 12224–12230. <https://doi.org/10.1523/JNEUROSCI.3579-08.2008>
- Kiefer, M., Trumpp, N., Herrnberger, B., Sim, E.-J., Hoenig, K., & Pulvermüller, F. (2012). Dissociating the

- representation of action-and sound-related concepts in middle temporal cortex. *Brain and Language*, 122, 120–125. <https://doi.org/10.1016/j.bandl.2012.05.007>
- King, J., & Just, M. A. (1991). Individual Differences in Syntactic Processing: The Role of Working Memory. *Journal of Memory and Language*, 30(5), 580–602. [https://doi.org/10.1016/0749-596X\(91\)90027-H](https://doi.org/10.1016/0749-596X(91)90027-H)
- King, M., Hernandez-Castillo, C. R., Poldrack, R. A., Ivry, R. B., & Diedrichsen, J. (2019). Functional boundaries in the human cerebellum revealed by a multi-domain task battery. *Nature Neuroscience*, 22(8), 1371–1378. <https://doi.org/10.1038/s41593-019-0436-x>
- Koechlin, E., & Jubault, T. (2006). Broca's Area and the Hierarchical Organization of Human Behavior. *Neuron*, 50(6), 963–974. <https://doi.org/10.1016/j.neuron.2006.05.017>
- Kolodny, O., & Edelman, S. (2018). The evolution of the capacity for language: The ecological context and adaptive value of a process of cognitive hijacking. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1743). <https://doi.org/10.1098/rstb.2017.0052>
- Kotz, S. A., Cappa, S. F., Von Cramon, D. Y., & Friederici, A. D. (2002). Modulation of the lexical-semantic network by auditory semantic priming: An event-related functional MRI study. *NeuroImage*, 17(4), 1761–1772. <https://doi.org/10.1006/nimg.2002.1316>
- Kotz, S. A., Meyer, M., & Paulmann, S. (2006). Lateralization of emotional prosody in the brain: an overview and synopsis on the impact of study design. *Progress in Brain Research*, 156. [https://doi.org/10.1016/S0079-6123\(06\)56015-7](https://doi.org/10.1016/S0079-6123(06)56015-7)
- Kreitzer, A. C. (2009). Physiology and Pharmacology of Striatal Neurons. *Annual Review of Neuroscience*, 32, 127–147. <https://doi.org/10.1146/annurev.neuro.051508.135422>
- Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational similarity analysis - connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience*, 2(4), 1–28. <https://doi.org/10.3389/neuro.06.004.2008>
- Kuhn, S. L., Raichlen, D. A., & Clark, A. E. (2016). What moves us? How mobility and movement are at the center of human evolution. *Evolutionary Anthropology*, 25(3), 86–97. <https://doi.org/10.1002/evan.21480>
- Kutas, M., & Federmeier, K. D. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences*, 4(12), 463–469. [https://doi.org/10.1016/s1364-6613\(00\)01560-6](https://doi.org/10.1016/s1364-6613(00)01560-6)
- Lachlan, R. F., & Nowicki, S. (2015). Context-dependent categorical perception in a songbird. *Proceedings of the National Academy of Sciences*, 112(6), 1892–1897. <https://doi.org/10.1073/pnas.1410844112>
- Lakoff, G., & Johnson, M. (1980). *Metaphors We Live By*. University of Chicago Press.
- Lambon Ralph, M. A., Sage, K., Jones, R. W., & Mayberry, E. J. (2010). Coherent concepts are computed in the anterior temporal lobes. *Proceedings of the National Academy of Sciences of the United States of America*, 107(6), 2717–2722. <https://doi.org/10.1073/pnas.0907307107>

- Larsson, M. (2015). Tool-use-associated sound in the evolution of language. *Animal Cognition*, 18, 993–1005. <https://doi.org/10.1007/s10071-015-0885-x>
- Lashley, K. S. (1951). The problem of serial order in behavior. In L. A. Jefres (Ed.), *Cerebral mechanisms in behavior* (pp. 112–147). Wiley.
- Lehéricy, S., Benali, H., Van De Moortele, P.-F., Pélégri-issac, M., Waechter, T., Ugurbil, K., & Doyon, J. (2005). Distinct basal ganglia territories are engaged in early and advanced motor sequence learning. *Proceedings of the National Academy of Sciences*, 102(35), 12566–12571. <https://doi.org/10.1073/pnas.0502762102>
- Leinonen, L., Hyvärinen, J., Nyman, G., & Linnankoski, I. (1979). I. Functional properties of neurons in lateral part of associative area 7 in awake monkeys. *Experimental Brain Research*, 34(2), 299–320. <https://doi.org/10.1007/BF00235675>
- Lepre, C. J., Ne Roche, H., Kent, D. V., Harmand, S., Quinn, R. L., Brugal, J.-P., Texier, P.-J., Lenoble, A., & Feibel, C. S. (2011). An earlier origin for the Acheulian. *Nature*, 477, 82–95. <https://doi.org/10.1038/nature10372>
- Lewis, J. W. (2006). Cortical Networks Related to Human Use of Tools. *The Neuroscientist*, 12(3), 211–231. <https://doi.org/10.1177/1073858406288327>
- Liberman, A. M., Cooper, F. S., Shankweiler, D. P., & Studdert-Kennedy, M. (1967). Perception and the speech code. *Psychological Review*, 74(6), 431–461. <https://doi.org/10.1037/h0020279>
- Liberman, A. M., Harris, K. S., Hoffman, H. S., & Griffith, B. C. (1957). The discrimination of speech sounds within and across phoneme boundaries. *Journal of Experimental Psychology*, 54(5), 358–368. <https://doi.org/10.1037/h0044417>
- Liberman, A. M., & Mattingly, I. G. (1985). The motor theory of speech perception revisited. *Cognition*, 21, 1–36. <https://doi.org/10.3758/PBR.15.2.453>
- Liberman, A. M., & Whalen, D. H. (2000). On the relation of speech to language. *Trends in Cognitive Sciences*, 4(5), 187–196. [https://doi.org/10.1016/S1364-6613\(00\)01471-6](https://doi.org/10.1016/S1364-6613(00)01471-6)
- Liepmann, H. (1908). *Drei Aufsätze aus dem Apraxie Gebiet*. Verlag Von S. Karger.
- Liepmann, H. (1920). *Ergebnisse der gesamten Medizin* (H. Brugsch (ed.); Urban & Sc, pp. 516–543). Urban & Schwarzenberg.
- Locatelli, M., Gatti, R., & Tettamanti, M. (2012). Training of manual actions improves language understanding of semantically related action sentences. *Frontiers in Psychology*, 3, 1–10. <https://doi.org/10.3389/fpsyg.2012.00547>
- Lorio, S., Kherif, F., Ruef, A., Melie-Garcia, L., Frackowiak, R., Ashburner, J., Helms, G., Lutti, A., & Draganski, B. (2016). Neurobiological Origin of Spurious Brain Morphological Changes: A Quantitative MRI Study. *Human Brain Mapping*, 37(5), 1801–1815. <https://doi.org/10.1002/hbm.23137>

- Lotto, A. J., Hickok, G. S., & Holt, L. L. (2009). Reflections on mirror neurons and speech perception. *Trends in Cognitive Sciences*, 13(3), 110–114. <https://doi.org/10.1016/j.tics.2008.11.008>
- Machery, E. (2007). Concept empiricism: A methodological critique. *Cognition*, 104, 19–46. <https://doi.org/10.1016/j.cognition.2006.05.002>
- Maffongelli, L., Ausilio, A. D., Fadiga, L., & Daum, M. M. (2019). The Ontogenesis of Action Syntax. *Collabra: Psychology*, 5(1), 1–11. <https://doi.org/doi.org/10.1525/collabra.215>
- Maffongelli, L., Bartoli, E., Sammler, D., Kölsch, S., Campus, C., Olivier, E., Fadiga, L., & D'Ausilio, A. (2015). Distinct brain signatures of content and structure violation during action observation. *Neuropsychologia*, 75, 30–39. <https://doi.org/10.1016/j.neuropsychologia.2015.05.020>
- Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology Paris*, 102(1–3), 59–70. <https://doi.org/10.1016/j.jphysparis.2008.03.004>
- Makuuchi, M., Bahlmann, J., Anwender, A., & Friederici, A. D. (2009). Segregating the core computational faculty of human language from working memory. *Proceedings of the National Academy of Sciences*, 106(20), 8362–8367. <https://doi.org/10.1073/pnas.0810928106>
- Makuuchi, M., & Friederici, A. D. (2013). Hierarchical functional connectivity between the core language system and the working memory system. *Cortex*, 49(9), 2416–2423. <https://doi.org/10.1016/j.cortex.2013.01.007>
- Marangolo, P., Bonifazi, S., Tomaiuolo, F., Craighero, L., Coccia, M., Altoè, G., Provinciali, L., & Cantagallo, A. (2010). Improving language without words: First evidence from aphasia. *Neuropsychologia*, 48(13), 3824–3833. <https://doi.org/10.1016/j.neuropsychologia.2010.09.025>
- Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in Cognitive Sciences*, 8(2), 79–86. <https://doi.org/10.1016/j.tics.2003.12.008>
- Martel, M., Cardinali, L., Bertonati, G., Jouffrais, C., Finos, L., Farnè, A., & Roy, A. C. (2019). Somatosensory-guided tool use modifies arm representation for action. *Scientific Reports*, 9(5517), 1–14. <https://doi.org/10.1038/s41598-019-41928-1>
- Martel, M., Cardinali, L., Roy, A. C., & Farnè, A. (2016). Tool-use: An open window into body representation and its plasticity. *Cognitive Neuropsychology*, 33(1–2), 82–101. <https://doi.org/10.1080/02643294.2016.1167678>
- Martel, M., Finos, L., Koun, E., Farnè, A., & Roy, A. C. (2021). The long developmental trajectory of body representation plasticity following tool use. *Scientific Reports*, 11, 559. <https://doi.org/10.1038/s41598-020-79476-8>
- Mårtensson, J., Eriksson, J., Bodammer, N. C., Lindgren, M., Johansson, M., Nyberg, L., & Lövdén, M. (2012). Growth of language-related brain areas after foreign language learning. *NeuroImage*, 63(1), 240–244. <https://doi.org/10.1016/j.neuroimage.2012.06.043>

- Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, 379(6566), 649–652. <https://doi.org/10.1038/379649a0>.
- Martins, M. J. D., Bianco, R., Sammler, D., & Villringer, A. (2019). Recursion in action : An fMRI study on the generation of new hierarchical levels in motor sequences. *Human Brain Mapping*, 40(9), 1–16. <https://doi.org/10.1002/hbm.24549>
- Martins, M. J. D., Krause, C., Neville, D. A., Pino, D., Villringer, A., Obrig, H., & Dias Martins, M. (2019). Recursive hierarchical embedding in vision is impaired by posterior middle temporal gyrus lesions. *Brain*, 3217–3229. <https://doi.org/10.1093/brain/awz242>
- Massen, C., & Prinz, W. (2007). Programming Tool-Use Actions. *Journal of Experimental Psychology: Human Perception and Performance*, 33(3), 692–704. <https://doi.org/10.1037/0096-1523.33.3.692>
- Matchin, W., & Hickok, G. (2020). The Cortical Organization of Syntax. *Cerebral Cortex*, 30(3), 1481–1498. <https://doi.org/10.1093/cercor/bhz180>
- McGrew, W. C., & Collins, D. A. (1985). Tool use by wild chimpanzees (*Pan troglodytes*) to obtain termites (*Macrotermes herus*) in the Mahale Mountains, Tanzania. *American Journal of Primatology*, 9(1), 47–62. <https://doi.org/10.1002/ajp.1350090106>
- Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2010). Captive chimpanzees use their right hand to communicate with each other: Implications for the origin of the cerebral substrate for language. *Cortex*, 46, 40–48. <https://doi.org/10.1016/j.cortex.2009.02.013>
- Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2013). On the origins of human handedness and language: A comparative review of hand preferences for bimanual coordinated actions and gestural communication in nonhuman primates. *Developmental Psychobiology*, 55(6), 637–650. <https://doi.org/10.1002/dev.21150>
- Meister, I. G., Wilson, S. M., Deblieck, C., Wu, A. D., & Iacoboni, M. (2007). The Essential Role of Premotor Cortex in Speech Perception. *Current Biology*, 17(19), 1692–1696. <https://doi.org/10.1016/j.cub.2007.08.064>
- Mendoza, G. N., & Merchant, H. (2014). Motor system evolution and the emergence of high cognitive functions. *Progress in Neurobiology*, 122, 73–93. <https://doi.org/10.1016/j.pneurobio.2014.09.001>
- Mengotti, P., Corradi-Dell’acqua, C., Negri, G. A. L., Ukmar, M., Pesavento, V., & Rumiati, R. I. (2013). Selective imitation impairments differentially interact with language processing. *Brain*, 136, 2602–2618. <https://doi.org/10.1093/brain/awt194>
- Meyer, D. E., & Schvaneveldt, R. W. (1971). Facilitation in recognizing pairs of words: evidence of a dependence between retrieval operations. *Journal at Experimental Psychology*, 90(2), 227–234. <https://doi.org/10.1037/h0031564>.
- Middleton, F. A., & Strick, P. L. (2000). Basal ganglia and cerebellar loops: Motor and cognitive circuits. *Brain Research Reviews*, 31(2–3), 236–250. [https://doi.org/10.1016/S0165-0173\(99\)00040-5](https://doi.org/10.1016/S0165-0173(99)00040-5)

- Miller, L. E., Montroni, L., Koun, E., Salemme, R., Hayward, V., & Farnè, A. (2018). Sensing with tools extends somatosensory processing beyond the body. *Nature*, *561*(7722), 239–242. <https://doi.org/10.1038/s41586-018-0460-0>
- Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in Neurosciences*, *6*, 414–417. [https://doi.org/10.1016/0166-2236\(83\)90190-X](https://doi.org/10.1016/0166-2236(83)90190-X)
- Moll, J., De Oliveira-Souza, R., Passman, L. J., Cunha, F. C., Souza-Lima, F., & Andreiuolo, P. A. (2000). Functional MRI correlates of real and imagined tool-use pantomimes. *Neurology*, *54*(6), 1331–1336. <https://doi.org/10.1212/WNL.54.6.1331>
- Morgan, T. J. H., Uomini, N. T., Rendell, L. E., Street, S. E., Lewis, H. M., Cross, C. P., Evans, C., Kearney, R., Torre, I. De, Whiten, A., & Laland, K. N. (2015). Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nature Communications*, *6*, 1–8. <https://doi.org/10.1038/ncomms7029>
- Moro, A. (2014). On the similarity between syntax and actions. *Trends in Cognitive Sciences*, *18*(3), 109–110. <https://doi.org/10.1016/j.tics.2013.11.006>
- 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*(1), 110–118. <https://doi.org/10.1006/nimg.2000.0668>
- Möttönen, R., & Watkins, K. E. (2009). Motor Representations of Articulators Contribute to Categorical Perception of Speech Sounds. *Journal of Neuroscience*, *29*(31), 9819–9835. <https://doi.org/10.1523/JNEUROSCI.6018-08.2009>
- Murray, E. A., & Mishkin, M. (1984). Relative contributions of SII and area 5 to tactile discrimination in monkeys. *Behavioural Brain Research*, *11*(1), 67–83. [https://doi.org/10.1016/0166-4328\(84\)90009-3](https://doi.org/10.1016/0166-4328(84)90009-3)
- Neely, J. (1976). Semantic priming and retrieval from lexical memory: Evidence for facilitatory and inhibitory processes. *Memory & Cognition*, *4*(5), 648–654. <https://doi.org/10.3758/BF03213230>
- Neville, H., Nicol, J. L., Barss, A., Forster, K. I., & Garrett, M. F. (1991). Syntactically Based Sentence Processing Classes: Evidence from Event-Related Brain Potentials. *Journal of Cognitive Neuroscience Volume*, *3*(2), 151–165. <https://doi.org/10.1162/jocn.1991.3.2.151>
- Ni, W., Fodor, J. D., Grain, S., & Shankweiler, D. (1998). Anomaly Detection: Eye Movement Patterns. *Journal of Psycholinguistic Research*, *27*(5), 515–539. <https://doi.org/10.1023/a:1024996828734>
- Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, *10*(9), 424–430. <https://doi.org/10.1016/j.tics.2006.07.005>
- Obayashi, S., Suhara, T., Kawabe, K., Okauchi, T., & Maeda, J. (2001). Functional Brain Mapping of Monkey Tool Use. *NeuroImage*, *14*, 853–861. <https://doi.org/10.1006/nimg.2001.0878>
- Ochipa, C., G Rothi, L. J., & Heilman, K. M. (1989). Ideational apraxia: a deficit in tool selection and use. *Annals*

- of *Neurology*, 25(2), 190–193. <https://doi.org/10.1002/ana.410250214>
- Orlov, T., Makin, T. R., & Zohary, E. (2010). Article Topographic Representation of the Human Body in the Occipitotemporal Cortex. *Neuron*, 68, 586–600. <https://doi.org/10.1016/j.neuron.2010.09.032>
- Osiurak, F., & Badets, A. (2016). Tool use and affordance: Manipulation-based versus reasoning-based approaches. *Psychological Review*, 123(5), 534–568. <https://doi.org/10.1037/rev0000027>
- Osiurak, F., Jarry, C., & Le Gall, D. (2011). Re-examining the gesture engram hypothesis. New perspectives on apraxia of tool use. *Neuropsychologia*, 49, 299–312. <https://doi.org/10.1016/j.neuropsychologia.2010.12.041>
- Pa, J., & Hickok, G. (2008). A parietal-temporal sensory-motor integration area for the human vocal tract: Evidence from an fMRI study of skilled musicians. *Neuropsychologia*, 46, 362–368. <https://doi.org/10.1016/j.neuropsychologia.2007.06.024>
- Papeo, L., & Hochmann, J.-R. (2012). A cross-talk between brain-damage patients and infants on action and language. *Neuropsychologia*, 50, 1222–1234. <https://doi.org/10.1016/j.neuropsychologia.2012.03.025>
- Papeo, L., Negri, G. A. L., Zadini, A., & Rumiati, R. I. (2010). Action performance and action-word understanding: Evidence of double dissociations in left-damaged patients. *Cognitive Neuropsychology*, 27(5), 428–461. <https://doi.org/10.1080/02643294.2011.570326>
- Papitto, G., Friederici, A. D., & Zaccarella, E. (2020). The topographical organization of motor processing: An ALE meta-analysis on six action domains and the relevance of Broca's region. *NeuroImage*, 206, 1–15. <https://doi.org/10.1016/j.neuroimage.2019.116321>
- Park, J. E. (2017). Apraxia: Review and Update Jung. *Journal of Clinical Neurology*, 13(4), 317–324. <https://doi.org/https://doi.org/10.3988/jcn.2017.13.4.317>
- Pascual-Leone, A., Walsh, V., & Rothwell, J. (2000). Transcranial magnetic stimulation in cognitive neuroscience - virtual lesion, chronometry, and functional connectivity. *Curr Op Neurobi*, 10(2), 232–237. [https://doi.org/10.1016/s0959-4388\(00\)00081-7](https://doi.org/10.1016/s0959-4388(00)00081-7)
- Pastra, K., & Aloimonos, Y. (2012). The minimalist grammar of action. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1585), 103–117. <https://doi.org/10.1098/rstb.2011.0123>
- Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know ? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, 8, 976–988. <https://doi.org/10.1038/nrn2277>
- Pazen, M., Uhlmann, L., van Kemenade, B. M., Steinsträter, O., Straube, B., & Kircher, T. (2020). Predictive perception of self-generated movements: Commonalities and differences in the neural processing of tool and hand actions. *NeuroImage*, 206(116309). <https://doi.org/10.1016/j.neuroimage.2019.116309>
- Peeters, R. R., Rizzolatti, G., & Orban, G. A. (2013). Functional properties of the left parietal tool use region. *NeuroImage*, 78, 83–93. <https://doi.org/10.1016/j.neuroimage.2013.04.023>

- Peeters, R. R., Simone, L., Nelissen, K., Fabbri-Destro, M., Vanduffel, W., Rizzolatti, G., & Orban, G. A. (2009). The Representation of Tool Use in Humans and Monkeys: Common and Uniquely Human Features. *Journal of Neuroscience*, 29(37), 11523–11539. <https://doi.org/10.1523/JNEUROSCI.2040-09.2009>
- Penfield, W., & Boldrey, E. (1937). Somatic Motor and Sensory Representation in Man. *Brain*, 60(4), 389–443. <https://doi.org/10.1093/brain/60.4.389>
- Perani, D., Schnur, T., Tettamanti, M., Gorno-Tempini, M., Cappa, S. F., & Fazio, F. (1999). Word and picture matching: a PET study of semantic category effects. *Neuropsychologia*, 37, 293–306.
- Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1999). Functional Specialization for Semantic and Phonological Processing in the Left Inferior Prefrontal Cortex. *NeuroImage*, 10(1), 25–35. <https://doi.org/10.1006/nimg.1999.0441>.
- Ponce de León, M. S., Bienvenu, T., Marom, A., Engel, S., Tafforeau, P., Alatorre Warren, J. L., Lordkipanidze, D., Kurniawan, I., Murti, D. B., Suriyanto, R. A., Koesbardiati, T., & Zollikofer, C. P. E. (2021). The primitive brain of early Homo. *Science*, 372(6538), 165–171. <https://doi.org/10.1126/science.aaz0032>
- Prabhakaran, S., Zarahn, E., Riley, C., Speizer, A., Chong, J. Y., Lazar, R. M., Marshall, R. S., & Krakauer, J. W. (2008). Inter-individual Variability in the Capacity for Motor Recovery After Ischemic Stroke. *Neurorehabilitation Neural Repair*, 22(1), 64–71. <https://doi.org/10.1177/1545968307305302>
- Pramstaller, P. P., Marsden, C. D., Pramstaller, P. P., & Marsden, C. D. (1996). The basal ganglia and apraxia. *Brain*, 119(Pt 1), 319–340. <https://doi.org/10.1093/brain/119.1.319>.
- Premack, D. (2007). Human and animal cognition: Continuity and discontinuity. *Proceedings of the National Academy of Sciences of the United States of America*, 104(35), 13861–13867. <https://doi.org/10.1073/pnas.0706147104>
- Price, C. J. (2010). The anatomy of language: A review of 100 fMRI studies published in 2009. *Annals of the New York Academy of Sciences*, 1191, 62–88. <https://doi.org/10.1111/j.1749-6632.2010.05444.x>
- Price, C. J. (2012). A review and synthesis of the first 20years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImage*, 62(2), 816–847. <https://doi.org/10.1016/j.neuroimage.2012.04.062>
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6, 576–582. <https://doi.org/10.1038/2201358a0>
- Pulvermüller, F. (2010). Brain embodiment of syntax and grammar: Discrete combinatorial mechanisms spelt out in neuronal circuits. *Brain and Language*, 112, 167–179. <https://doi.org/10.1016/j.bandl.2009.08.002>
- Pulvermüller, F. (2014). The syntax of action. *Trends in Cognitive Sciences*, 18(5), 219–220. <https://doi.org/10.1016/j.tics.2014.01.001>
- Pulvermüller, F., & Fadiga, L. (2010). Active perception: sensorimotor circuits as a cortical basis for language. *Nature Reviews Neuroscience*, 11(5), 351–360. <https://doi.org/10.1038/nrn2811>
- Pulvermüller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005). Functional links between motor and

- language systems. *European Journal of Neuroscience*, 21(3), 793–797. <https://doi.org/10.1111/j.1460-9568.2005.03900.x>
- Pulvermüller, F., Huss, M., Kherif, F., Moscoso del Prado Martin, F., Hauk, O., & Shtyrov, Y. (2006). Motor cortex maps articulatory features of speech sounds. *Proceedings of the National Academy of Sciences of the United States of America*, 103(20), 7865–7870. <https://doi.org/10.1073/pnas.0509989103>
- Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005). Brain Signatures of Meaning Access in Action Word Recognition. *Journal of Cognitive Neuroscience*, 17(6), 884–892. <https://doi.org/10.1162/0898929054021111>
- Pylkkänen, L. (2019). The neural basis of combinatorial syntax and semantics. *Science*, 366(6461), 62–66. <https://doi.org/10.1126/science.aax0050>.
- Quallo, M. M., Price, C. J., Ueno, K., Asamizuya, T., Cheng, K., Lemon, R. N., & Iriki, A. (2009). Gray and white matter changes associated with tool-use learning in macaque monkeys. *Proceedings of the National Academy of Sciences*, 106(43), 18379–18384. <https://doi.org/10.1073/pnas.0909751106>
- Raizada, R. D. S., & Poldrack, R. A. (2007). Selective Amplification of Stimulus Differences during Categorical Processing of Speech. *Neuron*, 56(4), 726–740. <https://doi.org/10.1016/j.neuron.2007.11.001>
- Rangarajan, V., Jacques, C., Knight, R. T., Weiner, K. S., & Grill-Spector, K. (2020). Diverse Temporal Dynamics of Repetition Suppression Revealed by Intracranial Recordings in the Human Ventral Temporal Cortex. *Cortex*, 30, 5988–6003. <https://doi.org/10.1093/cercor/bhaa173>
- Reynaud, E., Lesourd, M., Navarro, J., & Osiurak, F. (2016). On the neurocognitive origins of human tool use: A critical review of neuroimaging data. *Neuroscience and Biobehavioral Reviews*, 64, 421–437. <https://doi.org/10.1016/j.neubiorev.2016.03.009>
- Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in Cognitive Sciences*, 21(5), 188–194. [https://doi.org/10.1016/s0166-2236\(98\)01260-0](https://doi.org/10.1016/s0166-2236(98)01260-0).
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, 3(2), 131–141. [https://doi.org/10.1016/0926-6410\(95\)00038-0](https://doi.org/10.1016/0926-6410(95)00038-0)
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25(1A), 31–40. [https://doi.org/10.1016/0028-3932\(87\)90041-8](https://doi.org/10.1016/0028-3932(87)90041-8)
- Roby-Brami, A., Hermsdorfer, J., Roy, A. C., & Jacobs, S. (2012). A neuropsychological perspective on the link between language and praxis in modern humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1585), 144–160. <https://doi.org/10.1098/rstb.2011.0122>
- Rosenbaum, D. A., Cohen, R. G., Jax, S. A., Weiss, D. J., & Van Der Wel, R. (2007). The problem of serial order in behavior: Lashley's legacy. *Human Movement Science*, 26, 525–554. <https://doi.org/10.1016/j.humov.2007.04.001>

- Roy, A. C., & Arbib, M. A. (2005). *The syntactic motor system*. John Benjamins Publishing Company.
<https://doi.org/10.1075/gest.5.1.03roy>
- Roy, A. C., Craighero, L., Fabbri-Destro, M., & Fadiga, L. (2008). Phonological and lexical motor facilitation during speech listening: A transcranial magnetic stimulation study. *Journal of Physiology Paris*, 102, 101–105. <https://doi.org/10.1016/j.jphysparis.2008.03.006>
- Roy, A. C., Curie, A., Nazir, T., Paulignan, Y., des Portes, V., Fournieret, P., & Deprez, V. (2013). Syntax at Hand: Common Syntactic Structures for Actions and Language. *PLoS ONE*, 8(8), 1–11.
<https://doi.org/10.1371/journal.pone.0072677>
- Rueschemeyer, S. A., Lindemann, O., Rooij, D. Van, Dam, W. Van, & Bekkering, H. (2010). Effects of intentional motor actions on embodied language processing. *Experimental Psychology*, 57(4), 260–266.
<https://doi.org/10.1027/1618-3169/a000031>
- Rumiati, R. I., Zanini, S., Vorano, L., & Shallice, T. (2001). A form of ideational apraxia as a selective deficit of contention scheduling. *Cognitive Neuropsychology*, 18(7), 617–642.
<https://doi.org/10.1080/02643290126375>
- Rüschemeyer, S. A., Brass, M., & Friederici, A. D. (2007). Comprehending prehending: Neural correlates of processing verbs with motor stems. *Journal of Cognitive Neuroscience*, 19(5), 855–865.
<https://doi.org/10.1162/jocn.2007.19.5.855>
- Saccuman, M. C., Cappa, S. F., Bates, E. A., Arevalo, A., Rosa, P. Della, Danna, M., & Perani, D. (2006). The impact of semantic reference on word class: An fMRI study of action and object naming. *NeuroImage*, 32, 1865–1878. <https://doi.org/10.1016/j.neuroimage.2006.04.179>
- Sagi, Y., Tavor, I., Hofstetter, S., Tzur-Moryosef, S., Blumenfeld-Katzir, T., & Assaf, Y. (2012). Learning in the Fast Lane: New Insights into Neuroplasticity. *Neuron*, 73(6), 1195–1203.
<https://doi.org/10.1016/j.neuron.2012.01.025>
- Sainburg, T., Theilman, B., Thielk, M., & Gentner, T. Q. (2019). Parallels in the sequential organization of birdsong and human speech. *Nature Communications*, 10(3636), 1–11. <https://doi.org/10.1038/s41467-019-11605-y>
- Sambin, S., Teichmann, M., de Diego Balaguer, R., Giavazzi, M., Sportiche, D., Schlenker, P., & Bachoud-Lévi, A. C. (2012). The role of the striatum in sentence processing: Disentangling syntax from working memory in Huntington's disease. *Neuropsychologia*, 50(11), 2625–2635.
<https://doi.org/10.1016/j.neuropsychologia.2012.07.014>
- Santi, A., & Grodzinsky, Y. (2007). Working memory and syntax interact in Broca's area. *NeuroImage*, 37(1), 8–17. <https://doi.org/10.1016/j.neuroimage.2007.04.047>
- Saygin, A. P. (2013). Sensory and Motor Brain Areas Supporting Biological Motion Perception: Neuropsychological and Neuroimaging Studies. In J. Kerri & M. Shiffrar (Eds.), *People Watching: Social, Perceptual, and Neurophysiological Studies of Body Perception* (pp. 371–389). Oxford University Press.

- Schone, H. R., Maimon-Mor, R. O., Baker, C. I., & Makin, T. R. (2021). Expert tool users show increased differentiation between visual representations of hands and tools. *Journal of Neuroscience*, 41(13), 2980–2989. <https://doi.org/10.1523/JNEUROSCI.2489-20.2020>
- Scorolli, C., & Borghi, A. M. (2006). Sentence comprehension and action: Effector specific modulation of the motor system. *Brain Research*, 1130, 119–124. <https://doi.org/10.1016/j.brainres.2006.10.033>
- Seed, A., & Byrne, R. (2010). Animal tool-use. *Current Biology*, 20(23), R1032–R1039. <https://doi.org/10.1016/j.cub.2010.09.042>
- Sereno, M. I., Diedrichsen, J., Tachrount, M., Testa-Silva, G., D Arceuil, H., & De Zeeuw, C. (2020). The human cerebellum has almost 80% of the surface area of the neocortex. *Proceedings of the National Academy of Sciences of the United States of America*, 117(32), 19538–19543. <https://doi.org/10.1073/pnas.2002896117>
- Sereno, M. I., & Huang, R. S. (2014). Multisensory maps in parietal cortex. *Current Opinion in Neurobiology*, 24(1), 39–46. <https://doi.org/10.1016/J.CONB.2013.08.014>
- Serniclaes, W., Van Heghe, S., Mousty, P., Carr, R. E., & Sprenger-Charolles, L. (2004). Allophonic mode of speech perception in dyslexia. *Journal of Experimental Child Psychology*, 87, 336–361. <https://doi.org/10.1016/j.jecp.2004.02.001>
- Shields, J. (1991). Semantic-pragmatic disorder: A right hemisphere syndrome? *British Journal of Disorders of Communication*, 26(3), 383–392. <https://doi.org/10.3109/13682829109012023>
- Silvanto, J., & Cattaneo, Z. (2017). Common framework for “virtual lesion” and state-dependent TMS: The facilitatory/suppressive range model of online TMS effects on behavior. *Brain and Cognition*, 119, 32–38. <https://doi.org/10.1016/j.bandc.2017.09.007>
- Simmons, W. K., Ramjee, V., Beauchamp, M. S., Mcrae, K., Martin, A., & Barsalou, L. W. (2007). A common neural substrate for perceiving and knowing about color. *Neuropsychologia*, 45, 2802–2810. <https://doi.org/10.1016/j.neuropsychologia.2007.05.002>
- 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. *Journal of Cognitive Neuroscience*, 20(11), 2037–2057. <https://doi.org/10.1162/jocn.2008.20143>.
- Sitnikova, T., Kuperberg, G., & Holcomb, P. J. (2003). Semantic integration in videos of real-world events: An electrophysiological investigation. *Psychophysiology*, 40(1), 160–164. <https://doi.org/10.1111/1469-8986.00016>.
- Steele, J., Ferrari, P. F., & Fogassi, L. (2012). From action to language: Comparative perspectives on primate tool use, gesture and the evolution of human language. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1585), 4–9. <https://doi.org/10.1098/rstb.2011.0295>
- Steinhauer, K., & Drury, J. E. (2012). On the early left-anterior negativity (ELAN) in syntax studies. *Brain and*

- Language*, 120, 135–162. <https://doi.org/10.1016/j.bandl.2011.07.001>
- Stoll, H., de Wit, M. M., Middleton, E. L., & Buxbaum, L. J. (2020). Treating limb apraxia via action semantics: a preliminary study. *Neuropsychological Rehabilitation*, 31(7), 1–18. <https://doi.org/10.1080/09602011.2020.1762672>
- Stout, D., & Chaminade, T. (2012). Stone tools, language and the brain in human evolution. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 367(1585), 75–87. <https://doi.org/10.1098/rstb.2011.0099>
- Stout, D., Chaminade, T., Apel, J., Shafti, A., & Faisal, & A. A. (2021). The measurement, evolution, and neural representation of action grammars of human behavior. *Scientific Reports*, 11(13720), 1–13. <https://doi.org/10.1038/s41598-021-92992-5>
- Stromswold, K., Caplan, D., Alpert, N., Rauch, S., Biel, A., Coppola, M., Hanna, J., Jaros, B., Torrealano, L., Makris, N., Grimshaw, J., Marantz, A., Marsella, S., Mehler, J., Pinker, S., Schmidt, C., Snyder, W., & Young, A. (1996). Localization of Syntactic Comprehension by Positron Emission Tomography. *Brain and Lan*, 52(3), 452–473. <https://doi.org/10.1006/brln.1996.0024>
- Tagarelli, K. M., Shattuck, K. F., Turkeltaub, P. E., & Ullman, M. T. (2019). Language learning in the adult brain: A neuroanatomical meta-analysis of lexical and grammatical learning. *NeuroImage*, 193, 178–200. <https://doi.org/10.1016/j.neuroimage.2019.02.061>
- Teichmann, M., Dupoux, E., Kouider, S., Brugière, P., Boissé, M.-F., Baudic, S., Cesaro, P., Peschanski, M., Bachoud-Lévi, A.-C., Bachoud-Lévi, A.-C., & Avenir, E. (2005). The role of the striatum in rule application: the model of Huntington’s disease at early stage. *Brain*, 128, 1155–1167. <https://doi.org/10.1093/brain/awh472>
- Teichmann, M., Gaura, R., De, O., Supiot, R., Delliaux, M., Verny, C., Renou, P., Remy, P., & Bachoud-Le, A.-C. (2008). Language processing within the striatum: evidence from a PET correlation study in Huntington’s disease. *Brain*, 131, 1046–1056. <https://doi.org/10.1093/brain/awn036>
- Teichmann, M., Rosso, C., Martini, J. B., Bloch, I., Brugières, P., Duffau, H., Lehericy, S., & Bachoud-Lévi, A. C. (2015). A cortical-subcortical syntax pathway linking Broca’s area and the striatum. *Human Brain Mapping*, 36(6), 2270–2283. <https://doi.org/10.1002/hbm.22769>
- Tettamanti, M., & Moro, A. (2012). Can syntax appear in a mirror (system)? *Cortex*, 48, 923–935. <https://doi.org/10.1016/j.cortex.2011.05.020>
- Tettamanti, M., & Weniger, D. (2006). Broca’s area: a supramodal hierarchical processor? *Cortex*, 42(4), 491–494. [https://doi.org/10.1016/s0010-9452\(08\)70384-8](https://doi.org/10.1016/s0010-9452(08)70384-8)
- Thach, W. T., Goodkin, H. P., & Keating, J. G. (1992). The cerebellum and the adaptive coordination of movement. *Annual Review of Neuroscience*, 15, 403–442. <https://doi.org/10.1146/annurev.ne.15.030192.002155>
- Tremblay, P., & Dick, A. S. (2016). Broca and Wernicke are dead, or moving past the classic model of language neurobiology. *Brain and Language*, 162, 60–71. <https://doi.org/10.1016/j.bandl.2016.08.004>

- Tremblay, P., Sato, M., & Small, S. L. (2012). TMS-induced modulation of action sentence priming in the ventral premotor cortex. *Neuropsychologia*, 50(2), 319–326. <https://doi.org/10.1016/j.neuropsychologia.2011.12.002>
- Trumpp, N. M., Traub, F., & Kiefer, M. (2013). Masked Priming of Conceptual Features Reveals Differential Brain Activation during Unconscious Access to Conceptual Action and Sound Information. *PLoS ONE*, 8(5). <https://doi.org/10.1371/journal.pone.0065910>
- Trumpp, N. M., Traub, F., Pulvermüller, F., & Kiefer, M. (2013). Unconscious Automatic Brain Activation of Acoustic and Action-related Conceptual Features during Masked Repetition Priming Article. *Journal of Cognitive Neuroscience*, 26(2), 352–364. <https://doi.org/10.1162/jocn>
- Turkeltaub, P. E., & Coslett, B. H. (2010). Localization of sublexical speech perception components. *Brain and Language*, 114, 1–15. <https://doi.org/10.1016/j.bandl.2010.03.008>
- Ujhelyi, M. (1996). Is there any intermediate stage between animal communication and language? *Journal of Theoretical Biology*, 180(1), 71–76. <https://doi.org/10.1006/jtbi.1996.0079>
- Ullman, M. T. (2001). A neurocognitive perspective on language: The declarative/procedural model. *Nature Reviews Neuroscience*, 2(10), 717–726. <https://doi.org/10.1038/35094573>
- Ullman, M. T. (2004). Contributions of memory circuits to language: The declarative/procedural model. *Cognition*, 92(1–2), 231–270. <https://doi.org/10.1016/j.cognition.2003.10.008>
- Ullman, M. T. (2006). Is Broca's area part of a basal ganglia thalamocortical circuit? *Cortex*, 42(4), 480–485. [https://doi.org/10.1016/S0010-9452\(08\)70382-4](https://doi.org/10.1016/S0010-9452(08)70382-4)
- Ulrich, M., Hoenig, K., Grön, G., & Kiefer, M. (2013). Brain Activation during Masked and Unmasked Semantic Priming: Commonalities and Differences. *Journal of Cognitive Neuroscience*, 25(12), 2216–2229. <https://doi.org/10.1162/jocn>
- Umiltà, 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. *Proceedings of the National Academy of Sciences of the United States of America*, 105(6), 2209–2213. <https://doi.org/10.1073/pnas.0705985105>
- Ungerleider, L. G., & Mishkin, M. (1982). Two Cortical Visual Systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of Visual Behavior* (pp. 549–586). The MIT Press.
- Uomini, N. T., & Meyer, G. F. (2013). Shared Brain Lateralization Patterns in Language and Acheulean Stone Tool Production: A Functional Transcranial Doppler Ultrasound Study. *PLoS ONE*, 8(8), 1–9. <https://doi.org/10.1371/journal.pone.0072693>
- Valyear, K. F., Fitzpatrick, A. M., & McManus, E. F. (2017). The Neuroscience of Human Tool Use. In J. Kaas (Ed.), *Evolution of Nervous Systems: Second Edition* (Vol. 4, pp. 341–353). Elsevier. <https://doi.org/10.1016/B978-0-12-804042-3.00112-3>

- van Paridon, J., Ostarek, M., Arunkumar, M., & Huettig, F. (2021). Does Neuronal Recycling Result in Destructive Competition? The Influence of Learning to Read on the Recognition of Faces. *Psychological Science*, 32(3), 459–465. <https://doi.org/10.1177/0956797620971652>
- Varela, F. J., Thompson, E., & Rosch, E. (1991). *The embodied mind: Cognitive science and human experience*. MIT Press.
- Vicari, G., & Adenzato, M. (2014). Is recursion language-specific? Evidence of recursive mechanisms in the structure of intentional action. *Consciousness and Cognition*, 26(1), 169–188. <https://doi.org/10.1016/j.concog.2014.03.010>
- Vigneau, M., Beaucousin, V., Herve, P. Y., Duffau, H., Crivello, F., Mazoyer, B., & Tzourio-mazoyer, N. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage*, 30, 1414–1432. <https://doi.org/10.1016/j.neuroimage.2005.11.002>
- Vigneau, M., Beaucousin, V., Hervé, P. Y., Jobard, G., Petit, L., Crivello, F., Mellet, E., Zago, L., Mazoyer, B., & Tzourio-Mazoyer, N. (2011). What is right-hemisphere contribution to phonological, lexico-semantic, and sentence processing? Insights from a meta-analysis. *NeuroImage*, 54(1), 577–593. <https://doi.org/10.1016/j.neuroimage.2010.07.036>
- Wahl, M., Marzinzik, F., Friederici, A. D., Hahne, A., Kupsch, A., Schneider, G. H., Saddy, D., Curio, G., & Klostermann, F. (2008). The Human Thalamus Processes Syntactic and Semantic Language Violations. *Neuron*, 59(5), 695–707. <https://doi.org/10.1016/j.neuron.2008.07.011>
- Walenski, M., Europa, E., Caplan, D., & Thompson, C. K. (2019). Neural networks for sentence comprehension and production: An ALE-based meta-analysis of neuroimaging studies. *Human Brain Mapping*, 40(8), 2275–2304. <https://doi.org/10.1002/hbm.24523>
- Walker, C. B. F. (1987). *Reading the past cuneiform*. University of California Press.
- Walsh, V. (2003). A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, 7(11), 483–488. <https://doi.org/10.1016/j.tics.2003.09.002>
- Weisberg, J., Van Turenout, M., & Martin, A. (2007). A Neural System for Learning about Object Function. *Cerebral Cortex*, 17, 513--521. <https://doi.org/10.1093/cercor/bhj176>
- Wenger, E., Brozzoli, C., Lindenberger, U., & Lövdén, M. (2017). Expansion and Renormalization of Human Brain Structure During Skill Acquisition. *Trends in Cognitive Sciences*, 21(12), 930–939. <https://doi.org/10.1016/j.tics.2017.09.008>
- Wenger, E., Kühn, S., Verrel, J., Mårtensson, J., Bodammer, N. C., Lindenberger, U., & Lövdén, M. (2016). Repeated Structural Imaging Reveals Nonlinear Progression of Experience-Dependent Volume Changes in Human Motor Cortex. *Cerebral Cortex*, 27(5), 1–15. <https://doi.org/10.1093/cercor/bhw141>
- Wernicke, C. (1874). *Der Aphasische Symptomencomplex: Eine Psychologische Studie Auf Anatomischer Basis*. Kessinger Publishing.

- Wernicke, C. (1881). *Lehrbuch der geirnkrankeiten fur aerzte und studirende*. Kassel Fischer.
- Wernicke, C. (1969). The Symptom Complex of Aphasia. In R. S. Cohen & M. W. Wartofsky (Eds.), *Proceedings of the Boston Colloquium for the Philosophy of Science 1966/1968* (pp. 34–97). Springer. https://doi.org/10.1007/978-94-010-3378-7_2
- Wilson, S. M., Saygin, A. P., Sereno, M. I., & Iacoboni, M. (2004). Listening to speech activates motor areas involved in speech production. *Nature Neuroscience*, 7(7), 701–702. <https://doi.org/10.1038/nn1263>
- Wolpert, D. M., Diedrichsen, J., & Flanagan, J. R. (2011). Principles of sensorimotor learning. *Nature Reviews Neuroscience*, 12(12), 1–13. <https://doi.org/10.1038/nrn3112>
- Wymbs, N. F., Bassett, D. S., Mucha, P. J., Porter, M. A., & Grafton, S. T. (2012). Article Differential Recruitment of the Sensorimotor Putamen and Frontoparietal Cortex during Motor Chunking in Humans. *Neuron*, 74(5), 936–946. <https://doi.org/10.1016/j.neuron.2012.03.038>
- Xu, T., Yu, X., Perlik, A. J., Tobin, W. F., Zweig, J. A., Tennant, K., Jones, T., & Zuo, Y. (2009). Rapid formation and selective stabilization of synapses for enduring motor memories. *Nature*, 462(7275), 915–919. <https://doi.org/10.1038/nature08389>
- Yamazaki, Y., Hikishima, K., Saiki, M., Inada, M., Sasaki, E., Lemon, R. N., Price, C. J., Okano, H., & Iriki, A. (2016). Neural changes in the primate brain correlated with the evolution of complex motor skills. *Scientific Reports*, 6(31084), 1–10. <https://doi.org/10.1038/srep31084>
- Zaccarella, E., & Friederici, A. D. (2017). The neurobiological nature of syntactic hierarchies. *Neuroscience and Biobehavioral Reviews*, 81, 205–212. <https://doi.org/10.1016/j.neubiorev.2016.07.038>
- Zatorre, R. J., Fields, R. D., & Johansen-Berg, H. (2012). Plasticity in gray and white: neuroimaging changes in brain structure during learning. *Nature Neuroscience*, 15(4), 528–536. <https://doi.org/10.1038/nn.3045>
- Zeki, S. (1991). Cerebral akinetopsia (visual motion blindness): A review. *Brain*, 114(2), 811–824. <https://doi.org/10.1093/brain/114.2.811>
- Zihl, J., Von Cramon, D., Mai, N., & Schmid, C. H. (1991). Disturbance of movement vision after bilateral posterior brain damage: Further evidence and follow up observations. *Brain*, 114(5), 2235–2252. <https://doi.org/10.1093/brain/114.5.2235>