



Review

Manual praxis in stone tool manufacture: Implications for language evolution



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ABSTRACT

Alternative functions of the left-hemisphere dominant Broca's region have induced hypotheses regarding the evolutionary parallels between manual praxis and language in humans. Many recent studies on Broca's area reveal several assumptions about the cognitive mechanisms that underlie both functions, including: (1) an accurate, finely controlled body schema, (2) increasing syntactical abilities, particularly for goal-oriented actions, and (3) bilaterality and fronto-parietal connectivity. Although these characteristics are supported by experimental paradigms, many researchers have failed to acknowledge a major line of evidence for the evolutionary development of these traits: stone tools. The neuroscience of stone tool manufacture is a viable proxy for understanding evolutionary aspects of manual praxis and language, and may provide key information for evaluating competing hypotheses on the co-evolution of these cognitive domains in our species.

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1. Introduction

In the past 20 years, classical concepts of Broca's area for the motor function of language have been complicated by mounting evidence of other cognitive functions in the area (see [Arbib,](#)

[2006; Binkofski & Buccino, 2004; Schubotz & Fiebach, 2006](#)). Through experimental paradigms, including various lesion-based studies and several neuroimaging studies, researchers have found evidence of a human mirror neuron system, which likely includes classical Broca's area and adjacent tissues in the pre-frontal and motor cortices, as well as other parietal and temporal areas. Linked to the function of neurons in these areas is the human action-recognition system, which has been proposed as the

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perceptory-motor base of human language (Buccino, Binkofski, & Riggio, 2004; Molenberghs, Cunnington, & Mattingley, 2009, 2012; Rizzolatti & Arbib, 1998). Many aspects of action recognition—and action itself—in Broca's area are analogous to how human language functions, with the strongest parallels coming from manual praxis, or finely attuned awareness and function of the hands. Empirical evidence of parallels between manual praxis and language have led to multiple hypotheses regarding the possible co-evolution of the two in humans (Arbib, 2011; Corballis, 2003, 2007, 2010). Still, we have much more to learn about Broca's area and its functions, especially if we are to understand the area's evolutionary past.

1.1. Broca's area: location, cytoarchitecture, and connectivity

One of the current issues in studying action in Broca's area is the definition of the area itself, which is still heavily based on the original cytoarchitectonic Brodmann areas (BA) 44 and 45, or the *pars opercularis* and *pars triangularis*, in the inferior frontal gyrus (for a review, see Amunts & Zilles, 2006). Within the context of alternative functions in Broca's area, it is necessary to address some recent motivations for reassessing the validity of the classical delineation of areas 44 and 45 as Broca's area. In particular, many of these studies derive from the relationship between cortical areas in humans and non-human primates, such as macaques, and particularly how they relate to the mirror neuron system (see Section 1.2). For example, many studies have shown that areas in the macaque lateral prefrontal cortex, specifically area F5 (the proposed homolog to Broca's area), have functions similar to pre-central areas in humans, ranging from fine sensorimotor control to “higher order control processes that regulate the selection among multiple competing responses and stimuli based on conditional operations” (Petrides, 2005:781). In general, the macaque homolog to Broca's area, as well as its cortical and subcortical connections, has suggested a long evolutionary history for processing multimodal input in primates, which includes visual and auditory stimuli, among others, but has been extended in our species to include spoken language (Petrides & Pandya, 2001). Despite these similarities, pre-frontal areas in the human brain have undergone extensive modification throughout our species' evolution, leading to vast behavioral differences in both praxis and language. As evidenced by the following studies, Broca's area is uniquely developed in *Homo sapiens*, and understanding this development is essential to assessing human behavioral and cognitive singularity.

In 1999 K Amunts and others updated the cytoarchitectonic map of Broca's area and its right hemisphere homolog in humans (based on 34 brains, age range 3.5 months to 85 years), which serves as probabilistic comparative material for many locational studies today (Amunts et al., 1999). Another important finding of this study was a re-assessment of the well-established left–right asymmetry, which was significant for area 45, but not significant in BA 44 (Amunts et al., 1999). Broca's area is classically associated heavily with the left hemisphere, leading to the left-lateralized dominance of language in most humans, but its right hemisphere homolog is gaining more recognition in studies on language and, interestingly, manual praxis (see Section 2.3; Keller, Crow, Foundas, Amunts, & Roberts, 2009). Additionally, evidence of BA 44 activation is more common in action-recognition studies than BA 45, so the area's lack of asymmetry may reflect a lesser degree of linguistic specialization, although this hypothesis has not been directly tested.

It is of paramount importance to interpret experimental paradigms within anatomical contexts, but outside its probabilistic location, the functional parcellation of Broca's area, as well as its distinctions from – and connections to – other parts of the brain, is extremely complex (see Keller et al., 2009). Novel approaches in brain mapping support experimental findings with details on

how Broca's area relates to the motor system and other cortical areas in humans. In 2010, Amunts and others reassessed Broca's area and surrounding tissues with a multiple-receptor mapping technique (reliant upon cytoarchitecture, connectivity, and neurotransmitter levels). They found significant differences in neurotransmitter levels between the hemispheres, most pronounced in BA 44, which is contradictory to the previously mentioned bilateral symmetry of the area, and suggested that functional lateralization is not always dependent upon gross anatomical asymmetries. In this study, BA 45 was further split into anterior and posterior parts, and BA 44 into dorsal and ventral parts, which correspond nicely to other intra-areal distinctions (both in connectivity and function) (Amunts et al., 2010). They also found evidence supporting the division of surrounding areas including the frontal orbitalis (areas 46 and 47) and BA 6 (classically the pre-motor cortex, or PMC, and the supplementary motor area, or SMA), and noticed a gradient-like transition between areas 44 and 45 and these areas, with high anatomical similarities to classical Broca's at its borders with each area, and more interareal distinctions present at each area's periphery (Amunts et al., 2010).

Subcortical connections of BA 44 and 45 are also relevant to studies on action function in the area. As Amunts et al. showed in 2010, Broca's area has a unique relationship to pre-motor and supplementary motor cortices, likely supporting its function in manual and orofacial motor tasks. These links, however, would not be possible without subcortical connections to the basal ganglia, thalamus, and corticospinal tract. In a diffusion-weighted imaging (DWI) study, researchers were able to show that the anterior (semantics-associated) segment of Broca's area connects differently to subcortical regions than the more posterior (phonological/syntactical) segment, although *pars triangularis* and *pars opercularis* tracts overlapped significantly (Ford et al., 2013). They state that this cortico-thalamo-cortical circuitry likely subserves a computational grammar which is useful in language and, as argued here, extends to manual praxis as well (Ford et al., 2013:6). With regard to the corticospinal tract (CST), less work has been done, but a DTI study of a hemorrhagic patient with global aphasia and paralysis confirmed the presence of an intact tract from Broca's area to the CST, which was damaged severely in the left hemisphere (Jang, 2009). These studies highlight the basal motor functions of Broca's area, which are often overshadowed by its higher cognitive functions, but are extremely important in linking praxis and language, which both require complex motoric control (see Section 2.1).

Outside of prefrontal cortex, and particularly relevant to language, connectivity between Broca's area and posterior areas (e.g. Wernicke's area in the superior temporal gyrus), has also been divided into several neural tracts (see Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006). One DTI study highlights a classical, well-known pathway which is strongly left lateralized, the arcuate fascicle (Glasser & Rilling, 2008), which has been further linked to two additional pathways in a DWI study, where BA 44 tracts dorsally to perisylvian parietal regions and BA 45 tracts more medially to other pre-central areas (Anwander, Tittgemeyer, von Cramon, Friederici, & Knösche, 2007). A third combined fMRI-DTI study also found anterior, superior, and inferior fascicles that are handedness-independent in terms of laterality, supporting a more integrated “functional connectome” for the area (Lemaire et al., 2013:435). While more work is needed on the cortical and subcortical nature of this fronto-posterior connectome, empirical evidence suggests that these features are inherent to many human functions, including manual praxis and language.

Additionally, there has been a push to understand the functional differences in Broca's area within the context of cortico-cortical connectivity, and recent *in vivo* tractographic studies have suggested that BA 44 and 45 link to BA 9, 8 and 6 (SMA and

pre-SMA), also in an anterior-to-posterior gradient (Ford, McGregor, Case, Crosson, & White, 2010:1230). The laterality of Broca's area, especially as it relates to handedness, is a large topic within neuroscience, as will be discussed later, but increased studies on pre-central cortico-cortical connections suggest that some areas can be separated by hemisphere, while others cannot (Anwander et al., 2007). In a DWI study of Broca's connectivity to M1, SMA, and pre-SMA, anterior and posterior polar connections (from Broca's to pre-SMA and M1) differed between hemispheres, while the middle segment (from Broca's to SMA) was bilaterally indistinguishable (Anwander et al., 2007). In this study, intra-areal distinctions were made for both BA 44 and 45, similar to cytoarchitectonic and other data, leading to an overall consensus that the opercular cortex (BA 44/47) likely supports a more ancestral, primitive grammar, while BA 45 has specialized more for the complex grammars necessary for human language (Anwander et al., 2007).

Taking into account the formation of neural networks and Hebbian learning processes in the brain, it is likely that defining Broca's area—and areas in the brain in general—is far more complex than previously thought (Ross, 2010). In a Hebbian-learning based computational model, researchers formed a classical left perisylvian language network, which included left hemisphere Brodmann areas 41, 42, 22 (post-central), 44, 45, 4, and 6 (pre-central), yielding several specific but overlapping distributed circuits for speech sounds (Garagnani, Wennekers, & Pulvermüller, 2008; Pulvermüller & Fadiga, 2010). What is most relevant about this model is that they assessed how multimodal deficits in these networks can stem from localized lesions centered in isolated areas, including isolated pre-motor (BA 4/6) and pre-frontal (BA 44/45) areas, respectively (Garagnani et al., 2008; Pulvermüller & Fadiga, 2010). This suggests that while there are interareal distinctions, localized changes in the brain can have rather widespread effects via interareal connections; linking this to neurotransmission and connectivity data discussed above suggests, overall, that “localization of functions in the brain is a clinically robust but very dynamic, four-dimensional phenomenon that is driven by large-scale neural networks learning” how to efficiently process complex behavioral tasks (Ross, 2010:233).

A dynamic, gradient-based approach for studying the brain is becoming increasingly important as we raise our general knowledge, but it is particularly important for studies on action in Broca's area, where most neuroimaging studies show highest density of neural activation in BA 44 and 45. However, reliable activation in surrounding areas is present across many paradigms, that change through learning (see Caspers, Zilles, Laird, & Eickhoff, 2010; Kelly & Garavan, 2005; Lewis, 2006; Molenberghs et al., 2009, 2012; Vogt et al., 2007). Informed by these concepts, this paper will discuss the parallels between manual praxis and language within a larger context of an extended *Broca's network* including classical BA 44 and 45, as well as BA 4, 6 and 47 and their right hemisphere homologs, instead of solely focusing on Broca's area *sensu stricto* (see Ford et al., 2010; Lemaire et al., 2013).

1.2. Studying action in Broca's: the mirror neuron system

Increases in technology have allowed us to learn much about our brains, but the limitations of neuroimaging technologies must be constantly addressed. For example, fMRI studies have become increasingly popular in recent decades, due to their non-invasive nature and spatio-temporal efficiency, but fMRI scanning is very difficult to study in action-based contexts. Due to movement artifacts and other practical considerations, studying action directly in the brain must be limited to short sequences that require little to no head or body movement to minimize imaging corrections. This means that in most studies, it is *action observation* that provides evidence of non-linguistic, motor-based functions in Broca's and

other areas. Although many experimental paradigms involve small-scale movement sequences in subjects, most of the relevant literature on action in relation to Broca's area inherently adopts a dependency on what we believe to be the human mirror neuron system (MNS), because most tasks are based on observation.

In their seminal 1998 study, G. Rizzolatti and M. Arbib discuss single motor neurons in the rhesus macaque neocortex that fire when both performing *and observing* a range of tasks involving the hands, face, and feet. The two propose that this neuronal “congruence between observed and executed actions” (Rizzolatti & Arbib, 1998:188) forms the basis of mimetic capability (Rizzolatti & Arbib, 1998:192) in primates, forming a direct link between action perception and motor-based performance representations in the brain; obviously, this is highly adaptive for social interactions, learning, and other fundamental primate characteristics. One interesting aspect of this study is the *specificity* with which mirror neurons fire—for example, one for index finger and thumb “fine” grasping, another for clockwise rotation of an object, and yet another for counterclockwise rotation. Other key aspects of macaque mirror neurons are that *manual grasping tasks* showed highly specific activation in temporal, parietal, and frontal regions, specifically including area F5, the macaque homolog to Broca's area (Petrides, 2005; Petrides & Pandya, 2001; Rizzolatti & Arbib, 1998). These characteristics led to decades of research concerned with finding a human mirror neuron system (MNS) and understanding its role in human cognition (see Bookheimer, 2002; Cappa & Pulvermüller, 2012; Corballis, 2003, 2007, 2010; Grodzinski & Amunts, 2006; Maeda, Mazziotta, & Iacoboni, 2002; Willems & Hagoort, 2007).

Evidence of the MNS in humans comes from several studies based in transcranial magnetic stimulation (TMS), electroencephalography (EEG), magnetoencephalography (MEG), behavioral (neuropsychological), PET, and fMRI technologies (see Binkofski & Buccino, 2006 for a review), with the main goals of comparing data from macaque MNS studies to those in humans. For example, the mirror neuron system was discovered in macaques, a genus that is evolutionarily separated from modern *H. sapiens* by at least 30 million years, suggesting that action-recognition is a relatively archaic evolutionary adaptation in primates. This presents a difficult contrast to the relatively recent nature and perhaps uniqueness of human language and technology, and begs the question: how reliant are these cognitive domains on action-recognition? While the presence alone of a human MNS is insufficient evidence for linking praxis and language to Broca's area in our species, specific research on the MNS as it relates to the two has proven that action and language are inextricably linked in the brain, with BA 44/45, as well as other areas implicated in the MNS, as the primary neural substrates.

It is likely true that the human MNS is as highly specific as the macaque system, although invasive techniques prevent clinical confirmation of this phenomenon. Still, many researchers studying human action-recognition believe that Broca's area has cognitive functions outside of language, and more specifically that BA 44 is likely a central node in the mirror neuron system in the frontal lobe, and is homologous to macaque area F5, where mirror neurons were originally discovered (Arbib, 2011; Binkofski et al., 2000; Fadiga & Craighero, 2000, 2003; Iriti, 2006; Johnson-Frey et al., 2003; Keysers & Gazzola, 2010; Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Nishitani, Amunts, & Hari, 2005; Rizzolatti, Fogassi, & Gallese, 2002). Work on mirror neurons is an important part of research on the action-recognition system in humans and other primates, and has highlighted some very unique links between action observation, action output, and interestingly—object manipulation—in Broca's and other cortical areas (Fadiga & Craighero, 2000, 2003; Fadiga, Craighero, & Olivier, 2005; Frey, 2008; Hubbard, Wilson, Callan, & Dapretto, 2009; Johnson-Frey, 2003; Villarreal et al., 2008).

Much like in the macaque, researchers have found evidence of a somatotopic organization of observation-based neural activation in the human motor system, with orofacial observation activating orofacial motor systems, manual action observation activating manual motor areas, and action-observation of the feet activating lower-limb motor areas. This characteristic has led to the claim that, via proprioceptive feedback within the MNS, “a ‘personal’ knowledge of the action [is] observed, in the sense that it is mapped on the observer’s motor repertoire and therefore the observer has a direct, personal experience [of observed actions] in motor terms” (Buccino et al., 2004:374; Caspers et al., 2010; Maravita & Iriki, 2004; Vogt et al., 2007). This personal motor representation of others’ actions is exceptionally strong for manual and linguistic stimuli, and there is even evidence that *solely upon hearing action-related spoken words*, such as “lick, pick, and kick,” mirror neurons in the motor cortex (including areas 44, 45, 6, and others) activate in a somatotopic way (see Caspers et al., 2010; Corballis, 2010; Kilner et al., 2009; Tettamanti et al., 2005).

All together, these data suggest that an action-recognition system, likely based on the function of mirror neurons, exists in humans and other primates, with particular evidence that the human MNS has expanded its sensitivity to unique modalities, specifically language. According to Rizzolatti and Arbib, “human language...evolved from a basic mechanism that was not originally related to communication: the capacity to recognize actions” (Rizzolatti & Arbib, 1998:193). This paper will discuss relevant research paradigms that support a link between action and language in Broca’s area, highlight three main parallels between a specific form of action—manual praxis—and language, and suggest further avenues of research if we are to elucidate the evolutionary relationship between these cognitive functions.

2. Reworking Broca’s: neural mechanisms underlying manual praxis and language

At least 139 studies, including clinical research, virtual lesion studies (reversible inactivation through TMS), and neuroimaging studies (based on both PET and fMRI technologies), have been conducted linking action-recognition to language in Broca’s area and other neural substrates in the past decades (Bookheimer, 2002; Caspers et al., 2010; Lewis, 2006; Molenberghs et al., 2012). While it is outside the scope of this paper to delve into each in detail, I will review three conclusions or assumptions underlying these studies, which many believe form a definitive cognitive link between manual praxis and language.

One characteristic of interest is the development and extension of the primate body schema, which in humans includes *incredibly* fine control of both manual systems, or the fingers and hands, and orofacial systems, or facial musculature and the gustatorial apparatus. A second is a higher capacity for understanding and using syntax, including the classical concept of linguistic syntax, but also linked to *syntax of action*, particularly for goal-directed/oriented behavior. A third parallel between manual praxis and language is less understood, and includes other evidence like bilaterality and connectivity of neural substrates, often through research specifically on Broca’s area, but based more on widely distributed neural networks that have yet to be fully studied. Important considerations of the following studies must be listed, often related to the research procedures chosen and their implicit weaknesses. As mentioned before, these considerations derive from universal experimental design limitations currently present in the neurosciences, and thus cannot often be addressed; however, some methodologies are stronger than others, especially with regards to an evolutionary scope.

There are many studies on language motor function in Broca’s area, many on manual motor function in Broca’s area, and many on the links between the two. Particularly relevant to this review are studies that compare two types of manual praxis to language: “intransitive action” involves manual tasks where no object manipulation is present (this includes all forms of communicative gesture as well as random hand movements, conscious or unconscious), while “transitive action” involves object manipulation (including simple examples like touching or grasping an object, as well as complex, goal-oriented procedures, often involving tool use). Intransitive and transitive actions have regularly been contrasted with the intent of understanding how communicative gesture is processed in the brain (Knapp & Corina, 2010; Króliczak, Piper, & Frey, 2011; Pazzaglia, Smania, Corato, & Aglioti, 2008; Willems & Hagoort, 2007), but some paradigms contrast the two in order to illustrate the importance of *transitive* (vs. intransitive) activation in Broca’s area, specifically within the context of human evolution (Enticott, Kennedy, Bradshaw, Rinehart, & Fitzgerald, 2010; Lewis, 2006).

Another matter to consider is the traditional use of right-hand exclusive paradigms, which include using only right-hand dominant subjects for research, as well as right-hand imagery for experimental stimuli. This is a common practice throughout neuroscience in general, but is particularly common in language-related research as it allows for more controlled experimentation (consider left-handers’ variable hemispheric dominance for language tasks vs. right-handers’ almost-universal left hemisphere dominance) (see Willems, Van der Haegen, Fisher, & Francks, 2014). Handedness itself is a complex issue, as self-reporting through classic tests often used in neuroscience (like the Edinburgh Handedness Inventory and The Waterloo Handedness Questionnaire), are too simplistic and are often inaccurate (see Annett, 1998; Guillard, 1987; McGrew & Marchant, 1996). Some studies do exist on left-hand imagery (and less often use left-hand dominant subjects), but the overall prevalence of right-hand paradigms still reflects a weakness in the relevant literature on action and language in Broca’s and other areas. This practice may bias concepts of laterality in neural activation, but more importantly, it ignores a unique aspect of manual praxis in humans: differential bimanual coordination (see Section 3). These issues in no way refute the findings of previous studies, but addressing them may provide a basis for further elucidating parallels between manual praxis and language in the brain, and could particularly clarify the bilaterality of network function and hemisphere activation, which is important if we wish to directly link the two cognitive functions in evolutionary time.

2.1. The extended body schema

One aspect of recent studies on the role of Broca’s area in manual praxis and language involves an *embodied* approach to cognition, where perception and action are intricately linked in our brains, and we are constantly aware of our body schemas as we go through our days. This theoretical foundation is important for studies on action-recognition via the MNS, because it posits an isomorphism between observed actions and our own motor representations of those actions (see Arbib, 2011; Caspers et al., 2010; Corballis, 2003, 2007, 2010; Fazio et al., 2009; Kemmerer & Gonzalez-Castillo, 2010; Kemmerer, Rudrauf, Manzel, & Tranel, 2012; Kilner et al., 2009; Vaesen, 2012). Thus, studies showing activation in Broca’s for task-observation reflect our own motor representations of them and often involve manual tasks. Considering the specificity of the MNS in macaques and the dedication of human neocortex to the sensorimotor control of our hands and faces, it is likely that we have an extended neural system attuned

to bilateral orofacial and manual functions, specifically involving bilateral BA 44 and 45.

Evidence for embodied action-recognition for both manual praxis and language in Broca's area comes from several lesion-based and fMRI studies. As stated earlier, I will particularly focus on evidence of highly attuned awareness to manual systems engaged in transitive action, or manual motor control for object manipulation. One important theoretical consideration for transitive action and the primate body schema is the concept of plasticity, whereby in the present context humans can functionally extend their inherent body structure by manipulating objects, or tools, with their hands (Iriki, 2005). An extremely special aspect of this body plasticity is that it is not fixed, i.e. we can pick up an object when it is useful and discard it when it is not, which requires perceptual flexibility. Many primates exhibit body schema plasticity, as do other animals, but plasticity can be particularly paralleled to the open nature of human language (Iriki, 2005, 2006; Maravita & Iriki, 2004). There is ample evidence of fine motor circuitry required for speech specifically based in Broca's and other pre-central areas,¹ but much fewer studies focus on how human embodiment extends its specificity to manual systems. Despite this, the functional role of neural areas in transitive action observation, performance, and analysis implicates a similar extended neural schema for human hands, and the specific activation of Broca's area further associates language and praxis.

In a study of 38 aphasic patients with varying levels of apraxia (ranging from none, to partial, to severe), a photo-based functional association test was administered to see if Broca's aphasics lose semantic knowledge of tool and their uses, and if they become less capable of understanding novel tool's potential uses (Goldenberg & Spatt, 2009). Thirty-three of 38 patients performed below-normal on associating functions to tools, and over half the patients showed additional dissociation between common- and novel-tools and their functions. All of these characteristics showed significant correlation with lesion locations in Broca's area, with other, less significant correlations to temporal and parietal regions, suggesting that semantic knowledge of tools exists in BA 44/45 (Goldenberg & Spatt, 2009).

In a second lesion-based study of 226 subjects with widely distributed bilateral brain damage, researchers assessed deficits in six conceptual/lexical tasks: naming actions, word–picture matching for verbs, word attribute tasks, word comparison, picture attribute tasks, and picture comparison (Kemmerer et al., 2012). Sixty-one patients showed impairment in at least one of the six tasks, with picture comparison, naming actions, and word comparison being the most difficult. What is interesting about this study is that left-hemisphere IFG lesions were significantly correlated with deficits in all 6 tasks, and in comparison to stimuli related to fruits, vegetables, and animals, stimuli for *actions and tools* showed significantly higher impairments. There were also significant links between the right homolog of extended Broca's network (particularly BA 47 and anterior cingulate cortex) and task impairment for picture-related tasks. The authors conclude by stating that the left IFG associated to all six tasks, and deficits in each task were linked bilaterally to hand-related cortical areas (Kemmerer et al., 2012).

Several fMRI paradigms have provided evidence of extended praxis circuits in Broca's network. One study attempted to address the modality-dependence of activation in Broca's area, and specifically assess the concept of BA 44 encoding visually-based and auditory-based motor goals of the hands and mouth as implicated

by its role in the MNS (Baumgaertner, Buccino, Lange, Mcnamara, & Binkofski, 2007). Nineteen healthy right-handed subjects were scanned while watching videos of – or reading sentences about – transitive actions in comparison to non-biological control stimuli. They found that both visual and verbal stimuli showed similar activation patterns in the brain, most prominently in the *pars opercularis* (BA 44), but including other areas in extended Broca's network, and conclude by stating that the *pars opercularis* is likely involved in “the polymodal conceptual processing of goal-oriented hand actions” (Baumgaertner et al., 2007:887).

Another study tested whether action-recognition and language production had common neural substrates, and scanned 12 healthy right-handed subjects completing two tasks: one was silently generating verbs stimulated by a noun visual cue, and the other was observing pictures of manually active (e.g. drinking from a cup) vs. passive (e.g. sitting down) tasks. Additionally for manual stimuli, subjects were either directed to “rest” or “move” after stimulus, so this study actually reflects a simple motor sequence (right-hand grasp of a cup) within fMRI (Hamzei et al., 2003). Active stimuli showed increased IFG activation vs. passive stimuli, and overlapped strongly with verb generation activation, which according to the authors supports the hypothesized neural link between action recognition and verb formation in the IFG, particularly for manual actions (Hamzei et al., 2003).

Additional studies by S. Frey have corroborated the role of Broca's area in human transitive action, based on fMRI experiments. In one study on 18 right-handed subjects, activation was compared for observation of images of hands touching objects and tools vs. hands grasping objects and tools, in order to detect the specificity of manual praxis-related activation, and compare more general object manipulation (touch/non-tool), to a more specific goal-oriented action (grasp/tool) (Johnson-Frey et al., 2003). As mentioned before, goal orientation has been implicated as a main component of human tool use, and may have unique neural underpinnings in Broca's area, especially if it is a polymodal processing hub for praxis and language. Significant findings of this study are that, after the precentral gyrus, the *pars triangularis* (BA 45) and *pars opercularis* (BA 44) were the most commonly activated areas (73% and 65%, respectively) bilaterally. Differences in blood-oxygen-level dependent (BOLD) signals were detected between touching and grasping, but no differences were detected between object types. This study implies that much like the macaque MNS, manual action recognition in humans is highly specific, as manual grasps are processed differently than simple touching in the IFG, perhaps related to goal-orientation (Johnson-Frey et al., 2003).

In another fMRI study, Frey and colleagues contrasted tool-use planning to tool-use execution vs. controls (e.g. subjects heard “hammer” or “spoon” among others, and then heard “go” for pantomime execution or “nogo” for planning only, for all stimuli) (Johnson-Frey, Newman-Norlund, & Grafton, 2005). This study also reflects a direct comparison of action-observation to action itself in Broca's area, and while they used only right-handed subjects, they also had subjects complete non-dominant hand pantomimes. Significant bilateral activation was shown in Broca's network and its right hemisphere homolog (most strongly in BA 44/45) for all tool vs. control tasks (both “go” and “nogo”), as expected, and execution showed stronger BOLD signals vs. planning in the left hemisphere. However, when contrasting tool planning and tool execution in Broca's right homolog, significantly elevated activity was found for *planning*, specifically when the non-dominant hand was used (Johnson-Frey et al., 2005). This finding, as well as similar assessments of bilaterality for manual praxis in Broca's network, will be discussed in more detail in Section 2.3.

Overall, neuroscientific studies on transitive action in the human brain have aided us in understanding how the MNS manifests in our species, as well as how it relates to action recognition

¹ See research on motor production and processing of phonemes, such as Bailey and Hahn (2005), Cogan et al. (2014), Ghosh, Tourville, and Guenther (2008), Sato, Tremblay, and Gracco (2009), and Wang, Green, and Samal (2013), for evidence of controlled body schemas in language function in humans.

and, in some cases, action itself. We have confirmed a robust link between human language and manual praxis, specifically for goal-oriented, object-directed actions. This is supported by reliable and repeated activation in extended Broca's network across diverse paradigms. As mentioned before, at its base this includes manual and orofacial motor systems in BA 4, 6 and 47, but also in classical areas BA 44 and 45, which likely represent higher-level polymodal processing via unique prefrontal and post-central interareal connections. This suggests that functionally, Broca's network (as well as its temporal and parietal projections) has allowed for uniquely embodied human cognition, based in a finely controlled body schema and highly attuned action recognition that extend to both language and manual praxis.

2.2. Syntax and goal-oriented behavior

The next link between manual praxis and language comes from the concept of syntax, which—in linguistics—can refer to both the basic arrangement of words in a predictable nested hierarchy, as well as the compounded use of these hierarchies to communicate increasingly complex ideas (for example, consider the role of recursion in enabling time or locational displacement). This process is essential to human language and has been highly developed and expanded, presumably to facilitate the exchange of increasingly sophisticated information (Friederici, 2001; Kemmerer, 2012). The role of Broca's area in conjunction with the PFC for processing linguistic syntax is long-established (Grodzinsky, 2000). However, the most basic syntactic functions can also be extended to the deliberate ordering of *actions*, often to achieve an overarching goal. Many believe that this “goal-oriented” action is implicit in human manual praxis (consider making a cup of coffee with a coffee machine), and is also functionally linked to the human PFC, including Broca's area. The concept of syntax is extremely important in the human capacity to “select and coordinate actions or thoughts in relation to internal goals” because we must hierarchically organize various behaviors (i.e. pick certain possible actions over others, like adding coffee to the filter before turning on the machine) to efficiently achieve our expected outcomes (Koechlin & Jubault, 2006:963). Thus, goal-directed behavior, which is reliant upon basic syntax, is necessary in achieving many everyday manual tasks (Clerget, Windericx, Fadiga, & Olivier, 2009; Fazio et al., 2009; Koechlin & Jubault, 2006; Moro, 2013).

Much like we can consider a basic syntax of action for manual functions, we can extend the concept of goal orientation to language. In language, whether spoken or gestured, the speaker has to effectively communicate their intentions to a listener (or listeners), and often, those listeners must communicate back, at the very least to confirm their understanding. Syntax certainly became more refined in language over our species' evolution, but many researchers have argued that at its base, language is a highly derived extension of goal-oriented behaviors in which a syntax of action played a seminal role, using manual praxis as a prime basal candidate. Studies on syntax in Broca's area have led researchers to designate the area as a polymodal syntax hub in the brain, which functions for nesting elementary manual actions (a visual-dominant modality) as well as complex linguistic elements (an auditory-dominant modality) (Fazio et al., 2009:1987).

Direct evidence for fundamental hierarchical action processing in Broca's area relies upon experimental paradigms comparing non-biological sequences (where no human agent is present) to biologically-based actions of increasing syntactical complexity (where human agents complete tasks ranging from simple to complex). In neuroimaging studies of healthy subjects, neural activation is compared between simplistic operations and multi-step, more complex ones. Additionally, performance-based tests on clinical subjects with damage in BA 44 and 45 corroborate the role of

Broca's area in sequencing increasingly complex biologically-based actions in contrast to non-biological sequences, linking Broca's network to hierarchically organized action-recognition in an *embodied* manner.

In a virtual lesion study using transcranial magnetic stimulation, 13 right-handed subjects were asked to re-order still images taken from video clips of non-biological sequences (ex. a bicycle falling over) and both intransitive and transitive biological actions (ex. touching one's nose or opening a cupboard with a key, respectively) (Clerget et al., 2009). They contrasted TMS-impairment of left BA 44 in sequencing non-biological, intransitive, and transitive sequences, and found that virtual lesions only affected syntactic abilities for biological actions, meaning that it is particularly biological-action syntax that taxes area 44. Additionally, they found reaction times (RTs) differed significantly for transitive vs. intransitive actions, suggesting that object-related manual syntax is strongly correlated with activity in the *pars opercularis* (Clerget et al., 2009).

Other studies comparing non-biological sequence reconstruction to biological sequences have shown a similar trend in activation, and a combined behavioral-fMRI study with a similar experimental design on six aphasic patients *without apraxia* and six healthy controls showed that patients performed significantly worse in reconstructing tools, tool use, and manual actions (Fazio et al., 2009). Like the previous study, no significant difference was found between patients and controls for non-biological sequences, but significantly higher deficits were particularly attributed to *tool-related* tasks for patients. This study suggests that even in the absence of manual apraxia, the understanding of transitive manual praxis in those with Broca's area damage is impaired. The authors claim that this provides evidence that the syntactical properties of Broca's area may be evolutionarily linked to goal-directed action (Fazio et al., 2009:1986).

These studies strongly imply that manually-based syntax is processed in BA 44, and further provide evidence for cognitive links between praxis and language, but shed little light on the specificity and possible differentiation within Broca's area in response to action. Another fMRI study on increasingly complex syntactical operations compared how manual complexity of tasks corresponded to neural activation when observing those tasks. This study was an attempt to directly link action observation to first-person motor representations of action, and confirm Broca's area as part of the human MNS (Molnar-Szakacs, Kaplan, Greenfield, & Iacoboni, 2006). Additionally, reliant upon the specificity of the macaque mirror system, perhaps differential spatial patterns of activation could be found in Broca's area for *minute* differences between similar manual tasks. For this study, 12 healthy subjects were scanned watching videos of two transitive tasks: *seriated cup processing* reflected lower-level manual dexterity, while *stacking rings* reflected higher-level complexity; these designations were supported by a behavioral study of RTs in healthy subjects, showing that stacking rings was consistently harder to complete. Activation in the extended Broca's network (including BA 44, 45, 6 and 9) was found across all subjects for both tasks, but BOLD signal changes differed between stimuli, with stronger activation during observation of the more complex task, but overall showing little interareal distinction for similar manual tasks in comparison to syntax differentiation (Molnar-Szakacs et al., 2006). Interestingly, activation was strongly bilateral in all patients, which the authors state is compatible with other studies on bilaterality of the human MNS (Molnar-Szakacs et al., 2006).

Considering the wide distribution of activation for manual syntax in Broca's and adjacent areas, and Molnar-Szakacs's suggestion of differing BOLD signals for complexity, can BA 44 and 45 be differentiated in their *syntactical roles* for manual tasks? In an imagery-based combined cytoarchitectonic fMRI study of six healthy

subjects, manual motor imagery showed left-lateralized activation of many pre-motor areas, which was strongest in BA 44, but also included BA 45, 47, and 6, as well as their right-hemisphere homologs (Binkofski et al., 2000). The authors argue that BA 44 subserves recognition and execution of manual imagery, and that bilateral activation in Broca's area suggests that it is a node in a "large-scale network subserving action" (Binkofski et al., 2000:283).

As stated before, hierarchical sequencing forms a strong cognitive platform for parallelism between manual praxis and language in humans, but many discuss these syntax-based parallels particularly within the context of goal-orientated behavior. The previously mentioned paradigms all address the importance of goal-orientation for their experiments, as syntax is a necessary component of completing many of the stimulus tasks. Still, little has been done to specifically address how goal-orientation interacts with syntax in the brain, other than the repeated suggestion that dlPFC activation found in many of these studies reflects evidence of inhibitory or task-switch functional activation (Johnson-Frey et al., 2005; Stout, Toth, Schick, & Chaminade, 2008; Villarreal et al., 2008). Kemmerer approaches this subject, not within neuroscience, but from a linguistic perspective, by showing that we can see how goal-orientation specifically related to human biological action and manual praxis affects human language systems in terms of syntactic typology (Kemmerer, 2012). He argues that the strong prevalence of subject–object–verb (SOV) and subject–verb–object (SVO) word order across the globe—which encompass 89% of known languages—derives from the role of Broca's area in sequencing biological actions, particularly transitive ones. He further states that "from an evolutionary perspective, once BA 44 [and perhaps Broca's network in general] became adept at extracting the skeletal structure of goal-directed actions, it could then apply that ability to other cognitive domains" (Kemmerer, 2012:61), which is consistent with others' claims that language shared, and even co-opted, the more generalized action-recognition system in the brain over our evolution, particularly in the IFG and surrounding areas (see Caspers et al., 2010; Lewis, 2006; Molenberghs et al., 2012; Rizzolatti and Arbib, 1998).

To many, these aforementioned parallels between manual praxis and language in terms of both body schema and syntax, combined with the general concept of evolutionary parsimony, suggest a co-evolution of the two systems in humans. Despite this, the wide-spread locations of neural activation, especially when contrasted with the seemingly heightened role of BA 44 in comparison to other areas in Broca's network, show that we still have much to learn about how praxis networks specifically relate to language ones, and especially how these networks relate *within* each of these cognitive domains. While we are far from learning these details, addressing their importance pushes us to develop novel testing paradigms that will further elucidate Broca's alternative functions, particularly in an evolutionary sense.

2.3. Bilaterality and connectivity of Broca's area

One final parallel between manual praxis and language involves the bilaterality and connectivity of Broca's area, which is a colossal topic on its own within the literature. Ever since the work of Paul Broca on left-IFG lesions and "aphemia," we have considered language to be a left-hemisphere lateralized task, historically leading to the classification of the left hemisphere as the dominant one in most humans (Broca, 2011 (1865):230; Broca, 2006 (1861)). The leftward asymmetry of Broca's area is still confirmed by many studies, although there is now a plethora of evidence for right-hemispheric functions (in Broca's homolog and other areas) for language, including prosodic and affective evaluation of speech, especially when syntactic or semantic ambiguities are present. The now bilateral, although still left-hemisphere dominant neural

activation for language is paralleled in studies on manual praxis, more specifically for transitive action, which has massive evolutionary implications, including models on the evolution of handedness in our species (Corballis, 2003).

In several of the previously discussed neuroimaging studies, significant activation in Broca's right hemisphere homolog was found, potentially complicating concepts of a functional isomorphism between manual praxis and language in the brain (Binkofski et al., 2000; Johnson-Frey et al., 2003, 2005; Kilner et al., 2009; Maess, Koelsch, Gunter, & Friederici, 2001; Molnar-Szakacs et al., 2006; Villarreal et al., 2008; Vogt et al., 2007). Due to this, I believe there is a tendency to down-play right hemisphere activation in action-recognition studies in general. Despite this, many studies specifically on the laterality of activation in Broca's network and its right hemisphere homolog (and BA 44 and 45 alone) have been conducted in recent years. These studies often include subjects of either handedness, as well as right- and left-hand stimuli, but it is outside the scope of this paper to address handedness-effects on language and praxis in detail. Overall, much like work on the anatomical nature of Broca's area, results of laterality studies further complicate our interpretations of alternate functions in the area, and open further avenues of inquiry.

In order to frame right-hemisphere significance in manual praxis, especially within the context of parallelisms with language, it is important to address the role of Broca's right hemisphere homolog in language itself. As mentioned before, evidence of right-hemisphere participation in language often functionally relates to prosody and higher-level semantics, which are necessary, but perhaps complementary, functions to syntactical processing controlled by the left-hemisphere (Amunts, Schleicher, Ditterich, & Zilles, 2003; Friederici, 2001; Gelfand & Bookheimer, 2003; Hoyte, Kim, Brownell, & Wingfield, 2004; Hubbard et al., 2009; Nicholson, Baum, Cuddy, & Munhall, 2002; Ross & Monnot, 2008; Stout et al., 2008).

In an fMRI study on syntactic, semantic, and prosodic processing in the brain, Friederici (2001) tested activation differences between four linguistic stimuli in all right-handed subjects: normal sentence hearing, sentences with function words but no real content words (syntax), lists of content words with no functional words (semantics), and pseudoword lists with neither functional nor content words. For syntax based stimuli, the predicted left opercular (BA 44) activity was shown, but across all stimuli, similar activation in the IFG across hemispheres was found, showing that interhemispheric differences were more pronounced in other brain regions, such as inferior precentral regions, the planum temporale, and the planum polare. In a second test, the same stimuli were used, only some had been "delexicalized," with only prosodic information preserved. In these cases, significant rightward shifts were found in the IFG and other areas, proving that Broca's right-hemisphere homolog is used in prosodic evaluation of various sentence forms (Friederici, 2001). Accordingly, she suggests that left-hemisphere increases associate with syntax, while right-hemisphere increases associate with prosody (Friederici, 2001). Additional lesion-based studies have confirmed this claim, where those with damage in Broca's right homolog show decreased abilities to distinguish different meanings in syntactically identical phrases with prosodic shifts (see Hoyte et al., 2004).

Does the functional specialization of Broca's area and its right homolog for language extend to manual praxis? Put simply, there is considerable evidence that complementary hemispheric roles do exist for manual tasks, but the relationship between each hemisphere is far less understood, especially when considering human handedness. Between 85% and 90% of living humans are right-hand dominant, and as mentioned before, handedness is possibly linked to language lateralization in our species (see Section 2; Annett, 1998; Corballis, 2003). Many studies have attempted to address

handedness-dependent and -independent asymmetries in neural activity related to language, but much more work is needed on the bilaterality of praxis networks in the brain, particularly on the relationship between the contralateral motor system and its links to Broca's network. Studies on representations of tools (both physically and semantically) in the brain show bilateral, but left-lateralized characteristics. Interestingly, the bilaterality of praxis-related activity in the brain can even predict language laterality in both left- and right-handers (Gonzalez & Goodale, 2009).

In a meta-analysis of 64 paradigms, Lewis (2006) assessed cortical regions implicated in various aspects of transitive action involving tools in humans. He divided the studies into five experimental categories: tool pantomime, tool imagery (subjects "imagined" using tools), tool viewing, tool naming, and hearing tools (Lewis, 2006). He also assessed effects of right- and left-handedness, both in subjects and in stimuli. Left IFG was the most commonly reported activation across all paradigms (71% of reported foci were left, while only 29% were right), with left posterior middle temporal gyri (pMTG) and other temporo-parietal areas also showing common activation (also with right homolog evidence) (Lewis, 2006). Like many of the researchers he cites, he believes that overall, tool-networks parallel language networks in that they are primarily left-lateralized, but both tasks have important right hemisphere activation. Importantly, he states that the only exclusively left lateralized activation found in all studies was in the inferior parietal lobule (IPL), and that IFG activation is largely bilateral (Lewis, 2006). He concludes by mentioning that handedness biases in living humans, and their inherent influences on neuroimaging studies, can limit and complicate data, suggesting that more work should be done to address this issue (Lewis, 2006; also see Willems et al., 2014).

How does activation in Broca's area differ for left-handers vs. right-handers? In an observation-imagery based fMRI study, 16 right-handed and 16 left-handed healthy subjects were instructed to read a word (which corresponded to either a manual verb or a non-manual verb), close their eyes, and imagine performing that task (Willems, Toni, Hagoort, & Casasanto, 2009). As predicted, manual vs. non-manual stimuli showed higher activation in Broca's network, with left-handers showing a right-hemisphere bias and right-handers showing a left-hemisphere bias. Still, all manual vs. non-manual activations were bilateral in nature, and it was only the degree which differed with handedness. This study suggests laterality biases are dependent upon hand preference, which provides necessary support for the embodied cognition theoretical framework adopted by many, but this study was only focused on dominant-hand imagery, and thus does not address activation when either right-handed or left-handed subjects consider their non-dominant hand.

Many of the manual actions we perform daily, whether transitive or not, are not restricted to one hand, and even within unimanual actions, humans rarely isolate all tasks to their dominant hand while completely ignoring the other. Especially considering the bimanual nature of most manual actions, it is necessary to understand how we neurally represent dominant hand actions vs. non-dominant ones, and determine whether this relates to the laterality of Broca's area. An fMRI study on 14 right-handed and 14 left-handed subjects addressed contrasts between unimanual and bimanual actions as well as dominant vs. non-dominant hand differences, specifically within tool pantomiming (Vingerhoets et al., 2012). They first found that bimanual (vs. unimanual actions) show increased, left-lateralized activity in the IFG (consistent with other left-dominant tool-based paradigms) regardless of handedness. There was also no major difference in activation for unimanual dominant and unimanual non-dominant actions. For example, when the non-dominant hand is used by subjects of either handedness, there are only minor hemispheric shifts in IFG activation, and

left hemisphere dominance extends to actions even of the left hand (where contralateral right hemisphere activation should increase). Overall, between-group comparisons of left- and right-handers only showed differences in the *degree* of lateralization, with left-handers showing more bilateral activation in general as opposed to right-hemisphere dominance (Vingerhoets et al., 2012).

In another fMRI study of 14 left-handed subjects, unimanual dominant and non-dominant manual actions were contrasted (half intransitive and half transitive), and then compared to right-handed subject data from another study (Martin, Jacobs, & Frey, 2012). Overall, they found that activation in the IFG and other areas was decidedly bilateral for left-handers when compared to right handers, but also found that this was *effector-specific*, where degree of lateralization was dependent upon the type of task (Martin et al., 2012). Tasks requiring precision gripping, for example, showed stronger left-lateralization in the IFG across all subjects. They argue that this suggests that the left hemisphere is crucial in grasp planning irrespective of hand dominance (Martin et al., 2012). These studies extend the unique bilaterality of language to those for manual praxis, and suggest that more studies contrasting unimanual vs. bimanual actions and dominant vs. non-dominant hands should be done with regards to effector-specificity in grasping.

In relation to work on effector-specificity and non-dominant hand performance, particularly for precision grasping, Gonzalez, Whitwell, Morrissey, Ganel, and Goodale (2007) have conducted work on how grasp size affects hand choice in both left- and right-handers. Interestingly, they have shown consistent evidence that grasping small objects is commonly performed with the right hand across subjects. While this is not surprising for right-hand dominant subjects, they also showed that in left-hand dominant subjects, up to 50% of precision grasping is completed with the right hand (Gonzalez et al., 2007). In an attempt to explain this anomalous preference, an illusion-based study was conducted where healthy subjects were asked to grab objects with size-contrast illusions (Ponzo and Ebbinghaus illusions). They found that regardless of hand dominance, grip aperture in the left hand was more susceptible to size illusion, and claimed that right-handed movements were less susceptible to visual illusions than left-handed ones, even in left-handers (Gonzalez, Ganel, & Goodale, 2006). They argue that this is evidence of the left-lateralized, yet bilateral praxis network which manifests uniquely in left-handers. In a combined precision-grasp dichotic-listening study, they were further able to significantly predict the degree of language lateralization by degree of right-hand use, especially in left-handed subjects. In this study, the more subjects tended to use their right hand for precision grasping, the more left-lateralized their language tasks appeared (Gonzalez & Goodale, 2009). Overall, it has been shown that manual praxis, even when handedness is considered, shows strong parallels with language in terms of bilaterality, and the more we expand experimental paradigms to include left-handed subjects and imagery, the more we can learn about how laterality manifests in these cognitive domains.

The functional differentiation of cerebral hemispheres is not unique to humans, but the unique nature of laterality and language is a huge topic within neuroscience, and has been related to anatomy as well as handedness, biological sex, learning, etc. Particularly relevant to the alternative, action-based, functions of Broca's area is the claim that auditory articulatory-learning (i.e. learning through motor repetition of sounds) vs. perceptual learning (i.e. simply learning by hearing) may be related to the laterality of language (Pulvermüller, Kiff, & Shtyrov, 2012). A specific aspect of this claim is that the arcuate fascicle, which is necessary for action-perception linkage in language and left-lateralized, is highly influenced by motor-based vs. perception-based learning (Pulvermüller & Fadiga, 2010).

There has been hardly any study specifically on this subject, but an EEG study of healthy right-handed subjects sought to address these concepts, and contrasted laterality during the perception of pseudowords learned via articulatory (motor-based) vs. perceptual (non-motor based) processes (Pulvermüller et al., 2012). The findings of this study show that while both learning cases lead to similar behavioral success, neural mechanisms underlying active and passive linguistic learning are vastly different, with left hemispheric increases for motor-based language learning in Broca's and other areas and a strongly *bilateral* representation for perceptually learned pseudowords (Pulvermüller et al., 2012). In a Hebbian-based computer learning model, it was also shown that left lateralization of language partially derives from action-based learning via the arcuate fascicle (Pulvermüller & Fadiga, 2010). Ultimately, the authors state that linguistic representations "should be left-lateralized *because* they emerged from action-perception learning," overall suggesting that leftward asymmetries in Broca's area are simply due to a learning bias (Pulvermüller et al., 2012:880).

While this argument is rather bold, it may further connect manual praxis and language in terms of cognition, and may also address differential laterality between the two. For example, a central tenet of this claim is that language is much better learned in an active sense, where one must match their own motor phonemes to those they perceive via motor-based learning; considerable behavioral evidence confirms this in non-experimental settings, such as babbling in infants (Berwick, Friederici, Chomsky, & Bolhuis, 2013; Corballis, 2010; Gentilucci & Dalla Volta, 2008; Nishitani et al., 2005). This characteristic can also be linked to manual praxis, where "practice makes perfect," and it is only through repetitive motor trials that complex actions are learned, most often with right-hand (left-hemisphere) dominance (see Kelly & Garavan, 2005; Passingham, Toni, & Rushworth, 2000; Vaesen, 2012; Vogt et al., 2007). Considering these links further validates the MNS and action-recognition as the basis for language evolution in humans because they are inherent in perception–action learning. Additionally, linking generalized hemispheric characteristics, such as the role of the right-hemisphere in visuospatial acuity, one could posit a link between action–perception learning in the left hemisphere, linked to language and right-hand dominance, and passive, perception-based learning in the right hemisphere to higher level (spatially-based) linguistic processes and the complementary (framing) role of the non-dominant left hand in many humans (see Arbib, 2011; MacNeilage, Studdert-Kennedy, & Lindblom, 1984; Thornton, 2012; Vallortigara & Rogers, 2005). Still, far more work needs to be done on the role of learning in praxis and language, specifically related to Broca's area, in order to gain empirical support of these concepts.

While the laterality of manual praxis and language are extremely complex, overall they represent closer parallels between the two systems than divergence, as does fronto-posterior connectivity. This characteristic has perhaps been less explicitly studied, but there are vast amounts of evidence showing similarities between language and manual praxis in various post-central regions, including the superior temporal sulcus/gyrus (STS/STG) posterior middle temporal gyrus (pMTG), and superior parietal lobule (SPL), among others (see Caspers et al., 2010; Glasser & Rilling, 2008; Lewis, 2006; Molenberghs et al., 2009, 2012; Peeters, Rizzolatti, & Orban, 2013; Ramayya, Glasser, & Rilling, 2010 for overviews). In fact, much as these meta-analyses suggest, there are several regions that may be just as important as Broca's network in subserving manual praxis and language in humans, including posterior association cortex BA 40 and 22 (which includes Wernicke's area).

Although these other areas are more broadly referred to in the literature, and more work is needed to distinguish them to the

degree that we have for BA 44, 45, and other frontal regions, the fact that parietal and temporal areas are repeatedly implicated in transitive action studies is enough to consider them an additional neural isomorphism between language and manual praxis, especially when we consider these findings within the context of the fronto-posterior functional connectome (see Section 1.1). Overall, the claim that praxis and language rely upon shared neural substrates in large scale left-lateralized perisylvian networks is rapidly gaining support within neuroscience. In the future, more work should be done to delineate linguistic and non-linguistic functions in Wernicke's and surrounding areas, specifically as they relate to action-recognition and the MNS, goal-orientated behavior, and transitive action.

2.4. Evolutionary implications

A main motivation of research on action-recognition and manual praxis in Broca's (and other) areas centers around perhaps one of the most important questions we have about ourselves as a species: how and why did language evolve? The links between language and manual praxis have led to several competing hypotheses about the co-evolution of the two cognitive domains. Two leading hypotheses on the evolution of language as related to action-recognition in Broca's network are: the gestural origins of speech, which posits that increasing complexity of manual praxis allowed human ancestors to communicate more and more effectively via gestures, and after perhaps an expansion of orofacial sensorimotor systems, spoken language overtook gesture and became the primary form of communication (Arbib, 2011; Gentilucci & Dalla Volta, 2008). In contrast, the syntax-based theory for the evolution of language assumes a more paralleled evolution between language and manual praxis, with *syntax*, and not gesture, as the common substrate. In this scenario, it was the increased capacity for hierarchical complexity—including mental displacement in time and space—that drove manual gesture and linguistic complexity forward together (Arbib, 2011; Corballis, 2010; Frey, 2008; Stout & Chaminade, 2007, 2012).

After decades of research and continually mounting evidence for various parallels between language and manual praxis in Broca's and other areas, no clear evidence in support of one theory over another has yet been found. In fact, it seems that we actually have more questions than answers, which is due to inherent limitations in the study of language and evolution in general. First, techniques that would provide us with better spatio-temporal resolution (such as single-cell recording) are often too invasive for human subjects, and there is such a large disparity between us and the other non-human primates we study (for example, work on mirror neurons in macaques), that comparative studies only provide weak proxies for transitive action and especially language (see Peeters et al., 2009). However, there is one highly obscure point of evidence that has not yet been fully examined, which is perhaps the best line of evidence we have for examining the co-evolution of manual praxis and language: stone tool manufacture.

3. Lithic technology and human evolution: toolmaking as manual praxis

Stone tools, or lithic technologies, are one of the most abundant and continuous forms of evidence for the cultural and cognitive evolution of humans and their hominid ancestors (Holloway, 1981:290), and paleoanthropologists have been studying various aspects of stone tool manufacture and use for centuries. Appearing some time around 2.6 million years ago (mya) (Roche et al., 1999; Semaw et al., 1997), lithic technology reflects over 90% of hominid technology use, as it was only between 6000 and 8000 years ago

that *H. sapiens* replaced stone tools with those made of bronze and other metals (Ambrose, 2001; Bordes, 1968; Toth & Schick, 1986). In an attempt to understand significant behavioral and cognitive aspects of stone tool manufacture, among other things, paleoanthropologists and archaeologists have developed experimental archaeology, which is a subdiscipline concerned with the modern-day recreation of stone tools similar to those found at various sites around the globe which represent millions of years of hominid technological advances (Toth & Schick, 1993).

In experimental archaeology, living humans—called flintknappers or knappers—recreate stone tools, ranging from the oldest and simplest cobble-flaked tools to ornate arrowheads from Neolithic periods, using a mix of traditional techniques. This process is called flintknapping, and requires highly controlled differential bimanual coordination, where the non-dominant (most often left) hand manipulates a particular type of stone, or a core (typically a silicate-based material with predictable conchoidal fracture), which will become the tool, and the dominant (typically right) hand uses a harder percussion material (commonly made of harder rocks, bone, or wood) to break off flakes in succession, removing thin pieces of the core until a desired “finished product” is made (Andrefsky, 1998; Whittaker, 2004).

An important consideration should be made regarding the physics of lithic fracture, which has also extensively been studied (see Cotterell & Kamminga, 1990 for a review). In order to remove flakes from even very soft rocks, for example, a flintknapper has to find an acute angle on a lithic edge (preferably less than 70°, although this can vary with different hammer types) to percuss from, and right- or obtuse-angles will rarely result in a useful flake removal, if they do at all. Once a suitable edge angle is found, the knapper orients the core and prepares for a rapid and precise blow with the dominant hand, which must also be correctly aimed (in terms of hammer angle), placed (in terms of where it will contact the core) and time (in terms of how fast the hammer must go to remove a flake). Any deviation in this *precision grip*—for example a *misplaced* blow—will often result in no flake removal or incorrect/non-usable flake removal (consider misplacing an 80 mph baseball pitch and hitting the batter instead of the strike zone). Likewise, a *misaimed* blow will often result in unworkable edge angles, reducing the possibility of future percussions. *Mistimed* blows can be too soft and fail to remove flakes or too hard and shatter the flake or even an entire core.

Much work has been dedicated to how flintknappers learn these traits of conchoidal fracture, and how novice knappers differ from experts, who often take upwards of ten years (and sometimes longer) to become comfortable with the process of stone tool manufacture. These studies generally highlight that stone tool manufacture is an *extremely* difficult skill to learn, and cite several reasons as to why this is (see Geribàs, Mosquera, & Vergès, 2010a; Nonaka, Bril, & Rein, 2010; Stout, 2005; Stout & Semaw, 2006). Interestingly, many of these reasons derive from the physics of lithic fracture as they relate to previously discussed motor and cognitive functions—namely body schema extension and syntactical capability. By studying how novices and experts approach stone tool manufacture, as well as how increasingly complex lithic technologies correspond to higher demands on praxis systems, it has been shown that bimanual coordination, as well as planning, task-switch, and even higher-order characteristics such as aesthetics, are inherent in lithic production (see Ambrose, 2010).

Differential bimanual coordination is arguably the most acute and unique aspect of human manual praxis, and certainly reflects a finely controlled body schema, where both hands simultaneously complete different, yet complementary tasks to achieve an overarching goal (e.g. threading a needle and sewing, using scissors to cut a piece of paper, etc.) (Guiard, 1987). As stated before, current neuroscientific paradigms fail to address how differential

bimanual coordination is modulated by the brain, especially in comparison to language. This is often because of experimental limitations which are further complicated by human handedness, but it is important to acknowledge that typical right- and left-hand coordination roles are in accord with the more general hemispheric roles, with the left hemisphere linked to precision sensorimotor capacities and the right hemisphere linked to visuospatial acuity and large-scale contextualization (Arbib, 2011; Thornton, 2012; Vallortigara & Rogers, 2005).

Adopting this manual complementation concept in stone tool manufacture also explains major differences between novice and expert knappers, as well as the cognitive changes required to make a simple vs. a more complex tool. In several studies, the major difference between novices and experts is that novices tend to rely heavily on their dominant hand, and rarely manipulate the core with their non-dominant one (often ignoring edge angle) (see Geribàs, Mosquera, & Vergès, 2010b; Nonaka et al., 2010). Thus, novices require several more percussions and flake removals to complete a tool. In contrast to this, experts use their supportive, non-dominant hand almost more than their percussive one, turning the core over repeatedly, choosing where to remove flakes in the most efficient manner (reliant upon edge angle), and resulting in fewer, but *better-placed* percussive blows. These differences explain why novice knappers can rarely produce higher-order stone tools, which require bifacial flaking (removal of pieces from both sides of the core) and precise motor and ideological understanding of conchoidal fracture (see Geribàs et al., 2010a, 2010b).

Also relevant to the percussive efficiency in experts is the previously discussed concept of body schema plasticity, where a motor-extension of the body (in this case, a hammerstone) is adopted, and subsequently can be manipulated with as much ease as our own body parts (see Section 2.1; Iriki, 2005, 2006; Maravita & Iriki, 2004). Taking into account the negative results of a misaimed, misplaced, or mistimed blow, a highly precise and finely controlled manual schema for dominant-hand object manipulation would be highly adaptive in an evolutionary sense. The same is true for the complementary non-dominant hand, although perhaps less precision would be required in this case (reconsider the evidence of right-hand preference for precision grasping even in left-handers, Section 2.3).

As evidenced by these experimental archaeology-based studies, stone tool manufacture represents perhaps one of the most manually complex transitive action systems in humans, and arguably taxes the finely controlled human body schema much more than the stimuli present in many existing neuroimaging studies on manual praxis in Broca's area. In order to determine whether this is also true for syntax, we must further consider the differences in manufacture techniques between simpler lithic tools and more complex ones. For the purposes of this paper, the contrast between Mode I, or Oldowan tools, with Mode II, or Acheulean tools, is most relevant, as it reflects the second major cognitive shift related to hominid lithic technology (with the first shift being associated to the initial appearance of stone tool manufacture). To make an Oldowan tool, a flintknapper simply has to remove a few flakes (and sometimes just a single one) from a core, which—as discussed above—at the very least requires differential bimanual coordination. Thus, it is likely that upon the advent of Oldowan tools 2.6 mya, hominids already had a uniquely attuned body schema for manual systems, although we are currently unable to reliably track how such a unique behavior emerged.

Despite their importance for studies on Broca's area in terms of body schema, Oldowan techniques require very few percussions, have little hierarchical nesting of events, and reflect very basic goal-orientation (see Geribàs et al., 2010a; Holloway, 1981:295; Stout, 2005; Stout & Semaw, 2006). In contrast to this, making an Acheulean tool (especially the handaxes that typify later Acheulean

sites, starting around 1.6 mya) requires upwards of 50 percussions and relies upon several nested hierarchies for which a distinct, although not universal, syntax has been found (Holloway, 1981, 2012). As mentioned before, when removing flakes, expert knappers rotate the core more often in their non-dominant hand, and this has been attributed to increased planning ahead and foresight regarding workable edge angles. There are several small-scale goals associated with Acheulean tool manufacture, that when compounded (in an integrated fashion) comprise the overarching, hierarchical goal of finishing the tool (see Gowlett, 2006; Holloway, 1969, 2012; Pelegrin, 2005). These include: removal of the outermost layer of the core (cortex), generalized bifacial thinning via large flake removal, smaller-scale, more detailed thinning and shaping, and often (although not necessary) additional preparation of the cutting edge, sometimes accompanied by retouch after the tool becomes blunt after use.

In order to complete a handaxe (and all other bifaces, including those from other Paleo-Meso- and Neo-lithic periods), a knapper must switch back and forth between these four tasks, deciding which among them best enables their progression after *each percussive blow* (consider how expert Chess players think ahead several moves and constantly adjust their strategies throughout a game). This becomes increasingly important if, for whatever reason, they make a mistake (i.e. if they inaccurately remove a flake and create a poor edge angle, or create an unstable platform that increases the risk of fracturing the entire core into unusable pieces). As mentioned before, novices show poor understanding of edge and platform preparation because they ignore their non-dominant, framing hand roles, and as a result, bifacial lithic production is typically achieved only by experts with many years' experience (see Geribàs et al., 2010a; Stout, 2005; Stout & Semaw, 2006). This hierarchical nesting of events has existed in our hominid ancestors for millions of years, and reflects an early expansion of the syntax of action for manual praxis, which as previously discussed relies heavily upon Broca's area. The transition from Oldowan tools to Acheulean tools is correlated with a twofold increase in cranial capacity (and up to threefold by the later Acheulean) in hominid fossil remains (Holloway, 1969, 1996), and is frequently studied in a cognitive context, as well as a paleoarchaeological one. Although vastly different in terms of syntax, the appearance of these tool types is restricted to the oldest technological period, the Lower Paleolithic (or Old Stone Age), which does not reflect the exponential development of later lithic technologies, including those made by modern *H. sapiens*.

Despite this, Lower Paleolithic manufacture likely requires the two cognitive parallels between praxis and language, which would suggest that the third parallel, neuroanatomical connectivity and bilaterality, was also present to some degree in the earliest stages of stone toolmaking. Furthermore, the conceptual shift between Oldowan and Acheulean tool manufacture can be applied to comparisons between the Lower Paleolithic with later technologies in all three parallels because at their base, later tool types—ranging from relatively simple to extremely complex—required similar cognitive shifts in the understanding of lithic fracture mechanics and step-wise goal-orientation, whereby the expansion of a flintknapper's mental framework and “tool-kit” led to vast technological developments, as well as the probable expansion and lateralization of Broca's area.

3.1. The technological hypothesis for language evolution

Combined with other fossil data (e.g. endocasts, skeletal indicators of hominid handedness, and behavioral data from paleoarchaeological sites), a clear progression for manual praxis via stone toolmaking can be tracked over millions of years of our evolution. Many have suggested that stone tool manufacture may have

even been a significant driver for hominid cognitive evolution, which includes the appearance and expansion of social learning, symbolism, and even aesthetics, among other “uniquely human” characteristics (see Holloway, 1969 as an early generative paper on this subject). These topics have since been widely addressed within the anthropological literature,² but the specific role of lithic technology in the evolution of language with respect to neural architecture is relatively rare. As mentioned earlier, there is no universally accepted hypothesis regarding the evolution of language, and there is no hard evidence of language progression in humans and other hominids before writing, as words and gestures do not fossilize (see Holloway, 2008; Rilling, 2008; Toth & Schick, 1986; Wynn, 2002). However, informed by the isomorphism between manual praxis and language in Broca's area, along with an understanding of lithic manufacture as the longest-standing form of transitive action in hominids, perhaps we can study language evolution through a third co-evolutionary hypothesis: the “technological hypothesis” for language evolution.

The archeological record suggests that lithic technology was highly adaptive in hominids, and from the appearance of Oldowan tools, hominids became progressively more reliant upon lithic technology for various aspects of survival. It is widely accepted that selective pressures gave advantages to those individuals with enhanced toolmaking capabilities (i.e., individuals who were “better” with their hands at making stone tools were more likely to survive and produce offspring who were also talented knappers). Considering the cognitive bases of stone tool manufacture—the capacity for an embodied action-recognition in conspecifics (body schema), and the increased capability for goal-orientation (syntax)—it is evident that selection for skilled hominid knappers was simultaneously favoring larger, more complex neural praxis systems, which are reliably rooted in Broca's extended network in modern humans.

The technological hypothesis for language evolution argues that adaptive selection of skilled stone toolmakers was a *primary driver* of this overall extension of large-scale praxis networks, which expanded to communicative, and ultimately linguistic, functions (Stout & Chaminade, 2012; Vaesen, 2012). Much like the gestural and syntactical origins hypotheses, Broca's area and other left-hemisphere dominant perisylvian areas expanded uniquely in hominids to subserve alternate cognitive functions (in this case, lithic technology manufacture), and were co-opted by language. In contrast to these two hypotheses, however, the technological hypothesis has millions of years' worth of physical evidence that we can study. Considering these points, why is stone tool manufacture—as an evolutionarily robust form of manual praxis and possible driver of language evolution—not of more interest to neuroscience? More inter-disciplinary collaboration is needed to introduce lithic technology into cognitive neuroscience and related fields, with several main goals, some of which have recently been highlighted.

The first of our goals should be to gain a general understanding of the neural mechanisms that underlie stone tool manufacture. Weaknesses of studying the neural bases of stone toolmaking are likely a main contribution to its underrepresentation in the literature, as currently fMRI studies (which are the most common contemporary form of study in the neurosciences) are incompatible with stone tool manufacture, mostly due to aforementioned subject movement artifacts. Still, a few works by Stout and others (Stout & Chaminade, 2007, 2012; Stout, Toth, Schick, Stout, & Hutchins, 2000; Stout et al., 2008), Uomini and Meyer (2013),

² Lithic technology as it relates to hominid cognitive evolution is a vast topic, and reviewing it in detail is outside the scope of this paper. For an introduction, see Coolidge and Wynn (2009), Davidson (2010), de Beaune, Coolidge, and Wynn (2009), Gibson and Ingold (1993), Haidle (2011), Holloway (1969), Rilling (2008), Roux and Bril (2005), Vaesen (2012), and Wynn (2002).

and others are now confirming through various neuroimaging technologies that much like other forms of manual praxis, stone tool manufacture highly parallels language perception and production in the brain. Considering the anthropological literature on cognitive aspects of stone tool manufacture, it is possible that flintknapping may represent the strongest neural isomorphism between manual praxis and language, which may help us to better understand and evaluate the competing evolutionary hypotheses in the existing literature. In order to confirm or refute the viability of the technological hypothesis for language evolution, more studies on the neural mechanisms underlying stone tool manufacture are needed.

3.2. The neuroscience of stone tool manufacture

There are numerous incompatibilities between stone tool manufacture and neuroimaging technologies, because making a stone tool requires strong, fast, precise manual percussions with the dominant hand, as well as complex movements by the non-dominant one. These actions could be used in a blocked experimental design, but the short time periods used for traditional stimuli are still problematic. Movement artifacts represent the largest issue in studying the neural mechanisms underlying stone tool manufacture, particularly with fMRI. Still, a few PET paradigms have been used in the past decade (Stout & Chaminade, 2012; Stout et al., 2000, 2008), as well as an observation-based fMRI study (Stout, Passingham, Frith, Apel, & Chaminade, 2011), and an fTCD study, which measures cerebral blood flow changes during tasks (Uomini & Meyer, 2013). These studies represent the relevant literature on stone tool manufacture as a form of manual praxis in the brain, and show several similarities with the previously discussed studies paralleling other forms of praxis to language.

In 2000, the first neuroimaging study of stone tool manufacture was conducted using ^{15}O PET technology on a single male right-handed subject with over 20 years of knapping experience (Stout et al., 2000). Three experimental blocks were conducted: a control, where the subject viewed a lithic core without imagining or planning tool manufacture, a second where he was shown a partially worked core and instructed to imagine finishing the tool, and a third where the subject actually knapped a core (at half-force, because even with PET technology, full-force knapping resulted in inaccurate imaging). Scanned data were conformed to MRI data of the subject taken separately, and showed several left-lateralized activations, some of which were in Broca's network (although none in BA 44/45 specifically), with others in previously discussed post-central regions (such as BA 40 and 22). Similar to comparative studies on action-planning and action-execution, such as Johnson-Frey et al. (2005), when the imagery task was compared to knapping, the latter showed increased responses overall, but in the same locations (Stout et al., 2000). This suggests that in lieu of studying knapping itself, which is susceptible to movement artifacts even via PET technology, stone tool manufacture can be studied accurately through imagery-only paradigms. The paralleled results of these studies also lend support to the validity of action-observation experiments as proxies for studying action itself.

In a subsequent FDG-PET study, Stout et al. (2008) tested three right-handed expert knappers under three conditions: a control where subjects hit a cobble with a hammerstone without removing flakes, an Oldowan manufacture task, and an Acheulean manufacture task. This study addresses the same hypotheses present in neuroimaging studies on the syntactical nature of manual tasks, such as Binkofski et al. (2000) and Molnar-Szakacs et al. (2006), but is not observation-based, and does not include non-biological tasks. In this regard, it is a more direct assessment of syntactical processing for manual actions, although it suffers from weaker spatio-temporal resolution. Similar to previous works based in action-

observation, increased activity was shown for Oldowan and Acheulean tasks when compared to controls in several regions, and left hemisphere BA 4 and 6 showed highest similarity between Oldowan and Acheulean tasks. Interestingly, both tasks showed bilateral activation in Broca's network, whereas only Acheulean manufacture showed activation specific to Broca's area (BA 45), which was right lateralized (Stout et al., 2008). As mentioned before, bimanual coordination tasks are vastly underrepresented in neuroimaging studies, especially those where subjects complete an action component. This FDG-PET study assesses how increasing praxic syntax is modulated by the brain, and in that regard it parallels previous works. However, it also indicates how increasing manual coordination is neurally represented, for which there is little comparative lateralization data (Vingerhoets, 2012). The authors urge more studies on the lateralized nature of their findings, perhaps attributed to the increased non-dominant left hand role in Acheulean manufacture, but state that their results:

[P]rovide evidence of increased sensorimotor and cognitive demands related to the changing nature of expert performance and to the complexity of toolmaking methods, and suggest important relationships between... technological change and evolving hominin brain size, functional lateralization and language capacities (Stout et al., 2008:1944).

The data from this study were later used as comparative material for the only fMRI study related to stone tool manufacture, which was solely observation-based, like many of the previously discussed works on action in Broca's area.

In order to see how learning and knowledge of stone tool manufacture are represented in the brain, Stout and others conducted an fMRI study where complete novices and trained subjects assessed short video clips of Oldowan and Acheulean stone tool manufacture, compared to a percussive (but non-flake-removing) control task (Stout & Chaminade, 2007; Stout et al., 2011). The original intent was for trained subjects to be capable of manufacturing Acheulean handaxes, but none of them were successful in learning this technique after an 8 week training period, so data from the previous FDG-PET study was used as well, comprising expert knapper data. All subjects watched clips of the three tasks, and were asked either to imagine completing the next action, or to evaluate whether or not the knapper was successful in achieving their goal (Stout et al., 2011). When compared to controls, bilateral *pars opercularis* and right-lateralized *pars triangularis* activation was found, which was stronger for Acheulean stimuli than Oldowan stimuli, and particularly strong in trained subjects. Subjects also showed more generalized Broca's network and post-central activation in areas such as BA 6 and BA 40, among others, which was highest in trained subjects. Contrasting Acheulean vs. Oldowan observation showed significant activation in left BA 44 and 45 in all three subject classes, likely compatible with its hierarchical complexity. The authors state that activation in Broca's area reflects "multi-level action parsing [based on]... a strong motivation to attend to, analyze, and understand all Toolmaking stimuli" (Stout et al., 2011:1335). Along with the more traditional action-observation based studies on manual praxis, this may implicate the MNS in supporting an embodied understanding of conspecific actions, highly attuned to transitive manual tasks and possibly to primitive (or even proto-) language. As suggested by the current data and archaeological record, this capability was likely present by the first appearance of lithic technologies, and certainly established by the time Acheulean bifaces appear in the archaeological record.

The final study was particularly interested in correlating the laterality of language with that of stone tool manufacture, which is important considering that all of the previous studies showed surprising (albeit, not unprecedented) activation in Broca's right

homolog associated to flintknapping (Uomini & Meyer, 2013). Another important aspect of this study is that it provides correlated data on two highly lateralized cognitive tasks, rather than attempting to control for laterality in order to study already-known loci of activation. For this study, ten expert flintknappers (two left-handers) underwent transcranial Doppler sonography (fTCD) while manufacturing Acheulean handaxes (movement artifacts are inconsequential for this technology) and silent cued word generation (representing a common linguistic task). fTCD measures cerebral blood flow change through the right- and left-middle cerebral arteries (MCAs), with no interhemispheric transfer, and can thus indicate functional blood flow velocity changes for each hemisphere. From these data, laterality indices (LIs) were made for each task, where the absolute blood flow for each hemisphere is compared to assess left- or right-asymmetries (Uomini & Meyer, 2013). Blood flow velocity changes were highly correlated between Acheulean tool manufacture and the language task across time (particularly between 2 and 7 s), suggesting that tool manufacture and language are both reliant upon goal-orientation. However, the tasks showed *opposite* LI's, with language being leftwardly asymmetric and lithic manufacture being rightwardly asymmetric, although no mention is made about differences in LI's between right- and left-handers (Uomini & Meyer, 2013). Still, “[s]ignificant correlations in the degree of asymmetric activation on sites of neural overlap would strengthen claims of biological association between cognitive functions” (Vingerhoets, 2012:243), and non-related cognitive tasks show *un-correlated* LI's under the same experimental procedures, further suggesting that laterality is an important avenue of future work on praxis and language (see Meyer, Spray, Fairlie, & Uomini, 2014).

Combined with the existing fMRI and PET data, it seems that stone tool making has anomalous lateralization, ranging from relatively strong bilateral activity to atypical right-hemisphere dominance. Despite this, it is clear that the task involves classical Broca's area, as well as its right-hemisphere homolog and its local and long-range connections, in much the same way as previously assessed manual and linguistic tasks. More work is needed to assess the role of bimanual coordination in driving cerebral lateralization patterns, including more study on flintknapping itself, but also dependent upon comparative data from more general bimanual research paradigms on both left- and right-handers. Additionally, novel approaches (such as fTCD analysis) and alternative technologies should be encouraged in cases where fMRI is incompatible with research designs that would improve our understanding of action in the brain.

4. Conclusion

While much more research is needed, current experimental evidence has drawn strong, repeated, and reliable associations between Broca's area and its classically associated linguistic functions with alternative functions related to action-recognition and manual praxis in humans and non-human primates. Based on the area's anatomy and connectivity, the extension of BA 44 and 45 into an extended Broca's network including surrounding pre-frontal and motor areas (such as BA 47 and 6), and their long-range connections to post-central areas, has shown that language and praxis further rely on similar, widely distributed bilateral areas in the brain. Broca's area is a central node in these neural systems, and it is unlikely that these parallels are a result of mutually exclusive evolutionary histories for both uniquely expanded human cognitive domains. Still, little is known about the co-evolutionary mechanisms that created these two systems in our species and our hominid ancestors, and we must develop novel experimental approaches if we want to justify the proposed links between praxis and language in evolutionary contexts.

All current neuroscientific studies on stone tool manufacture show similarities with the more general neuroscientific literature on the parallels between transitive manual praxis and language in Broca's network and other areas in the human brain, suggesting that studies on the neural substrates of lithic manufacture are of value to paleoanthropologists and neuroscientists alike. Still, some stark differences do exist: the elevated role of Broca's right hemisphere homolog in lithic-based studies needs to be addressed, as little explanation of this phenomenon currently exists. While it may reflect the expanded role of the non-dominant (often) left hand in stone tool manufacture, little comparative data on bimanual coordination in BA 44/45 exists. In terms of the co-evolution of these systems in hominids, perhaps the bilateral nature of activation in stone tool manufacture reflects the less specialized, and thus less lateralized, praxis-based platform implicated by other studies on the laterality of manual praxis in Broca's area. This could be considered additional evidence of Broca's area as a polymodal processing hub that was originally adapted to action-observation of orofacial and manual systems, and subsequently co-opted for language, which lead to unique human lateralities (perhaps through active learning via the arcuate fasciculus). In order to evaluate these concepts, more work of this nature needs to be done, as it has thus far provided clear-but-limited evidence of partially overlapping networks, “strongly suggesting that [manual praxis and language] share a foundation in...human capacities for complex, goal-directed action and are likely to have evolved in a mutually reinforcing way” (Stout et al., 2008:1947).

Broca's area is a central hub in multiple distributed bilateral, but left-hemisphere dominant, networks responsible for manual praxis and language. Despite the stark behavioral differences between praxis and language in humans, the underlying cognitive principles, such as fine attunement of the body schema and acute syntactical control, are the same. Competing hypotheses regarding the co-evolution of praxis and language would strongly benefit from more studies and novel experimental paradigms, as it is clear that we still have much to learn about how manual praxis and language correspond to neural networks. Still, increased study of stone tool manufacture, specifically in Broca's area and its temporal and parietal conjunctions, may provide us with invaluable information on how language evolved in our lineage. Current evidence within this subject supports the syntax-based theory over the gestural origin of speech theory, with a final suggestion that we should also focus on the technological hypothesis of language origins as the most parsimonious explanation of the three parallels between praxis and language in Broca's and other areas.

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