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The relationship between language and other high-level cognitive functions: review of neuroimaging and patient evidence

Short title: Language vs. other cognitive functions

Evelina Fedorenko[a,b,c] & Rosemary Varley[d] (UCL)

[a] Massachusetts General Hospital
[b] Harvard Medical School
[c] Center for Academic Research and Training in Anthropogeny (CARTA)
[d] University College London

Abstract (172 words)

Humans are endowed with a rich repertoire of cognitive abilities. Many of these are shared with other animals, while a few appear to be unique to our species. Among the latter is our ability to translate complex thoughts into language, a code that allows us to exchange those thoughts with one another, plausibly laying the foundation of human culture and civilization. Given that language evolved against the backdrop of many evolutionarily older systems and mechanisms, a natural question arises as to the degree to which our language system is separable from other cognitive systems. In particular, does language rely on a set of specialized brain regions, or does it share neural machinery with other functions? Based on converging evidence from neuroimaging studies and investigations of individuals with aphasia, we here argue that a set of brain regions on the lateral surfaces of the left frontal and temporal cortices selectively support high-level linguistic processing. We therefore conclude that language is separable from the rest of the cognitive arsenal in the adult human brain.

Keywords: language; syntax; semantics; functional specificity; numerical cognition; cognitive control; Theory of Mind; music; navigation; fMRI; neuropsychology; aphasia

Please send correspondence to Ev Fedorenko (MGH, HMS, Psychiatry Department, Building 149, East 13th Street, Charlestown, MA 02129, USA; Charlestown, MA 02129; evelina.fedorenko@mgh.harvard.edu).

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1. Introduction

Many non-human animals – ranging from those genetically similar to us, like chimpanzees (e.g., Call, 2001; Tomasello et al., 2003; Hurley & Nudds, 2006; Penn & Povinelli, 2007; Matsuzawa, 2009; Whiten, 2011) and bonobos (e.g., Hare & Yamamoto, 2015; Roffman et al., 2015), to our more distant relatives, like marine mammals (e.g., Herman, Pack & Morrel-Samuels, 1993; Reiss & Marino, 2001; Schusterman, Thomas & Wood, 2013) or birds (e.g., Bluff et al., 2007; Taylor et al., 2007) – are capable of complex thoughts and behaviors. Furthermore, all animal species have a way to exchange information with one another (e.g., Kaplan, 2014). These communication systems are highly variable in their media, scope, and complexity (e.g., Endler, 1993; Hauser, 1997; Hauser & Konishi, 1999; Bradbury & Vehrencamp, 2011). Most would agree, however, that human language is unparalleled in the animal kingdom in its complexity and generative power (e.g., Snowdon, 1990; Deacon, 1997; Hauser et al., 2002; Premack, 2007; Kinsella, 2009). Of course, language is a relatively recent development on the evolutionary timescale, having emerged only 100,000-200,000 years ago (e.g., Atkinson 2011; Perreault & Mathew, 2012; cf., for example, our divergence from chimpanzees, which occurred between 5 and 7 million years ago; Kumar et al., 2005). Consequently, much of our cognitive and neural machinery was already in place when the language system evolved. To date, however, debates continue as to the relationship between language and other cognitive abilities. These debates concern a number of distinct questions, and some have been perhaps unnecessarily heated due to the conflation of some of the relevant issues, as we discuss in Section 4. We here tackle one specific question: does language processing rely on its own specialized brain regions or does it instead make use of machinery that is also used to perform other cognitive tasks? Note that we are here concerned with mature human brains. We touch on the role of language in the *development* of specifically human cognitive competences in Section 4.

Two methods most directly speak to the question of whether there exist brain regions that are selectively engaged during language processing. The ***first*** is functional magnetic resonance imaging (fMRI), which can be used to examine co-activation between language and other cognitive processes. If a brain region supports both linguistic processing, and, say, musical processing, then it should be active during tasks tapping both of these cognitive processes. If, on the other hand, a brain region selectively supports linguistic processing, then it should be active when people process language, and much less so, or not at all, when people process music. The ***second*** method relies on individuals with acquired brain damage and allows us to ask whether damage to the language system affects performance in other domains. If the language system – or some of its components – are critical for arithmetic processing or processing structure in music, then damage to these brain regions should lead to deficits in these non-linguistic abilities. If, on the other hand, the language system is not necessary for non-linguistic abilities,

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then focal damage to the language system should *only* affect language comprehension and/or production, leaving intact performance on non-linguistic tasks.

We here review evidence from these two methodologies, occasionally drawing on data from other approaches, focusing on the relationship between language and five other cognitive abilities that have been argued – over the years – to share cognitive and neural machinery with language: arithmetic processing, executive functions, Theory of Mind, music processing, and spatial navigation. The nature of and the reasons for the alleged overlap between linguistic and other processes have varied across domains. In particular, the hypothesized overlap comes in at least two flavors. In some cases, language has been argued to share representations and/or computations with other domains. For example, language, music and arithmetic all rely on structured representations characterized by features like compositionality and recursion (e.g., Hauser et al., 2002) or complex hierarchical structure (e.g., Maess et al., 2001; Patel, 2003; Maruyama et al., 2012). In the case of Theory of Mind, some aspects of linguistic syntax have been argued by some to be a critical component of our representations of others' mental states (e.g., De Villiers & De Villiers, 2000). Language also shares some cognitive requirements with domain-general executive functions like inhibition (e.g., Novick et al., 2005).

However, in other cases, linguistic representations have been hypothesized to play a key role in other domains in spite of the fact that there may be no similarity whatsoever between the representations in the two domains. In particular, language has been argued to serve as a medium for integrating information across various specialized systems (e.g., Hermer & Spelke, 1999; Carruthers, 2005). In this way, in addition to their role in interpersonal communication, language representations have a significant intra-cognitive role. This kind of relationship was, for example, hypothesized to hold between language and spatial navigation (e.g., Hermer & Spelke, 1999).

We argue, based on the available evidence, that in a mature human brain a set of regions – most prominently, those located on the lateral surfaces of the left frontal and temporal cortices – selectively support linguistic processing, and damage to these regions affects an individual's ability to understand and produce language, but not to engage in a wide variety of complex non-linguistic tasks.

Before we proceed, it is important to clarify what we mean by "language". There are two points to make here. ***First***, we are focusing on *high-level* language processing, which includes extracting meaning from linguistic utterances and generating meaningful linguistic utterances when communicating with others (e.g., Fedorenko et al., 2010; regions schematically marked in red in Fig. 1, adapted from Fedorenko & Thompson-Schill, 2014). We are thus excluding from consideration i) auditory and visual perceptual regions concerned with the initial analysis of linguistic signals (marked in yellow and green in Fig. 1, respectively), as well as ii) articulatory motor regions concerned with the latest stages of speech production (marked in pink in Fig. 1). Of course, the question we ask here about the high-level language processing regions can be – and has been – asked with respect to those lower-level perceptual / motor regions. Briefly: it appears that some degree of specificity characterizes both auditory (e.g., Overath et al., 2015; Peretz et al., 2015; Norman-Haignere et al., 2015) and visual (e.g., Baker et al., 2007; Hamame et al., 2013) perceptual regions. The answer is somewhat equivocal for the motor regions, and the degree of functional specificity of parts of motor / pre-motor cortex for speech production over other motor behaviors, like non-speech oral movements, remains unclear. Some have argued for such specificity in parts of the speech articulation system – specifically, the superior precentral gyrus of the insula – based on patient evidence (e.g., Dronkers, 1996; cf. Hillis et al., 2004), but findings from fMRI generally do not support this claim (e.g., Bonilha et al., 2006; Fedorenko et al., 2014). Yet, dissociations between speech production and the production of non-speech oral movements have been reported (e.g., Whiteside et al., 2015). Furthermore, a recent fMRI study (Longcamp et al., 2014) has reported selectivity for letters over non-letter symbols in written production. Thus, the question clearly deserves further investigation.

And ***second***, although high-level language processing subsumes many potentially distinct computations, we here talk about it *holistically*. To elaborate: language comprehension and production can each be broken down into many mental operations (e.g., during comprehension, we need to recognize the words, understand how the words relate to one another by analyzing the morphological endings and/or word order, and construct a complex meaning representation). These operations must, at least to some extent, be *temporally* separable, with some preceding others (e.g., Swinney et al., 1997; Fodor, 1983; Marslen-Wilson, 1987), although the top-down effects of predictive processing are well accepted (e.g., Maslen-Wilson, 1975; Altman & Kamide, 1999; Hale, 2001; DeLong et al., 2005; VanBerkum et al., 2005; Dikker et al., 2005; Levy, 2008; Smith & Levy, 2013). It is also possible that these different operations are *spatially* separable, being implemented in distinct parts of the language network. Indeed, some results from the neuropsychological patient literature suggest that this must be the case (e.g., Caramazza, 1990; cf. Plaut, 1995). However, no compelling evidence exists, in our opinion, for either i) a consistent relationship between particular brain regions and particular mental operations in the patient literature, or ii) for the spatial separability of different components of high-level language processing in fMRI (e.g., Fedorenko et al., 2012c; Blank et al., 2015; Bautista & Wilson, 2016). Moreover, the language processing brain regions form a deeply integrated functional system, as evidenced by both a) strong anatomical connectivity (e.g., Saur et al., 2008), and b) high correlations in neural activity over time during both rest and naturalistic cognition (e.g., Blank et al., 2014; Tie et al., 2014). Thus, we here consider the high-level language processing system as a whole, without discussing particular brain regions within it.

We now proceed to review the evidence for the separability of the brain regions that support high-level language processing from those that support other cognitive abilities.

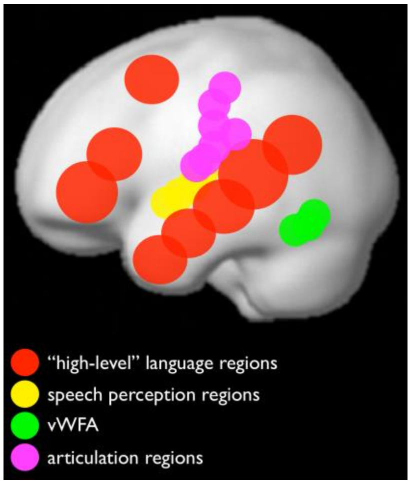

Figure 1. A schematic illustration of the approximate locations of brain regions that support perceptual (yellow, green), motor (pink) and high-level (red) aspects of language processing.

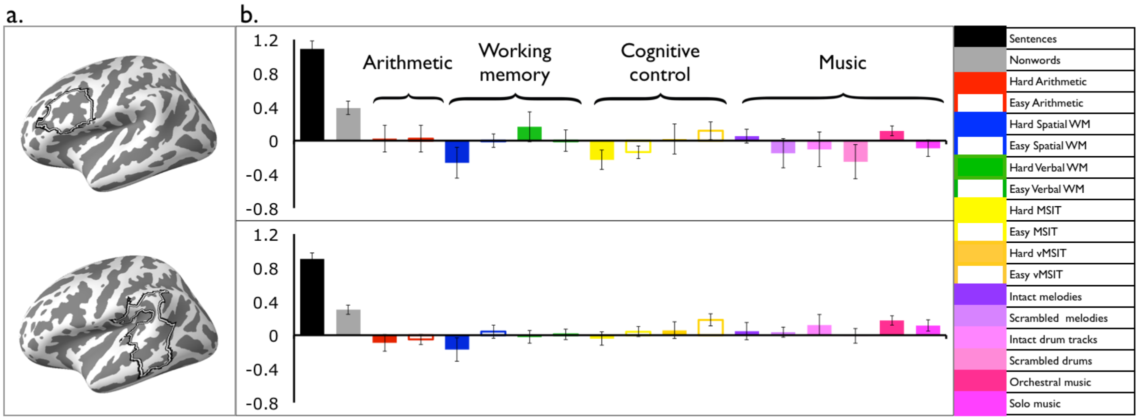

Figure 2. Functional response profiles of two high-level language processing brain regions.
(a). Two functional "parcels" derived from a group-level representation of language activations (the LIFG and the LMidPostTemp parcels from Fedorenko et al., 2010) and used to constrain the selection of subject-specific voxels. Individual regions of interest were functionally defined: each parcel was intersected with the individual activation map for the language localizer contrast (sentences > nonword lists; Fedorenko et al., 2010) and top 10% of voxels were taken to be that participant's ROI.

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(b). Responses to the language localizer conditions and a broad range of non-linguistic tasks. Responses to the sentences and nonwords conditions were estimated using across-runs cross validation (e.g., Nieto-Castañon & Fedorenko, 2012), so that the data to define the ROIs and to estimate their responses were independent. The data for the arithmetic, working memory (WM) and cognitive control (MSIT) tasks were reported in Fedorenko et al. (2011), and the data for the music conditions come from Norman-Haignere et al. (in preparation; see also Fedorenko et al., 2011, 2012).

2. Review of the evidence

2.1 Language vs. arithmetic processing

Previous work in numerical cognition has identified two distinct core systems underlying different aspects of numerical competence: i) a small exact number system, which is based on attention and allows the tracking of small quantities of objects with exact information about position and identity (e.g., Wynn, 1990; Xu et al., 2004; Feigenson et al., 2004); and ii) a large approximate number system (sometimes referred to as the analog magnitude estimation system), which provides noisy estimates of large sets (e.g., Whalen et al., 1999). These core abilities are shared across species (e.g., Gallistel, 1990; Hauser and Carey, 2003) and are present in pre-linguistic infants (Feigenson et al., 2004). Consequently, the autonomy of language from these core numerical abilities has not been controversial.

However, in addition to these evolutionarily conserved systems, humans have developed means to represent exact quantities of arbitrary set size, using verbal representations (i.e., words for numbers). Although not universal (e.g., Gordon et al., 2002; Pica et al., 2004; Frank et al., 2008), this ability to represent exact quantities is present in most cultures. Because these representations are verbal in nature, it has been proposed that exact arithmetic relies on the neural system that underlies linguistic processing (e.g., Dehaene, 2003). Indeed, neuroimaging studies and studies in bilingual speakers provided some evidence in support of this view (e.g., Dehaene & Cohen, 1997; Dehaene et al., 1999; Stanescu-Cosson et al., 2000; Van Harskamp & Cipolotti, 2001; Delazer et al., 2003). For example, Dehaene and colleagues (1999) had participants perform an exact vs. approximate arithmetic addition task. The exact > approximate contrast produced activation in a number of brain regions including parts of the left inferior frontal cortex (although the observed region fell quite anteriorly to "Broca's area" as defined traditionally). Based on the fact that other studies have found inferior frontal activations for verbal / linguistic tasks, Dehaene et al. argued that the regional activations they observed reflected engagement of the language system in exact calculations. Such indirect inferences can be dangerous, however: similar activation locations across studies – especially when operating at the level of coarse anatomy (e.g., talking about activations landing within "the inferior frontal gyrus", "the superior temporal sulcus" or "the angular gyrus", each of which encompasses many cubic centimeters of brain tissue) – cannot be used to conclude that the *same* brain region gave rise to the relevant activation patterns. For example, both faces and bodies produce robust responses within the fusiform gyrus, yet clear evidence exists of category selectivity for each type of stimulus in distinct, though nearby, regions (e.g., Schwarzlose et al., 2005). To make the strongest case for overlap, one would therefore need to, at the very least, directly compare the relevant cognitive functions within the same study, and ideally, within each brain individually (e.g., Fedorenko et al., 2010) because inter-individual variability can give rise to apparent overlap at the group level even when the activations are entirely non-overlapping in any given individual (e.g., Nieto-Castañon & Fedorenko, 2012).

A neuropsychological investigation that is characterized by a similar problematic inference was reported by Baldo & Dronkers (2006), who examined a large set of individuals with left hemisphere strokes and found a) a correlation in performance between a language comprehension task and an arithmetic task, and b) overlap in brain regions whose damage was associated with linguistic and arithmetic deficits (including in the left inferior frontal gyrus). As has been discussed extensively in the literature in the 1980s and 1990s (e.g., Coltheart, 1985; Shallice, 1988), however, dissociations are more powerful than associations because an association can arise from damage to nearby but distinct regions. Curiously, Baldo & Dronkers actually observe a dissociation in their data, with some patients being impaired on the language comprehension task but not arithmetic comprehension, and other patients showing the opposite pattern of results. However, they take their overall results as evidence of overlap in the mechanisms for processing language and arithmetic.

A major challenge to the view that the language system underlies our exact arithmetic abilities came from a study where patients with extensive damage to left-hemisphere language regions and with consequent severe aphasia were shown to have preserved ability to perform exact arithmetic (Varley et al., 2005). In particular, three such patients were able to solve a variety of mathematical problems that involved addition, subtraction, multiplication and division, small and large numbers, whole numbers and fractions, and expressions with brackets. Particularly astonishing was the dissociation in these patients between their lack of sensitivity to structural information in language vs. mathematical expressions: although profoundly agrammatic in language, they retained knowledge of features such as the embedded structure of bracket expressions and the significance of order information in non-commutative math operations of subtraction and division. This study strongly suggested that brain regions that support linguistic, including grammatical, processing are not needed for exact arithmetic.

A number of brain imaging studies have provided converging evidence for this view. An early PET study (Zago et al., 2001) examined the activation patterns during simple digit reading, retrieval of simple arithmetic facts, and arithmetic computations, and failed to observe any activation in the perisylvian cortices. More recently, Fedorenko, Behr & Kanwisher (2011) had participants perform a language understanding task in fMRI, which was used to localize language-responsive regions of interest in each participant individually. They then examined the responses of these brain regions while participants engaged in solving easier (with smaller numbers) or harder (with larger numbers) arithmetic addition problems. They found that the language regions responded during the arithmetic conditions at the same level as, or below, a low-level baseline condition (i.e., when participants did not engage in any task; Fig. 2), strongly suggesting that the language system is not active when we engage in exact arithmetic. Similarly, Monti, Parsons & Osherson (2012) found that linguistic, but not algebraic, syntax produced activations in the inferior frontal cortex. The latter instead produced responses in bilateral parietal brain regions. Finally, Maruyama et al. (2012) manipulated the syntactic complexity of algebraic operations and also found activations in parietal (and occipital) regions, but not within the fronto-temporal language system.

In summary, it appears that brain regions that respond robustly during linguistic processing are not generally (cf. Trbovich & LeFevre, 2003) active when we solve arithmetic problems. Furthermore, damage – even extensive damage – to the language regions appears to leave intact our arithmetic abilities. We therefore conclude that linguistic processing occurs in brain circuits distinct from those that support arithmetic processing.

2.2 Language vs. logical reasoning and other executive functions

In addition to our ability to exchange thoughts with one another via language, humans differ from other animals in the complexity of our thought processes (e.g., Gray & Thompson, 2004). In particular, we are experts in organizing our thoughts and actions according to internal goals. This structured behavior has been linked with a large number of theoretical constructs, including working memory, cognitive control, attention, and fluid intelligence (e.g., Miller & Cohen, 2001; Duncan, 2010, 2012). What is the relationship between these so-called "executive functions" and the language system?

There are at least two reasons to suspect an important link. The ***first*** has to do with the anatomical substrates of executive control. In particular, prefrontal cortex has long been argued to be important (e.g., Miller & Cohen, 2001). Although, over the years, additional brain regions have been incorporated into the cognitive control "network", including regions in the parietal cortices, frontal lobes continue to figure prominently in any account of cognitive control and goal-directed behavior. Critically, as has long been known, some of the language-responsive regions occupy parts of the left inferior frontal cortex. One possibility is that language processing at least partially relies on domain-general circuits in the left frontal lobe (e.g., Kaan & Swaab, 2002; Novick et al., 2005).

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The ***second*** reason concerns the functional importance of cognitive control and working memory for language. We have long known that these domain-general mechanisms play a role in language processing (e.g., see Fedorenko, 2014, for a recent review). For example, super-additive processing difficulties have been reported when participants perform a language task at the same time as a demanding working memory or inhibitory task (e.g., Gordon et al., 2002; Fedorenko et al., 2006). And in fMRI studies, a number of groups have reported activation in these domain-general frontal and parietal circuits for some linguistic manipulations, especially for manipulations of linguistic difficulty (e.g., Rodd et al., 2005; Novais-Santos et al., 2007; January et al., 2009). This suggests that cognitive control mechanisms can and do sometimes support language processing, much like they support the processing of information in other domains.

So, how is this relationship between language and cognitive control implemented? Is there partial, or even complete, overlap between these functions in the left frontal lobe, or does language rely on brain regions that are distinct from those that support cognitive control?

In one fMRI study (Fedorenko et al., 2011), we identified language-responsive brain regions and then examined the responses of those regions when participants performed several classic working memory / inhibitory tasks. As expected, the language regions in the temporal lobe showed no response during these executive tasks (Fig. 2). However, importantly, the language regions in the left frontal lobe (including in and around Broca's area) showed a similar degree of selectivity, in spite of the fact that executive tasks robustly activated left frontal cortex in close proximity to the language-responsive regions (Fedorenko et al., 2012a).

Other fMRI studies provided additional support for the idea that language regions, including those in the inferior frontal cortex, are highly selective in function. For example, Monti et al. (2007, 2009) have examined the relationship between linguistic processing and logical reasoning, another ability that strongly draws on domain-general cognitive control resources (e.g., Goel, 2007), and found largely non-overlapping responses, with the language regions responding strongly during the processing of language stimuli and much less so during the processing of logical expressions.

Data from patients with brain damage generally support the conclusions drawn from brain imaging studies. For example, Varley & Siegal (2000) report a severely agrammatic aphasic man who was able to perform well on complex causal reasoning tasks. Furthermore, anecdotally, some of the severely aphasic patients that Varley and colleagues have studied over the years continue to play chess in spite of experiencing severe comprehension / production difficulties. And chess is arguably the epitome of human intelligence / reasoning, with high demands on attention, working memory, planning, deductive reasoning, inhibition, etc. On the flip side, Reverberi et al. (2009) found that patients with extensive lesions in prefrontal cortex and preserved linguistic abilities exhibited impairments in deductive reasoning. Thus, an intact linguistic system is not sufficient for reasoning.

It is worth noting that at least one patient investigation has argued that language is, in fact, necessary for complex reasoning. In particular, using the Wisconsin Card Sorting Task (Berg, 1948), Baldo et al. (2005) reported impairments in aphasic individuals, but not in patients with left-hemisphere damage but without aphasia. A plausible explanation for this pattern of results is that language regions lie in close proximity to domain-general cognitive control regions. This is true not only in the left frontal cortex, as discussed above (e.g., Fedorenko et al., 2012a), but also in the left temporo-parietal cortex. Thus, brain damage that results in aphasia is more likely to affect these nearby cognitive control structures than brain damage that does not lead to aphasia (and is thus plausibly further away from the cognitive control regions). As noted above, dissociations are more powerful than associations (e.g., Coltheart, 1985; Shallice, 1988), so the fact that there exist severely aphasic individuals who have intact executive functions constitutes strong evidence for the language system not being critical to those functions.

In summary, although both executive functions and language processing robustly engage brain structures in the left frontal cortex, they appear to occupy nearby but distinct regions within that general area of the brain, as evidenced by clear dissociations observed in fMRI studies and the preserved abilities of at least some severely aphasic individuals to engage in complex non-linguistic reasoning tasks.

2.3 Language vs. Theory of Mind

A sophisticated ability to take the subtleties of another's mental states into consideration when acting in the world, Theory of Mind (ToM), is yet another defining characteristic of humans (e.g., Saxe, 2006). Some have argued that certain linguistic (specifically, grammatical) representations are necessary for thinking about others' minds (e.g., de Villiers, 2000; de Villers & de Villers, 2000). Indeed, some evidence seems to support this contention. First, linguistic abilities (including both syntax and understanding meanings of mental state verbs like "think" and "believe") correlate with success on false belief tasks (e.g., Astington & Jenkins, 1999; Dunn et al. 1991; Astington & Baird, 2005; Milligan et al. 2007; Wellman et al. 2001). Furthermore, training children with no understanding of false beliefs on certain linguistic constructions allows them to pass the false-belief task (e.g., Appleton & Reddy, 1996; Clements et al., 2000; Hale & Tager-Flusberg, 2003; Slaughter & Gopnik, 1996). However, we are here concerned with adult brains, and even if linguistic representations were critical for the *development* of (at least some aspects) of ToM, it is still possible that in a mature brain linguistic representations are no longer necessary.

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Recent research in social neuroscience has identified a set of brain regions that appear to play a role in representing others' internal states, including thoughts, preferences, and feelings (e.g., Fletcher et al., 1995; Gallagher et al., 2000; Vogeley et al., 2001; Ruby and Decety, 2003; Saxe and Kanwisher, 2003; Ciaramidaro et al., 2007; Gobbini et al., 2007). These regions include right and left temporo-parietal junction (TPJ), the precuneus, and regions in medial prefrontal cortex. The right TPJ, in particular, is highly selective for thinking about someone else's thoughts and beliefs (Saxe and Wexler, 2005; Saxe and Powell, 2006; Perner et al., 2006; Young and Saxe, 2009; Jenkins and Mitchell, 2009; Bedny et al., 2009), in line with both a) early patient studies that showed that damage to this region led to deficits in ToM reasoning (Siegal, Carrington and Radel, 1996; Happé, Brownell & Winner, 1999), and b) recent 'virtual lesion' TMS experiments (e.g., Kalbe et al., 2010; Young et al., 2010).

The fact that the apparently core (most functionally selective) region within the ToM network – the right TPJ – is located in the non-language-dominant hemisphere already suggests that the language system is probably not critical for ToM reasoning. However, the *left* TPJ is still an important component of the network (e.g., Samson, Apperly, Chiavarino, & Humphreys, 2004), and a recent study reported overlap between the left TPJ and the language regions (Deen et al., 2015). However, numerous experiments with aphasic patients who suffered extensive damage to the left TPJ indicate retained ToM reasoning and residual insights into the knowledge states of others (Dronkers et al., 1998; Varley & Siegal, 2000; Varley, Siegal & Want, 2001; Apperly, Samson, Carroll, Hussian & Humphreys, 2006; Willems, Benn, Hagoort, Toni, & Varley, 2011). Typical probes of ToM, such as the changed location or changed contents tasks, involve inferences regarding the beliefs of others. In standard formats these tasks place heavy demands on linguistic processing. For example, the participant must detect the third person reference of the probe question and make fine semantic discriminations between verbs such as 'think/know'. However, when people with severe agrammatic aphasia are given cues as to the purpose of the probe questions, they reveal retained ability in inferring the beliefs (both true and false) of others (Varley & Siegal, 2000). Willems et al., (2011) extended these observations to people with global aphasia. They employed a non-linguistic task in which there was a mismatch in knowledge between participants as to the location and orientation of two tokens on a grid. The informed participant (the 'sender') had to recognize the knowledge state of the naïve 'receiver' and then, using their own token, signal the location/orientation of the receiver's token. Participants with severe aphasia were able to adopt both sender and receiver roles: as senders, they recognized the receiver's need for information and designed a message to convey the necessary knowledge. As receivers, they were able to interpreting the intentions behind movement of a token in order to correctly locate and orientate their token. Thus, although the potential theoretical significance of the overlap observed between language comprehension and Theory of Mind tasks in the left TPJ remains to be investigated, it appears that the language system is not critical for mentalizing, at least once the mentalizing abilities have developed.

2.4 Language vs. music processing

Language and music – two universal cognitive abilities unique to humans (e.g., McDermott & Hauser, 2005) – have been observed to share similarities. Apart from the obvious surface-level similarity, with both involving temporally unfolding sequences of sounds with a salient rhythmic and melodic structure (e.g., Handel, 1989; Patel, 2008), there is a deeper parallel: language and music exhibit similar structural properties, as has been noted for many years (e.g., Riemann, 1877, as cited in Swain, 1995; Lindblom & Sundberg, 1970; Fay, 1971; Bernstein, 1976; Sundberg & Lindblom, 1976; Lerdahl & Jackendoff, 1977, 1983; Roads, 1979; Krumhansl & Keil, 1982). In particular, in both domains relatively small sets of elements (words in language, notes and chords in music) are used to create a large, perhaps infinite, number of sequential structures (phrases and sentences in language, and melodies in music). And in both domains, this combinatorial process is constrained by a set of rules, such that healthy adult humans can judge the well-formedness of typical sentences and melodies.

Inspired by these similarities, many researchers have looked for evidence of overlap in the processing of structure in language and music. For example, a number of studies have used a structural-violation paradigm where participants listen to stimuli in which the presence of a structurally unexpected element is manipulated. For example, some early studies used event-related potentials (ERPs) and showed that structural violations in music elicit components that resemble those elicited by syntactic violations in language. These include the P600 (e.g., Janata, 1995; Patel et al., 1998; Fitzroy & Sanders, 2013; see Osterhout & Holcomb, 1993; Hagoort et al., 1993, for the original reports of the P600 response to syntactic violations in language), and the early anterior negativity, present more strongly in the right hemisphere (eRAN; e.g., Patel et al., 1998; Koelsch et al., 2000; Loui et al., 2005; Miranda & Ullman, 2007; see Neville et al., 1991; Friederici, Pfeifer & Hahne, 1993, for the original reports of the eLAN in response to syntactic violations in language; see Steinhauer & Drury, 2012, for a recent critical evaluation of the eLAN findings). Later studies observed a similar effect in MEG and suggested that it originates in or around Broca's area and its right-hemisphere homologue (e.g., Maess et al., 2001). Subsequently, fMRI studies also identified parts of Broca's area as one of the generators of the effect (Koelsch et al., 2002; Tillmann et al., 2003, 2006; see Herdener et al, 2012, for similar evidence from rhythmic violations), although other regions were also implicated, including ventrolateral premotor cortex (e.g., Koelsch, 2006), insular cortex, parietal regions (e.g., Koelsch et al., 2002; Tillman et al., 2003), and superior temporal regions (e.g., Koelsch et al., 2002; see also Sammler et al., 2009, 2013, for evidence from intracranial EEG recordings).

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A number of behavioral dual-task studies have also argued for language-music overlap based on super-additive processing difficulty when musical violations coincided with syntactic violations in language (e.g., Fedorenko et al., 2009; Slevc et al., 2009; Hoch et al., 2011; cf. Bonnel et al., 2001). Some patient studies have also been taken to support overlap, notably those investigating musical processing in aphasic patients with lesions in Broca's area. Patel et al. (2008) found subtle deficits in processing musical structure, which – as the authors acknowledge – could also be attributed to lower-level auditory processing deficits. And Sammler et al. (2011) observed an abnormal scalp distribution of the eRAN component and subtle behavioral deficits in patients with IFG lesions.

However, in spite of the intuitive appeal of the music/language overlap idea, we will argue that there is an alternative interpretation of the results summarized above, which a few of the studies have already alluded to (e.g., Tillmann et al., 2006). In particular, a note or word that is incongruent with the preceding musical or syntactic context is a salient event. As a result, the observed responses to such deviant events could reflect a generic mental process – such as attentional capture, detection of violated expectations, or error correction – that a) applies equally to language, music, and other, non-musical and non-linguistic, domains, and b) does not necessarily have to do with processing complex, hierarchically-structured materials. A closer look at the available evidence supports this interpretation.

The P600 ERP component that is sensitive to syntactic violations in language and music is also sensitive to violations of expectations in other domains, including arithmetic (Niedeggen & Rosler, 1999; Núñez-Peña & Honrubia, 2004) and sequential learning of complex structured sequences (Christiansen et al., 2012). For example, Niedeggen & Rosler (1999) observed a P600 in response to violations of multiplication rules, and Núñez-Peña & Honrubia (2004) observed a P600 to violations of a sequence of numbers that were generated following an easy-to-infer rule (e.g., adding 3 to each preceding number - e.g., 3 6 9 12 15 **19**). Furthermore, although studies manipulating both syntactic and semantic structure in language argued that structural processing in music selectively interferes with *syntactic* processing in language (e.g., Besson & Schon, 2001; Slevc et al., 2009), more recent studies suggest that structural processing in music can interfere with both syntactic and semantic processing in language (Hoch et al., 2011; Perruchet & Poulin-Charronnat, 2013), arguing against a syntax-specific interpretation.

Given that language, music, and arithmetic all rely on complex structured representations, responses to violations in these domains could nonetheless index some sort of cross-domain high-level structural processing. However, unexpected events that do not violate *structural* expectations also appear to elicit similar ERP components. For example, Coulson and colleagues (1998a,b) have argued that the P600 component is an instance of another, highly domain-general, ERP component, the P300 component (also referred to as the "P3"), which has long been known to be sensitive to rare and/or informative events irrespective of high-level structure (e.g., Pritchard, 1981). Kolk and colleagues have also argued for a domain-general interpretation of the P600 component (e.g., Kolk & Chwilla, 2007). For example, Vissers et al. (2006) have observed a P600 for spelling errors ("fone" instead of "phone"), which seems unlikely to involve anything we might call abstract structural processing.

Some uncertainty also exists with respect to the relationship between the eRAN component (e.g., Koelsch et al., 2000) and the mismatch negativity (MMN) component. The MMN component is observed when a stimulus violates a rule established by the preceding sequence of sensory stimuli (Näätänen et al., 1978; see Garrido et al., 2009 and Trainor & Zatorre, 2009 for recent overviews). Most of the work on the MMN has focused on the auditory domain (see e.g., Näätänen et al., 2007 for a review), but several studies have reported a visual MMN (e.g., Cammann, 1990; Astikainen et al., 2004; Czigler et al., 2004). In the auditory domain, although early studies employed relatively low-level manipulations (e.g., a repeated tone in a sequence of ascending tones (e.g., Tervaniemi et al., 1994), or a switch in the direction of a within-pair frequency change (Saarinen et al., 1992)), later studies have observed the MMN component for more abstract manipulations, such as violations of tonal (e.g., Trainor et al., 2002; Neuloh & Curio, 2004; Fujioka et al., 2005) or rhythmic (e.g., Vuust et al., 2005; van Zuijen et al., 2004) patterns, raising questions about how this component might relate to the eRAN. Some ERP studies have explicitly argued that eRAN is distinct from the MMN, with eRAN exhibiting a longer latency and a larger amplitude than the MMN (e.g., Koelsch et al., 2001; cf. Leino et al., 2007, who report a longer latency for the MMN than for eRAN), and with different dominant sources (posterior IFG for eRAN and primary auditory cortex for the MMN; Garza Villarreal et al., 2011). However, a number of other studies have reported multiple sources for the MMN, including both temporal and frontal components (see Alain et al., 1998 for the patient evidence implicating the frontal source). According to one proposal (Giard et al., 1990; also Gomot et al., 2000; Maess et al., 2007), two mental processes contribute to the MMN: a) a sensory memory mechanism (located in the temporal lobe; e.g., Schoenwisner et al., 2007), and b) an attention-switching process (located in the frontal lobes), which has been shown to peak later than the temporal component (Rinne et al., 2000).

In summary, two ERP components (the P600 and the early anterior negativity) have been linked to structural processing in music and language, and controversy exists for both of them regarding their interpretation and their relationship to components driven by relatively low-level deviants (P3 and MMN, respectively). This raises the possibility that responses thought to be the signature of structural processing in music and language may instead reflect domain-general cognitive processes that have little to do specifically with processing *structure* in music and other domains.

A similar picture emerges in neuroimaging studies. For example, Koelsch et al. (2005) demonstrated that timbre violations activate regions in the posterior IFG and superior temporal cortices that are similar to those activated by violations of tonal structure (see also Doeller et al., 2003; Opitz et al., 2002; Tillmann et al., 2003). Furthermore, a meta-analysis of activation peaks from fMRI studies investigating brain responses to unexpected sensory events (Corbetta & Shulman, 2002) reveals a set of brain regions that rather closely resemble those activated by structural violations in music (Fig. 3).

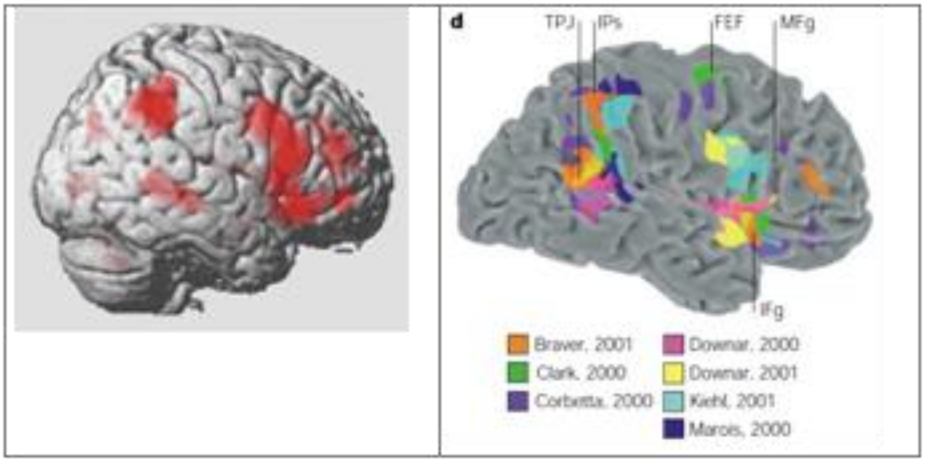

Figure 3. (a) The activation map for a contrast of structural violation vs. no structural violation in music from Koelsch et al. (2005, Fig. 2b). (b) The results of a meta-analysis of low-level unexpected events from Corbetta & Shulman (2002).

The frontal regions (including parts of Broca's area; Fedorenko et al., 2012a) and parietal regions that are present in both the activation map for the presence vs. absence of a structural violation in music, and Corbetta & Shulman's (2002) meta-analysis of activation peaks for unexpected events, have long been implicated in a wide range of cognitive demands, as discussed in Section 2.2 (e.g., Duncan, 2010, 2012).

In summary, evidence from the structural-violation paradigm is at present largely consistent with an interpretation in which the effects arise within domain-general brain regions that respond to unexpected events across domains (cf. Wang et al., 2015), including cases where the violations presumably have little to do with combinatorial processing or with complex hierarchical relationships among elements.

The structural-violation paradigm, albeit popular, has not, however, been the only paradigm used to study structural processing: another paradigm in music research that has been used to examine sensitivity to different types of structure involves comparing brain responses to intact and "scrambled" music. Scrambled variants of music are obtained by randomly rearranging segments of sound or elements of music, disrupting different types of musical structure depending on how the scrambling is performed. Comparisons of brain activity elicited by intact and scrambled music can thus be used to coarsely probe neural sensitivity to musical structure.

Using fMRI, Levitin & Menon (2003, 2005) compared brain responses to intact music and scrambled music generated by randomly reordering short segments of the musical sound waveform. They reported activation in the inferior frontal gyrus, around BA47, for the contrast of intact vs. scrambled music. Based on previous reports of high-level linguistic manipulations activating parts of BA47 (e.g., Fiez et al., 1995; Binder et al., 1997; Dapretto & Bookheimer, 1999), Levitin & Menon argued that the linguistic processes that engage parts of BA47 also function to process musical structure. However, they did not directly compare the processing of structure in music and language, leaving open the possibility that language and music manipulations could activate nearby but non-overlapping regions in the anterior parts of the inferior frontal gyrus.

Later studies that directly compared structured and unstructured language and music stimuli (Fedorenko et al., 2011; Rogalsky et al., 2011) in fact found little or no response to music in brain regions that are sensitive to the presence of structure in language, including regions in the left frontal lobe (Fedorenko et al., 2011; Norman-Haignere et al., in prep.; Fig. 2). Furthermore, in our recent work (Fedorenko et al., 2012b; see also Norman-Haignere et al., 2015), we reported several brain regions in the temporal cortices that respond more strongly to structured than unstructured musical stimuli (we randomly re-ordered the notes within pieces of music, disrupting most aspects of musical structure) but do not show sensitivity to the presence of structure in language stimuli. It therefore appears that distinct sets of brain regions support high-level linguistic vs. music processing.

This non-overlap is consistent with the dissociation between linguistic and musical abilities that has frequently been reported in the neuropsychological literature. In particular, patients that experience some difficulty with aspects of musical processing as a result of an innate or acquired disorder appear to have little or no trouble with high-level linguistic processing (e.g., Allen, 1878; Polk & Kertesz, 1993; Peretz, 1993; Peretz et al., 1994; Samson & Zatorre, 1994; Steinke et al., 1997; Griffiths et al., 1997; Liegeois-Chauvel et al., 1998; Patel et al., 1998; Wilson & Pressing, 1999; Piccirilli et al., 2000; Steinke et al., 2001; Wilson et al., 2002; Di Pietro et al., 2004; Warrier & Zatorre, 2004; Stewart et al., 2006; Phillips-Silver et al., 2011; see Peretz & Coltheart, 2003; Peretz & Hyde, 2003 for reviews). And conversely, aphasic patients – even those with severe language deficits – appear to have little or no difficulties with music perception (e.g., Brust, 1980; Marin, 1982; Basso & Capitani, 1985; Polk & Kertesz, 1993; Fedorenko et al., 2014). Perhaps the most striking case is that of the Russian composer Shebalin who suffered two left hemisphere strokes, the second of which left him severely aphasic. Shebalin nevertheless continued to compose music following his

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strokes, deemed to be comparable in quality to the music he composed before sustaining brain damage (Luria et al., 1965).

In summary, recent brain imaging studies suggest that non-overlapping sets of brain regions are sensitive to the presence of structure in language vs. music (Fedorenko et al., 2011; Rogalsky et al., 2011; Fedorenko et al., 2012b). These findings are consistent with evidence from brain-damaged populations. We therefore conclude that linguistic processing occurs in brain circuits distinct from those that support music processing.

2.5. Language vs. spatial navigation

The claim for a role for language in cross-domain integration has been explored in the area of navigation and reorientation. The environment provides a number of cues to location, including both geometric and landmark information. If these cues are processed by separate mechanisms (such as those dedicated to visuo-spatial processing and object recognition), it might be that only in the presence of relevant language forms that the two informational streams can be integrated, creating a capacity for flexible reorientating behaviour. Initial experimental findings supported this claim. Cheng (1986) reported that rats navigate on the basis of geometric information alone. Similarly, young children who had not yet mastered spatial language of the type 'right/left of X' also relied on the geometry of the environment (Hermer & Spelke, 1996). Furthermore, in a striking demonstration of the possible role of language, healthy adults when engaged in verbal shadowing failed to combine available landmark and geometric cues and attempted to reorient on the basis of geometric information alone (Hermer-Vazquez, Spelke, & Katsnelson, 1999). The capacity to incorporate landmark information into reorientation performance appeared to require linguistic resources.

Subsequent experiments did not always replicate these findings. For example, investigations with non-human species such as monkeys and fish revealed capacity to combine landmarks and geometry (Gouteux, Thinus-Blanc, & Vauclair, 2001; Sovrano, Bisazza, & Vallortigara, 2002). Learmonth, Newcombe and Huttenlocher (2001) found no effect of verbal shadowing when the dimensions of the search space were increased, indicating that reorientation in small search spaces is particularly vulnerable to disruption. Patients with global aphasia who had difficulties in comprehension and use of spatial terms both in isolation and in sentences were indistinguishable in reorientation performance from healthy controls (Bek, Blades, Siegal & Varley, 2010). These individuals were unable to produce terms such as 'left' or 'right', and made errors in understanding simple spatial phrases such as 'the match to the left of the box'. Despite these linguistic impairments, they were able to integrate landmark information (e.g., the blue wall) with ambiguous geometric information in order locate hidden objects.
. One possibility is that while language can be used to draw attention to particular aspects of an environment, other forms of cue can also perform this role. Shusterman, Lee and

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Spelke (2011) undertook a detailed exploration of the impact of different forms of verbal cues on the reorientation behavior of 4-year old children. They observed that a non-spatial linguistic cue that served only to direct a child's attention to landmark information was as effective in improving reorientation performance as verbal cues incorporating spatial information. This result suggests that, rather than language representations being a mandatory resource for informational integration, they provide more general scaffolding to learning. Furthermore, language is not the only resource to support attention to significant cues. Twyman, Friedman and Spetch (2007) report that non-linguistic training also supports children by drawing their attention to landmark information and enabling its combination with geometry in reorientation.

In a functional neuroimaging study of neural mechanisms that are associated with reorientation, Sutton, Twyman, Joanisse and Newcombe (2012) observed bilateral hippocampal activation during reorientation in virtual reality environments. Hippocampal activity increased in navigation of smaller spaces, confirming behavioral observations that reorientation in environments without distant visual cues is particularly challenging. Sutton et al. also report activations of perisylvian language regions including the left superior temporal and supramarginal gyri in conditions where environments contained ambiguous geometric information but no landmark cues. One interpretation of this result is that language resources are employed by healthy adults under conditions of cognitive challenge in order to support performance in intrinsically non-linguistic domains. For example, through encoding to linguistic forms, sub-elements of a problem can be represented and maintained in phonological working memory. However, the finding that informational integration is possible in profoundly aphasic adults indicates that language representations are not a mandatory component of reorientation reasoning. Klessinger, Szczerbinski & Varley (2012) provide a similar demonstration of use of language resources in support of calculation in healthy adults. Whereas competent calculators showed little evidence of phonological mediation in solving two-digit + two-digit addition problems, less competent calculators displayed phonological length effects (i.e., longer calculation times on problems with phonologically long vs short numbers). Thus, across a range of cognitive domains, language representations might be used in support of reasoning, particularly under conditions of high demand.

3. Functional specificity places constraints on possible mechanisms

The key motivation for investigating the degree of functional specialization in the human mind and brain is that such investigations critically constrain the hypothesis space of possible computations of each relevant brain region (e.g., Kanwisher, 2010). If only a particular stimulus or class of stimuli produce a response in some brain region, we would entertain fundamentally different hypotheses about what this region does, compared to a case where diverse stimuli produce similarly robust responses. For example, had we found a brain region within the high-level language processing language system that responded similarly strongly[1] during the processing of linguistic and musical stimuli, we could have hypothesized that this region is sensitive to some abstract features of the structure present in both kinds of stimuli (for example, dependencies among the relevant elements: words in language, tones and chords in music; or perhaps the engagement of a recursive operation). That would tell us that, at some level, we extract these highly abstract representations from these – very different on the surface – stimuli. The importance of these abstract representations / processes could then be evaluated in understanding the overall cognitive architecture of music and language processing. Similar kinds of inferences could be made in cases of observed overlap between language and other cognitive processes.

The fact that high-level language processing brain regions appear to *not* be active during a wide range of non-linguistic tasks suggests that these regions respond to some features that are only present in linguistic stimuli. We hypothesize that the language system stores our language knowledge representations. The precise nature of linguistic representations is still a matter of debate in the field of language research, although most current linguistic frameworks assume a tight relationship between the lexicon and grammar (e.g., Joshi, Levy, & Takahashi, 1975; Bresnan, 1982; Schabes, Abeille, & Joshi, 1988; Pollard & Sag, 1994; Goldberg, 1995; Bybee, 1998; Jackendoff, 2002, 2007; Culicover & Jackendoff, 2005; cf. earlier proposals like Jackendoff, 1977; Chomsky, 1981). Whatever their nature is though, detecting matches between the input and stored language knowledge is what plausibly leads to neural activity within the language system during language comprehension, and searching for and selecting the relevant language units to express ideas is what plausibly leads to neural activity during language production.

4. Issues that often get conflated with the question of functional specialization

The question of *whether in the adult human brain there exist brain regions that are specialized for linguistic processing* is sometimes conflated with and tainted by several issues that – albeit interesting and important – are nonetheless orthogonal (see e.g., Elman et al., 1996, for earlier discussions). We here attempt to briefly clarify a few such issues.

First, the existence of specialized language machinery does not imply the innateness of such machinery (see e.g., Karmiloff-Smith, 1992; Elman et al., 1996 for discussion).

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[1] It is worth noting that effect sizes are sometimes not appreciated enough in fMRI studies, which often focus on the *significance* of the effects. In some cases, two manipulations, A and B, may produce significant effects in a particular brain region, but if manipulation A produces a response that is several times stronger than manipulation B, this is critical for interpreting the role of the region in question in the cognitive processes targeted by the two manipulations.

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Functional specialization can develop as a function of our experience with the world. A clear example is the visual word-form area, vWFA, a region in the inferior temporal cortex that responds selectively to letters in one's native script (e.g., Baker et al., 2007). Recent experiments with macaques have also suggested that specialized circuits can develop via an experiential route (Srihasam et al., 2011). Given that language is one of the most frequent and salient stimuli in our environment from birth (and even in utero) and throughout our lifetimes, it is computationally efficient to develop machinery that is specialized for processing linguistic stimuli. In fact, our hypothesis introduced in Section 3 – that the fronto-temporal language system stores linguistic knowledge representations – is actually not compatible with the idea that our language machinery is present at birth.

It remains an important open question what the regions that in the adult brain show selectivity for high-level linguistic processing do prior to or at birth. A number of studies have reported responses to human speech in young infants characterized by at least some degree of selectivity over non-speech sounds and, in some cases, selectivity for native language over other languages (e.g., Dehaene-Lambertz et al., 2002; Dehaene-Lambertz et al., 2010; Kuhl et al., 2014; Schultz et al., 2014; cf. Christia et al., 2014). However, it is not clear whether these responses extend beyond the high-level auditory regions that are selective for speech processing in the adult brain but are not sensitive to the meaningfulness of the signal (e.g., Norman-Haignere et al., 2015). In any case, as noted above, infants have exposure to speech in the womb (e.g., Moon & Fifer, 2000), and some studies have shown sensitivity to sounds experienced prenatally shortly after birth (e.g., Partanen et al., 2013). As a result, even if speech responses in the infants occur in what-later-become high-level language processing regions, it is possible that these responses are experientially driven. Humans are endowed with sophisticated learning mechanisms and acquire a variety of complex knowledge structures and behaviors early in life. As a result, in order to postulate an innate capacity for language, or any other cognitive ability, strong evidence is required.

Second, the existence of specialized language machinery is orthogonal to whether and how this system interacts with other cognitive and neural systems. Most researchers these days – ourselves included – do not find plausible the idea that the language system is in some way *encapsulated* (cf. Fodor, 1981). However, *how* the language system exchanges information with other large-scale neural networks remains another important question for future research. Furthermore, the fact that there exist some brain regions that are specialized for language processing does not imply that it cannot *additionally* draw on domain-general resources, and in turn itself act as a co-opted/non-mandatory domain-general resource (2.5). In fact, as noted in Section 2.2, a number of linguistic manipulations have been shown to recruit the regions of the fronto-parietal executive system (see also Fedorenko, 2014, for a recent discussion).

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Third, the specificity of the language system does not imply that the relevant brain regions evolved specifically for language. This possibility cannot be excluded, but the evidence available to date does not unequivocally support it. In particular, although a number of researchers have argued that some brain regions in the human brain are not present in non-human primates (e.g., ***), others have suggested that a human brain is simply a scaled up versions of a non-human primate brain (e.g., Herculano-Houzel, 2012). Regardless of whether or not the human brain includes any species-specific regions, relative to the brains of our primate relatives humans possess massively expanded association cortices in the frontal, temporal and parietal regions (e.g., Buckner & Krienen, 2013). However, these association cortices house at least three spatially and functionally distinct large-scale networks: i) the fronto-temporal language system that we have focused on here, ii) the fronto-parietal domain-general cognitive control system (e.g., Duncan, 2010), and iii) the so-called "default mode network" (e.g., Buckner et al., 2008) that overlaps with the Theory of Mind network (e.g., Saxe, 2006) and has been also implicated in introspection and creative thinking. The latter two systems are present in non-human primates and appear to be structurally and functionally similar (e.g., Duncan, 2010; Mantini et al., 2011). How exactly the language system emerged against the backdrop of these other, not human-specific, high-level cognitive abilities remains a big question critical to understanding the evolution of our species.

And *fourth*, although in the fully formed adult brain damage to the language system does not appear to affect non-linguistic abilities, it is possible that in the course of development, language is critical for the formation of some cognitive capacities, such as our ability to explicitly represent others' mental states (as discussed in Section 2.3) or operate on large exact quantities. To investigate the role of language in the development of non-linguistic human capacities, one can a) look at the developmental time-courses of the relevant abilities to see if the mastering of particular linguistic devices leads to the emergence of the relevant non-linguistic ability, or b) examine the non-linguistic abilities in question in children who are delayed in their linguistic development, due to either a neurodevelopmental language disorder or lack of early linguistic input (e.g., Curtiss, 1977; Dronkers et al., 1998).

5. Conclusions

We have here reviewed evidence from brain imaging investigations and studies of patients with severe aphasia and argued that language processing relies on a set of specialized brain regions, located in the frontal and temporal lobes of the left hemisphere. These regions are not active when we engage in arithmetic processing, solve complex problems, listen to music, think about other people's mental states or navigate in the world. Furthermore, all these non-linguistic abilities further appear to remain intact following damage to the language system, suggesting that linguistic representations are not critical for these abilities. This highly selective functional response profile of the language regions suggests to us that these regions store domain-specific knowledge representations that mediate our linguistic comprehension and production abilities. The specificity of these regions further makes it possible to use them as a functional marker of activating linguistic representations, which is important in addressing questions about the role of language in various cognitive abilities.

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References

Alain, C., Woods, D., & Knight, R. (1999). A distributed cortical network for auditory sensory memory in humans. *Brain Research*, *812*(1-2), 23-37.

Allen, G. (1878). Note-deafness. *Mind*, *10*, 157–167.

Apperly, I., Samson, D., Carroll, N., Hussain, S., & Humphreys, G. (2006). Intact first- and second-order false belief reasoning in a patient with severely impaired grammar. *Social Neuroscience*, *1*(3-4), 334-348.

Appleton, M., & Reddy, V. (1996). Teaching Three Year-Olds to Pass False Belief Tests: A Conversational Approach. *Social Development*, *5*(3), 275-291.

Astikainen, P., Ruusuvirta, T., Wikgren, J., & Korhonen, T. (2004). The human brain processes visual changes that are not cued by attended auditory stimulation. *Neuroscience Letters*, *368*(2), 231-234.

Astington, J., & Baird, J. (2005). *Why language matters for theory of mind*. Oxford: Oxford University Press.

Astington, J., & Jenkins, J. (1995). Theory of mind development and social understanding. *Cognition & Emotion*, *9*(2-3), 151-165.

Atkinson, Q. (2011). Phonemic Diversity Supports a Serial Founder Effect Model of Language Expansion from Africa. *Science*, *332*(6027), 346-349.

Baker, C. I., Liu, J., Wald, L. L., Kwong, K. K., Benner, T., & Kanwisher, N. (2007). Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. *Proc Natl Acad Sci U S A*, *104*(21), 9087-92.

Baldo, J., Dronkers, N., Wilkins, D., Ludy, C., Raskin, P., & Kim, J. (2005). Is problem solving dependent on language?. *Brain And Language*, *92*(3), 240-250.

Basso, A., & Capitani, E. (1985). Spared musical abilities in a conductor with global aphasia and ideomotor apraxia. *Journal Of Neurology, Neurosurgery & Psychiatry*, *48*(5), 407-412.

Bedny, M., Pascual-Leone, A., & Saxe, R. (2009). Growing up blind does not change the neural bases of Theory of Mind. *Proceedings Of The National Academy Of Sciences*, *106*(27), 11312-11317.

Bek, J., Blades, M., Siegal, M., Varley, R., (2010). Language and spatial reorientation: Evidence from severe aphasia. *Journal of Experimental Psychology: Learning, Memory and Cognition 36* (3), 646-658.

Bek, J., Blades, M., Siegal, M., Varley, R., (2013). Dual-task Interference in Spatial Reorientation: Linguistic and Nonlinguistic Factors. *Spatial Cognition & Computation 13* (1), 26-49.

Berg, E. (1948). A Simple Objective Technique for Measuring Flexibility in Thinking. *The Journal Of General Psychology*, *39*(1), 15-22.

Bernstein, L. (1976). *The unanswered question*. Cambridge, Mass.: Harvard University Press.

Besson, M., & Schön, D. (2001). Comparison between language and music. In R. Zatorre & I. Peretz, *The biological foundations of music* (1st ed., pp. 232- 259). New York: The New York Academy of Sciences.

Binder, J., Frost, J., Hammeke, T., Cox, R., Rao, S., & Prieto, T. (1997). Human Brain Language Areas Identified by Functional Magnetic Resonance Imaging. *Neuroscience*, *17*(1), 353-362.

Bluff, L., Weir, A., Rutz, C., Wimpenny, J., & Kacelnik, A. (2007). Tool-Related Cognition in New Caledonian Crows. *Comparative Cognition & Behavior Reviews*, *2*, 1-25.

Bonilha, L., Rorden, C., Appenzeller, S., Carolina Coan, A., Cendes, F., & Min Li, L. (2006). Gray matter atrophy associated with duration of temporal lobe epilepsy. *Neuroimage*, *32*(3), 1070-1079.

Bonnel, A., Faita, F., Peretz, I., & Besson, M. (2001). Divided attention between lyrics and tunes of operatic songs: Evidence for independent processing. *Perception & Psychophysics*, *63*(7), 1201-1213.

Bradbury, J., & Vehrencamp, S. (2011). *Principles of animal communication* (2nd ed.). Sunderland, MA: Sinauer Associates.

Bresnan, J. (1982). *The Mental representation of grammatical relations*. Cambridge, Mass.: MIT Press.

Brust, J. (1980). Music and language: musical alexia and agraphia. *Brain*, *103*(2), 367-392.

Buckner, R.L. & Krienen, F.M. (2013). The evolution of distributed association networks in the human brain. *Trends in Cognitive Sciences,* 17(12), 648-665.

Buckner, R. L., Andrews-Hannah, J. R., & Schacter, D. L. (2008). The Brain's Default Network: Anatomy, Function, and Relevance to Disease. *Annals Of The New York Academy Of Sciences*, *1124*(1), 1-38.

Bybee, J. (1998). A Functionalist Approach to Grammar and Its Evolution. *Evolution Of Communication*, *2*(2), 249-278.

Call, J. (2001). Chimpanzee social cognition. *Trends In Cognitive Sciences*, *5*(9), 388-393.

Cammann, R. (1990). Is there a mismatch negativity (MMN) in visual modality?. *Behavioral And Brain Sciences*, *13*(02), 234-235.

Carruthers, P. (2005). Distinctively human thinking: Modular precursors and components. In P. Carruthers, S. Laurence, & S. Stitch (Eds.), The Innate Mind: Structure and contents (pp. 69–88). Oxford: Oxford University Press.

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, *23*(2), 149-178.

Chomsky, N. (1981). *Lectures on Government and Binding: The Pisa Lectures*. Holland: Foris Publications. Reprint. 7th Edition. Berlin and New York: Mouton de Gruyter, 1993.

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Christiansen, M., Conway, C., & Onnis, L. (2012). Similar neural correlates for language and sequential learning: Evidence from event-related brain potentials. *Language And Cognitive Processes*, *27*(2), 231-256.

Ciaramidaro, A., Adenzato, M., Enrici, I., Erk, S., Pia, L., Bara, B., & Walter, H. (2007). The intentional network: How the brain reads varieties of intentions. *Neuropsychologia*, *45*(13), 3105-3113.

Clements, W., Rustin, C., & McCallum, S. (2000). Promoting the Transition from Implicit to Explicit Understanding: A Training Study of False Belief. *Developmental Science*, *3*(1), 81-92.

Corbetta, M., & Shulman, G. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neuroscience*, *3*(3), 215-229.

Cosmides, L., Tooby, J., 1997. The Modular Nature of Human Intelligence. In: Scheibel, A., Schopf, J.W. (Eds.), The Origin and Evolution of Intelligence. Jones and Bartlett Publishers, Sudbury, MA, pp. 71-101.

Coulson, S., King, J.W., Kutas, M. (1998a). Expect the unexpected: Event-related brain response to morphosyntactic violations. Language and Cognitive Processes, 13(1), 21-58.

Coulson, S., King, J.W., Kutas, M. (1998b). ERPs and domain specificity: Beating a straw horse. Language and Cognitive Processes, 13(6), 653-672.

Culicover, P.W. and Jackendoff, R. (2005). *Simpler Syntax*. Oxford University Press.

Curtiss, S. (1982). Developmental dissociations of language and cognition.*Exceptional language and linguistics*, 285-312.

Czigler, I., Balázs, L., & Pató, L. (2004). Visual change detection: event-related potentials are dependent on stimulus location in humans. *Neuroscience Letters, 364*(3), 149-153.

Dapretto, M., & Bookheimer, S. (1999). Form and Content: Dissociating syntax and semantics in sentence comprehension. *Neuron*, *24*(2), 427-432.

de Villiers, J. (2000). Language and Theory of mind: what are the developmental relationships?. In S. Baron-Cohen, H. Tager-Flusberg & D. Cohen, *Understanding other minds: perspectives from autism and developmental cognitive neuroscience.* (1st ed., pp. 83-123). Cambridge: Cambridge University Press.

de Villiers, J., & de Villiers, P. (2000). Linguistic determinism and false belief. In P. Mitchell & K. Riggs, *Children's Reasoning and the Mind* (1st ed.). Hove, U.K.: Psychology Press.

Deacon, T. (1997). *The symbolic species*. New York: W.W. Norton.

Deen, B., Koldewyn, K., Kanwisher, N., & Saxe, R. (2015). Functional Organization of Social Perception and Cognition in the Superior Temporal Sulcus. *Cerebral Cortex*.

Dehaene, S., & Cohen, L. (1997). Cerebral Pathways for Calculation: Double Dissociation between Rote Verbal and Quantitative Knowledge of Arithmetic. *Cortex*, *33*(2), 219-250.

Dehaene, S., Jonides, J., Smith, E., & Spitzer, M. (1999). Thinking and problem solving. In M. Zigmond, F. Bloom, S. Landis, J. Roberts & L. Squire, *Fundamental Neuroscience* (1st ed., pp. 1543-1564). Waltham: Academic Press.

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology*, *20*(3-6), 487-506.

Delazer, M., Girelli, L., Granà, A., & Domahs, F. (2003). Number Processing and Calculation -- Normative Data from Healthy Adults. *The Clinical Neuropsychologist (Neuropsychology, Development And Cognition: Section D)*, *17*(3), 331-350.

Di Pietro, M., Laganaro, M., Leemann, B., & Schnider, A. (2004). Receptive amusia: temporal auditory processing deficit in a professional musician following a left temporo-parietal lesion. *Neuropsychologia*, *42*(7), 868-877.

Doeller, C., Opitz, B., Mecklinger, A., Krick, C., Reith, W., & Schröger, E. (2003). Prefrontal cortex involvement in preattentive auditory deviance detection:. *Neuroimage*, *20*(2), 1270-1282.

Dronkers, N. (1996). A new brain region for coordinating speech articulation. *Nature*, *384*(6605), 159-161.

Dronkers, N., Ludy, C., & Redfern, B. (1998). Pragmatics in the absence of verbal language: Descriptions of a severe aphasic and a language-deprived adult. *Journal Of Neurolinguistics*, *11*(1-2), 179-190.

Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: Mental programs for intelligent behaviour. *Trends in Cognitive Sciences*, *14*, 172-179.

Duncan, J., Schramm, M., Thompson, R., & Dumontheil, I. (2012). Task rules, working memory, and fluid intelligence. *Psychonomic Bulletin & Review*, *19*(5), 864-870.

Dunn, J., Brown, J., Slomkowski, C., Tesla, C., & Youngblade, L. (1991). Young Children's Understanding of Other People's Feelings and Beliefs: Individual Differences and Their Antecedents. *Child Development*, *62*(6), 1352.

Elman, J. L., Bates, E. A., Johnson, M. H., Karmiloff-Smith, A., Parisi, D., & Plunkett, K. (1996). *Rethinking innateness*. Cambridge, MA: MIT Press.

Endler, J. (1993). Some General Comments on the Evolution and Design of Animal Communication Systems. *Philosophical Transactions Of The Royal Society B: Biological Sciences*, *340*(1292), 215-225.

Fay, T. (1971). Perceived Hierarchic Structure in Language and Music. *Journal Of Music Theory*, *15*(1/2), 112.

Fedorenko, E., Fillmore, P., Smith, K., Bonilha, L. & Fridriksson, J. (2015). The superior precentral gyrus of the insula does not appear to be functionally specialized for articulation. *Journal of Neurophysiology.* DOI: 10.1152/jn.00214.2014

Fedorenko, E. (2014). The role of domain-general cognitive control in language comprehension. *Frontiers In Psychology*, *5*, 335

Fedorenko, E., & Thompson-Schill, S. (2014). Reworking the language network. *Trends In Cognitive Sciences*, *18*(3), 120-126.

Fedorenko, E., Behr, M., & Kanwisher, N. (2011). Functional specificity for high-level linguistic processing in the human brain. *Proceedings Of The National Academy Of Sciences*, *108*(39), 16428-16433.

Fedorenko, E., Duncan, J., & Kanwisher, N. (2012a). Language-Selective and Domain-General Regions Lie Side by Side within Broca's Area. *Current Biology*, *22*(21), 2059-2062.

Fedorenko, E., Frank, M. & Gibson, E. (2009). Syntactic complexity effects in Jabberwocky sentences. The 22nd CUNY Conference on Human Sentence Processing, Davis CA, March 2009.

Fedorenko, E., Gibson, E., & Rohde, D. (2006). The nature of working memory capacity in sentence comprehension: Evidence against domain-specific working memory resources. *Journal of Memory and Language*, *54*(4), 541-553.

Fedorenko, E., Hsieh, P.-J., Nieto-Castañon, A., Whitfield-Gabrieli, S. & Kanwisher, N. (2010). A new method for fMRI investigations of language: Defining ROIs functionally in individual subjects. *Journal of Neurophysiology*, 104, 1177-1194

Fedorenko, E., McDermott, J., Norman-Haignere, S., & Kanwisher, N. (2012b). Sensitivity to musical structure in the human brain. *Journal Of Neurophysiology*, *108*(12), 3289-3300.

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends In Cognitive Sciences*, *8*(7), 307-314.

Fiez, J., Raichle, M., Miezin, F., Petersen, S., Tallal, P., & Katz, W. (1995). PET Studies of Auditory and Phonological Processing: Effects of Stimulus Characteristics and Task Demands. *Journal Of Cognitive Neuroscience*, *7*(3), 357-375.

Fitzroy, A., & Sanders, L. (2013). Musical Expertise Modulates Early Processing of Syntactic Violations in Language. *Frontiers In Psychology*, *3*, 603.

Fletcher, P., Happé, F., Frith, U., Baker, S., Dolan, R., Frackowiak, R., & Frith, C. (1995). Other minds in the brain: a functional imaging study of "theory of mind" in story comprehension. *Cognition*, *57*(2), 109-128.

Fodor, J., (1981). The mind-body problem. *Scientific American*, *244*, 114-125.

Fodor, J., (1983). The Modularity of mind. MIT Press, Cambridge, MA.

Frank, M., Everett, D., Fedorenko, E., & Gibson, E. (2008). Number as a cognitive technology: Evidence from Pirahã language and cognition. *Cognition*, *108*(3), 819-824.

Friederici, A. D., Pfeifer, E., & Hahne, A. (1993). Event-Related brain potentials during natural speech processing: Effects of semantic, morphological and syntactic violations. *Brain Res Cogn Brain Res*, *1*(3), 183-92.

Fujioka, T., Trainor, L., Ross, B., Kakigi, R., & Pantev, C. (2005). Automatic Encoding of Polyphonic Melodies in Musicians and Nonmusicians. *Journal Of Cognitive Neuroscience*, *17*(10), 1578-1592.

Gallagher, H., Happé, F., Brunswick, N., Fletcher, P., Frith, U., & Frith, C. (2000). Reading the mind in cartoons and stories: an fMRI study of 'theory of mind' in verbal and nonverbal tasks. *Neuropsychologia*, *38*(1), 11-21.

Gallistel, C. (1990). *The organization of learning*. Cambridge, Mass.: MIT Press.

Garrido, M., Kilner, J., Stephan, K., & Friston, K. (2009). The mismatch negativity: A review of underlying mechanisms. *Clinical Neurophysiology*, *120*(3), 453-463.

Garza Villarreal, E., Brattico, E., Leino, S., Østergaard, L., & Vuust, P. (2011). Distinct neural responses to chord violations: A multiple source analysis study. *Brain Research*, *1389*, 103-114.

Giard, M., Perrin, F., Pernier, J., & Bouchet, P. (1990). Brain Generators Implicated in the Processing of Auditory Stimulus Deviance: A Topographic Event-Related Potential Study. *Psychophysiology*, *27*(6), 627-640.

Gobbini, M., Koralek, A., Bryan, R., Montgomery, K., & Haxby, J. (2007). Two Takes on the Social Brain: A Comparison of Theory of Mind Tasks. *Journal Of Cognitive Neuroscience*, *19*(11), 1803-1814.

Goel, V. (2007). Anatomy of deductive reasoning. *Trends In Cognitive Sciences*, *11*(10), 435-441.

Goldberg, A. E. (1995). *Constructions: A Construction Grammar Approach to Argument Structure*. Chicago: University of Chicago Press.

Gomot, M., Giard, M., Roux, S., Barthélémy, C., & Bruneau, N. (2000). Maturation of frontal and temporal components of mismatch negativity (MMN) in children. *Neuroreport*, *11*(14), 3109-3112.

Gordon, P.C., Hendrik, R., & Levine, W.H. (2002). Memory-load interference in syntactic processing. *Psychological Science*, *13*(5), 425-430.

Gouteux, S., Thinus-Blanc, C., & Vauclair, J. (2001). Rhesus monkeys use geometric and nongeometric information during a reorientation task. *Journal Of Experimental Psychology: General*, *130*(3), 505-519.

Gray, J., & Thompson, P. (2004). Neurobiology of intelligence: science and ethics. *Nature Reviews Neuroscience*, *5*(6), 471-482.

Griffiths, T.D., Rees, A., Witton, C., Cross, P.M., Shakir, R.A. & Green, G.G.R. (1997). Spatial and temporal auditory processing deficits following right hemisphere infarction. A psychophysical study. *Brain*, *120*(5), 785-794.

Hagoort, P., Brown, C., & Groothusen, J. (1993). The syntactic positive shift (sps) as an erp measure of syntactic processing. *Language And Cognitive Processes*, *8*(4), 439-483.

Hale, C., & Tager-Flusberg, H. (2003). The influence of language on theory of mind: a training study. *Developmental Science*, *6*(3), 346-359.

Hamame, C.M., Szwed, M., Sharman, M., Vidal, J., Perrone-Bertolotti, M., & Kahane, P. et al. (2013). Dejerine's reading area revisited with intracranial EEG: Selective responses to letter strings. *Neurology*, *80*(6), 602-603.

Handel, S. (1989). *Listening: An Introduction to the Perception of Auditory Events*. MIT Press.

Happé, F., Brownell, H., & Winner, E. (1999). Acquired `theory of mind' impairments following stroke. *Cognition*, *70*(3), 211-240.

Fedorenko, E., & Varley, R. (2016). Language and thought are not the same thing: Evidence from neuroimaging and neurological patients. Annals of the New York Academy of Sciences. 1369, 132-153.*doi:10.1111/nyas.13046*

Hare, B., & Yamamoto, S. (2015). *Bonobo Cognition and Behaviour*. Leiden: Brill Academic Pub.

Hauser, M. (1997). *The Evolution of Communication*. Cambridge, Mass.: MIT Press.

Hauser, M., & Carey, S. (2003). Spontaneous representations of small numbers of objects by rhesus macaques: Examinations of content and format. *Cognitive Psychology*, *47*(4), 367-401.

Hauser, M., & Konishi, M. (1999). *The Design of animal communication*. Cambridge, Ma.: MIT Press.

Hauser, M., Chomsky, N., & Fitch, W. (2002). The Faculty of Language: What Is It, Who Has It, and How Did It Evolve?. *Science*, *298*(5598), 1569-1579.

Herculano-Houzel, S. (2012). The remarkable, yet not extraordinary, human brain as a scaled-up primate brain and its associated cost. *Proceedings Of The National Academy Of Sciences*, *109*(Supplement_1), 10661-10668.

Herdener, M., Humbel, T., Esposito, F., Habermeyer, B., Cattapan-Ludewig, K., & Seifritz, E. (2012). Jazz Drummers Recruit Language-Specific Areas for the Processing of Rhythmic Structure. *Cerebral Cortex*, *24*(3), 836-843.

Herman, L., Pack, A., & Morrel-Samuels, P. (1993). Representational and conceptual skills of dolphins. In H. Roitblat, L. Herman & P. Nachtigall, *Language and Communication: Comparative Perspectives* (1st ed., pp. 273-298). Hillside, NJ: Lawrence Erlbaum.

Hermer-Vazquez, L., Spelke, E.S., Katsnelson, A.S., (1999). Sources of flexibility in human Cognition: Dual-Task Studies of Space and Language. *Cognitive Psychology*, *39*(1), 3-36.

Hillis, A., Work, M., Barker, P., Jacobs, M., Breese, E., & Maurer, K. (2004). Re-examining the brain regions crucial for orchestrating speech articulation. *Brain*, *127*(7), 1479-1487.

Hoch, L., Poulin-Charronnat, B., & Tillmann, B. (2011). The Influence of Task-Irrelevant Music on Language Processing: Syntactic and Semantic Structures. *Frontiers In Psychology*, *2*, 112.

Hurley, S., & Nudds, M. (2006). *Rational animals?*. Oxford: Oxford University Press.

Jackendoff, R. (1977). *X-bar-Syntax: A Study of Phrase Structure*. Linguistic Inquiry Monograph 2. Cambridge, MA: MIT Press.

Jackendoff, R. (2002). *Foundations of Language: Brain, Meaning, Grammar, Evolution*. Oxford University Press.

Jackendoff, R. (2007). A parallel architecture perspective on language processing. *Brain Research*, 1146, 2–22

Janata P. (1995). ERP measures assay the degree of expectancy violation of harmonic contexts in music. *Journal of Cognitive Neuroscience*, *7*(2), 153-164.

January, D., Trueswell, J. C., & Thompson-Schill, S. L. (2009). Co-Localization of stroop and syntactic ambiguity resolution in broca's area: Implications for the neural basis of sentence processing. J Cogn Neurosci, 21(12), 2434-44.

Jenkins, A., & Mitchell, J. (2009). Mentalizing under Uncertainty: Dissociated Neural Responses to Ambiguous and Unambiguous Mental State Inferences. *Cerebral Cortex, 20*(2), 404-410.

Joshi, A., Levy, L., & Takahashi, M. (1975). Tree adjunct grammars. *Journal Of Computer And System Sciences*, *10*(1), 136-163.

Kaan, E. & Swaab, T.Y. (2002). The brain circuitry of syntactic comprehension. *Trends in Cognitive Science, 6*(8), 350-356.

Kalbe, E., Schlegel, M., Sack, A., Nowak, D., Dafotakis, M., & Bangard, C. et al. (2010). Dissociating cognitive from affective theory of mind: A TMS study. *Cortex*, *46*(6), 769-780.

Kanwisher, N. (2010). Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings Of The National Academy Of Sciences*, *107*(25), 11163-11170.

Kaplan, G. (2014). Animal communication. *Wiley Interdisciplinary Reviews: Cognitive Science*, *5*(6), 661-677.

Karmiloff-Smith, A. (1992). *Beyond Modularity: A Developmental Perspective on Cognitive Science*. Cambridge, Mass.: MIT Press.

Kinsella, A. (2009). *Language evolution and syntactic theory*. Cambridge: Cambridge University Press.

Klessinger, N., Szczerbinski, M., & Varley, R. (2012). The role of number words: the phonological length effect in multidigit addition. *Memory & Cognition*, *40*(8), 1289-1302.

Koelsch, S. (2006). Significance of Broca's area and ventral premotor cortex for music-syntactic processing. *Cortex, 42*(4), 518-20.

Koelsch, S., Fritz, T., Schulze, K., Alsop, D., & Schlaug, G. (2005). Adults and children processing music: An fMRI study. *Neuroimage*, *25*(4), 1068-1076.

Koelsch, S., Gunter, T. C., von Cramon, D. Y., Zysset, S., Lohmann, G., & Friederici, A. D. (2002). Bach speaks: A cortical "language-network" serves the processing of music. Neuroimage, 17, 956-966.

Koelsch, S., Gunter, T., Friederici, A., & Schröger, E. (2000). Brain Indices of Music Processing: "Nonmusicians" are Musical. *Journal Of Cognitive Neuroscience, 12*(3), 520-541.

Koelsch, S., Gunter, T., v. Cramon, D., Zysset, S., Lohmann, G., & Friederici, A. (2002). Bach Speaks: A Cortical "Language-Network" Serves the Processing of Music. *Neuroimage*, *17*(2), 956-966.

Koelsch, S., Gunter, T.C., Schroger, E., Tervaniemi, M., Sammler, D. & Friederici, A.D. (2001). Differentiating ERAN and MMN: An ERP study. *NeuroReport, 12*(7), 1385-1389.

Kolk, H.H., Chwilla, D.J., (2007). Late Positivities in unusual situations: a commentary to (a) Kuperberg, Kreher, Sitnikova, Caplan and Holcomb and (b) Kemmerer, Weber-Fox, Price, Zdanczyk and Way. *Brain Language*, *100*(3), 257–262.

Fedorenko, E., & Varley, R. (2016). Language and thought are not the same thing: Evidence from neuroimaging and neurological patients. Annals of the New York Academy of Sciences. 1369, 132-153.*doi:*10.1111/nyas.13046

Krumhansl, C., & Keil, F. (1982). Acquisition of the hierarchy of tonal functions in music. *Memory & Cognition*, *10*(3), 243-251.

Kumar, S., Filipski, A., Swarna, V., Walker, A., & Hedges, S. (2005). Placing confidence limits on the molecular age of the human-chimpanzee divergence. *Proceedings Of The National Academy Of Sciences*, *102*(52), 18842-18847.

Learmonth, A.E., Newcombe, N.S., & Huttenlocher, J., (2001). Toddler's use of metric information and landmarks to reorient. *Journal of Experimental Child Psychology 80* (3), 225-244.

Leino, S., Brattico, E., Tervaniemi, M., & Vuust, P. (2007). Representation of harmony rules in the human brain: Further evidence from event-related potentials. *Brain Research*, *1142*, 169-177.

Lerdahl, F., & Jackendoff, R. (1977). Toward a Formal Theory of Tonal Music. *Journal Of Music Theory*, *21*(1), 111.

Lerdahl, F., & Jackendoff, R. (1983). *A generative grammar of tonal music*. Cambridge, MA: MIT Press.

Levitin, D. J., & Menon, V. (2003). Musical structure is processed in "language" areas of the brain: A possible role for brodmann area 47 in temporal coherence. *Neuroimage*, *20*(4), 2142-2152.

Levitin, D.J. & Menon, V. (2005). The neural locus of temporal structure and expectancies in music: Evidence from functional neuroimaging at 3 Tesla. *Music Perception*, *22*(3), 563-575.

Liegeois-Chauvel, C., Peretz, I., Babai, M., Laguitton, V., & Chauvel, P. (1998). Contribution of different cortical areas in the temporal lobes to music processing. *Brain*, *121*(10), 1853-1867.

Lindblom, B., & Sundberg, J. (1970). *Towards a generative theory of melody*. Stockholm: Dept. of Phonetics, Institute of Linguistics, University of Stockholm.

Longcamp, M., Lagarrigue, A., Nazarian, B., Roth, M., Anton, J.-L., Alario, F.-X. & Velay, J.-L. (2014). Functional specificity in the motor system : Evidence from coupled fMRI and kinematic recordings during letter and digit writing. *Human Brain Mapping*, 35, 6077-6087.

Loui, P., Grent-'t-Jong, T., Torpey, D., & Woldorff, M. (2005). Effects of attention on the neural processing of harmonic syntax in Western music. *Cognitive Brain Research*, *25*(3), 678-687.

Luria, A., Tsvetkova, L., & Futer, D. (1965). Aphasia in a composer. *Journal Of The Neurological Sciences*, *2*(3), 288-292.

Maess, B., Jacobsen, T., Schröger, E., & Friederici, A. (2007). Localizing pre-attentive auditory memory-based comparison: Magnetic mismatch negativity to pitch change. *Neuroimage*, *37*(2), 561-571.

Maess, B., Koelsch, S., Gunter, T.C. & Friederici, A.D. (2001). Musical syntax is processed in Broca's Area: An MEG study. Nature Neuroscience, 4, 540-545.

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Mantini, D., Gerits, A., Nelissen, K., Durand, J., Joly, O., & Simone, L. et al. (2011). DefaultMode of Brain Function in Monkeys. *Journal Of Neuroscience*, *31*(36), 12954-12962.

Marin, O.S.M. (1982). *Neurological aspects of music perception and performance*. The psychology of music. Academic Press, Inc. New York, NY.

Maruyama, M., Pallier, C., Jobert, A., Sigman, M., & Dehaene, S. (2012). The cortical representation of simple mathematical expressions. *Neuroimage*, *61*(4), 1444-1460.

Matsuzawa, T. (2009). The chimpanzee mind: in search of the evolutionary roots of the human mind. *Animal Cognition*, *12*(S1), 1-9.

McDermott, J., & Hauser, M. (2005). The origins of music: Innateness, uniqueness, and evolution. *Music Perception*, *23*(1), 29-59.

Miller, E., & Cohen, J. (2001). An integrative theory of prefrontal cortex function. *Annual Reviews Neuroscience*, *24*, 167-202.

Milligan, K., Astington, J., & Dack, L. (2007). Language and Theory of Mind: Meta-Analysis of the Relation Between Language Ability and False-belief Understanding. *Child Development*, *78*(2), 622-646.

Miranda, R., & Ullman, M. (2007). Double dissociation between rules and memory in music: An event-related potential study☆. *Neuroimage*, *38*(2), 331-345.

Monti, M. M., Osherson, D., Martinez, M., & Parsons, L. (2007). Functional neuroanatomy of deductive inference: A language-independent distributed network. *Neuroimage*, *37*(3), 1005-1016.

Monti, M., Parsons, L., & Osherson, D. (2009). The boundaries of language and thought in deductive inference. *Proceedings Of The National Academy Of Sciences*, *106*(30), 12554-12559.

Monti, M., Parsons, L., & Osherson, D. (2012). Thought Beyond Language: Neural Dissociation of Algebra and Natural Language. *Psychological Science*, *23*(8), 914-922.

Näätänen, R., Gaillard, A.W. & Mäntysalo, S. (1978). Early selective-attention effect on evoked potential reinterpreted. *Acta Psychologica*, *42*(4), 313–29.

Näätänen, R., Paavilainen, P., Rinne, T., & Alho, K. (2007). The mismatch negativity (MMN) in basic research of central auditory processing: A review. *Clinical Neurophysiology*, *118*(12), 2544-2590.

Neuloh, G., & Curio, G. (2004). Does familiarity facilitate the cortical processing of music sounds?. *Neuroreport*, *15*(16), 2471-2475.

Neville, H., Nicol, J., Barss, A., Forster, K., & Garrett, M. (1991). Syntactically Based Sentence Processing Classes: Evidence from Event-Related Brain Potentials. *Journal Of Cognitive Neuroscience*, *3*(2), 151-165.

Niedeggen, M., & Rosler, F. (1999). N400 Effects Reflect Activation Spread During Retrieval of Arithmetic Facts. *Psychological Science*, *10*(3), 271-276.

Fedorenko, E., & Varley, R. (2016). Language and thought are not the same thing: Evidence from neuroimaging and neurological patients. Annals of the New York Academy of Sciences. 1369, 132-153.*doi:10.1111/nyas.13046*

Nieto-Castañón, A., & Fedorenko, E. (2012). Subject-specific functional localizers increase sensitivity and functional resolution of multi-subject analyses. *Neuroimage, 63*(3), 1646-1669.

Norman-Haignere, S., Kanwisher, N. & McDermott, J. (submitted). Hypothesis-Free Decomposition of Voxel Responses to Natural Sounds Reveals Distinct Cortical Pathways for Music and Speech

Novais-Santos, S., Gee, J., Shah, M., Troiani, V., Work, M., & Grossman, M. (2007). Resolving sentence ambiguity with planning and working memory resources: Evidence from fMRI. *Neuroimage*, *37*(1), 361-378.

Novick, J.M., Trueswell, J.C., & Thompson-Schill, S.L. (2005). Cognitive control and parsing: Reexamining the role of Broca's area in sentence comprehension. *Cognitive, Affective, and Behavioral Neuroscience*, *5*(3), 263-281.

Núñez-Peña, M.I. & Honrubia, M.L. (2004). P600 related to rule violation in an arithmetic task. *Cognitive Brain Research, 18*(2), 130-141.

Opitz, B., Rinne, T., Mecklinger, A., von Cramon, D., & Schröger, E. (2002). Differential contribution of frontal and temporal cortices to auditory change detection: fMRI and ERP results. *Neuroimage*, *15*(1), 167-174.

Osterhout, L., & Holcomb, P. (1993). Event-related potentials and syntactic anomaly: Evidence of anomaly detection during the perception of continuous speech. *Language And Cognitive Processes*, *8*(4), 413-437.

Overath, T., McDermott, J., Zarate, J., & Poeppel, D. (2015). The cortical analysis of speech-specific temporal structure revealed by responses to sound quilts. *Nature Neuroscience*, *18*(6), 903-911.

Patel, A. (2003). Language, music, syntax and the brain. *Nature Neuroscience,* 6(7), 674-681.

Patel, A., Iversen, J., Wassenaar, M., & Hagoort, P. (2008). Musical syntactic processing in agrammatic Broca's aphasia. *Aphasiology*, *22*(7-8), 776-789.

Patel, A., Peretz, I., Tramo, M., & Labreque, R. (1998). Processing Prosodic and Musical Patterns: A Neuropsychological Investigation. *Brain And Language*, *61*(1), 123-144.

Penn, D., & Povinelli, D. (2007). Causal Cognition in Human and Nonhuman Animals: A Comparative, Critical Review. *Annual Review Of Psychology*, *58*(1), 97-118.

Peretz, I. & Coltheart, M. (2003). Modularity of music processing. *Nature Neuroscience, 6*(7), 688-691.

Peretz, I. & Hyde, K. (2003). What is specific to music processing? Insights from congenital amusia. *Trends in Cognitive Sciences*, 7(8), 362-367.

Peretz, I. (1993). Auditory atonalia for melodies. *Cognitive Neuropsychology*, *10*(1), 21-56.

Peretz, I., Kolinsky, R., Tramo, M., Labrecque, R., Hublet, C., Demeurisse, G., & Belleville, S. (1994). Functional dissociations following bilateral lesions of auditory cortex. *Brain*, *117*(6), 1283-1301.

Peretz, I., Vuvan, D., Lagrois, M., & Armony, J. (2015). Neural overlap in processing music and speech. *Philosophical Transactions Of The Royal Society B: Biological Sciences*, *370*(1664), 20140090-20140090.

Perner, J., Aichhorn, M., Kronbichler, M., Staffen, W., & Ladurner, G. (2006). Thinking of mental and other representations: The roles of left and right temporo-parietal junction. *Social Neuroscience*, *1*(3-4), 245-258.

Perreault, C., & Mathew, S. (2012). Dating the Origin of Language Using Phonemic Diversity. *Plos ONE*, *7*(4), e35289.

Perruchet P, Poulin-Charronnat B. (2013). Challenging prior evidence for a shared syntactic processor for language and music. *Psychon Bull Rev.*, *20*(2), 310-317.

Phillips-Silver, J., Toiviainen, P., Gosselin, N., Piche, O., Nozaradan, S., Palmer, C., & Peretz, I. (2011). Born to dance but beat deaf: a new form of congenital amusia. *Neuropsychologia*, *49*(5), 961-969.

Pica, P., Leme, C., Izard, V., & Dehaene, S. (2004). Exact and Approximate Arithmetic in an Amazonian Indigene Group. *Science*, *306*(5695), 499-503.

Piccirilli, M., Sciarma, T., & Luzzi, S. (2000). Modularity of music: evidence from a case of pure amusia. *Journal Of Neurology, Neurosurgery & Psychiatry*, *69*(4), 541-545.

Polk, M., & Kertesz, A. (1993). Music and Language in Degenerative Disease of the Brain. *Brain And Cognition*, *22*(1), 98-117.

Pollard, C., & Sag, I. A. (1994). *Head-driven phrase structure grammar*. Chicago: University of Chicago Press.

Premack, D. (2007). Human and animal cognition: Continuity and discontinuity. *Proceedings Of The National Academy Of Sciences*, *104*(35), 13861-13867.

Pritchard, W. (1981). Psychophysiology of P300. *Psychological Bulletin*, *89*(3), 506-540.

Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings Of The National Academy Of Sciences*, *98*(10), 5937-5942.

Rinne, T., Alho, K., Ilmoniemi, R., Virtanen, J., & Näätänen, R. (2000). Separate Time Behaviors of the Temporal and Frontal Mismatch Negativity Sources. *Neuroimage*, *12*(1), 14-19

Roads, C. (1979). Grammars as Representations for Music. *Computer Music Journal*, *3*(1), 48.

Rodd, J. M., Davis, M. H., & Johnsrude, I. S. (2005). The neural mechanisms of speech comprehension: Fmri studies of semantic ambiguity. *Cereb Cortex*, *15*(8), 1261-9.

Roffman, I., Savage-Rumbaugh, S., Rubert-Pugh, E., Stadler, A., Ronen, A., & Nevo, E. (2015). Preparation and use of varied natural tools for extractive foraging by bonobos (Pan Paniscus). *Am. J. Phys. Anthropol.*, *158*(1), 78-91.

Rogalsky, C., Rong, F., Saberi, K., & Hickok, G. (2011). Functional anatomy of language and music perception: Temporal and structural factors investigated using fMRI. *Journal of Neuroscience*, *31*(10), 3843-3852.

Fedorenko, E., & Varley, R. (2016). Language and thought are not the same thing: Evidence from neuroimaging and neurological patients. Annals of the New York Academy of Sciences. 1369, 132-153.*doi:*[*10.1111/nyas.13046*](https://doi.org/10.1111/nyas.13046)

Ruby, P., & Decety, J. (2003). What you believe versus what you think they believe: a neuroimaging study of conceptual perspective-taking. *European Journal Of Neuroscience*, *17*(11), 2475-2480.

Saarinen, J., Paavilainen, P., Schöger, E., Tervaniemi, M., & Näätänen, R. (1992). Representation of abstract attributes of auditory stimuli in the human brain. *Neuroreport*, *3*(12), 1149-1151.

Sammler, D., Koelsch, S., & Friederici, A. (2011). Are left fronto-temporal brain areas a prerequisite for normal music-syntactic processing?. *Cortex*, *47*(6), 659-673.

Sammler, D., Novembre, G., Koelsch, S., & Keller, P. (2013). Syntax in a pianist's hand: ERP signatures of "embodied" syntax processing in music. *Cortex*, *49*(5), 1325-1339.

Samson, D., Apperly, I., Chiavarino, C., & Humphreys, G. (2004). Left temporoparietal junction is necessary for representing someone else's belief. *Nature Neuroscience*, *7*(5), 499-500.

Samson, S., & Zatorre, R. (1994). Contribution of the right temporal lobe to musical timbre discrimination. *Neuropsychologia*, *32*(2), 231-240.

Saxe, R. (2006). Uniquely human social cognition. *Current Opinion In Neurobiology*, *16*(2), 235-239.

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in "theory of mind". *Neuroimage*, *19*(4), 1835-42.

Saxe, R., & Powell, L. (2006). It's the thought that counts: Specific brain regions for one component of theory of mind. *Psychological Science*, *17*(8), 692-699.

Saxe, R., & Wexler, A. (2005). Making sense of another mind: The role of the right temporo-parietal junction. *Neuropsychologia*, *43*(10), 1391-1399.

Schabes, Y., Abeille, A. & Joshi A.K. (1988). Parsing strategies with 'lexicalized' grammars: Application to tree adjoining grammars. *Proceedings of the 12th International Conference on Computational Linguistics*. Budapest, Hungary

Schonwiesner, M., Krumbholz, K., Rubsamen, R., Fink, G., & von Cramon, D. (2007). Hemispheric Asymmetry for Auditory Processing in the Human Auditory Brain Stem, Thalamus, and Cortex. *Cerebral Cortex*, *17*(2), 492-499.

Schusterman, R., Thomas, J., & Wood, F. (2013). *Dolphin cognition and behavior: A Comparative Approach*. Hillsdale: Taylor & Francis Group.

Schwarzlose, R., Baker, C., & Kanwisher, N. (2005). Separate Face and Body Selectivity on the Fusiform Gyrus. *Journal Of Neuroscience*, *25*(47), 11055-11059.

Shallice, T. (1988). From Neuropsychology to Mental Structure. Cambridge: CUP.

Shusterman, A., Ah Lee, S., & Spelke, E. (2011). Cognitive effects of language on human navigation. *Cognition*, *120*(2), 186-201.

Siegal, M., Carrington, J., & Radel, M. (1996). Theory of Mind and Pragmatic Understanding Following Right Hemisphere Damage. *Brain And Language*, *53*(1), 40-50.

Slaughter, V., & Gopnik, A. (1996). Conceptual Coherence in the Child's Theory of Mind: Training Children to Understand Belief. *Child Development*, *67*(6), 2967.

Slevc, L., Rosenberg, J., & Patel, A. (2009). Making psycholinguistics musical: Self-paced reading time evidence for shared processing of linguistic and musical syntax. *Psychonomic Bulletin & Review*, *16*(2), 374-381.

Snowdon, C. (1990). Language capacities of nonhuman animals. *Am. J. Phys. Anthropol.*, *33*(S11), 215-243.

Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2002). Modularity and spatial reorientation in a simple mind: Encoding of geometric and nongeometric properties of a spatial environment by fish. *Cognition*, *85*(2), 51–59.

Srihasam, K., & Livingstone, M. (2011). Anatomical correlates of early vs. late symbol training. *Journal Of Vision*, *11*(11), 1009-1009.

Stanescu-Cosson, R., Pinel, P., van de Moortele, P., Le Bihan, D., Cohen, L., & Dehaene, S. (2000). Understanding dissociations in dyscalculia: A brain imaging study of the impact of number size on the cerebral networks for exact and approximate calculation. *Brain*, *123*(11), 2240-2255.

Steinhauer, K. & Drury, J.E. (2012). On the early left-anterior negativity (ELAN) in syntax studies. *Brain and Language*, *120*(2), 135-162.

Steinke, W., Cuddy, L., & Jakobson, L. (2001). Dissociations among functional subsystems governing melody recognition after right-hemisphere damage. *Cognitive Neuropsychology*, *18*(5), 411-437.

Steinke, W.R, Cuddy, L.L., & Holden, R.R. (1997). Dissociation of musical tonality and pitch memory from nonmusical cognitive abilities. *Canadian Journal of Experimental Psychology, 51*(4), 316-334.

Stewart, L. (2006). Music and the brain: disorders of musical listening. *Brain*, *129*(10), 2533-2553.

Suddendorf, T., & Corballis, M. (2007). The evolution of foresight: What is mental time travel, and is it unique to humans?. *Behavioral And Brain Sciences*, *30*(03), 299-313.

Sundberg, J., & Lindblom, B. (1976). Generative theories in language and music descriptions. *Cognition*, *4*(1), 99-122.

Sutton, J. E., Twyman, A. D., Joanisse, M. F., Newcombe, N. S. (2012). Geometry three ways: An fMRI investigation of geometric information processing during reorientation. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 38* (6), 1530-1541.

Swain, J.P. (1995). The Concept of Musical Syntax. *Musical Quarterly*, 79(2), 281-308.

Taylor, A., Hunt, G., Holzhaider, J., & Gray, R. (2007). Spontaneous Metatool Use by New Caledonian Crows. *Current Biology*, *17*(17), 1504-1507.

Tervaniemi, M., Maury, S., & Näätänen, R. (1994). Neural representations of abstract stimulus features in the human brain as reflected by the mismatch negativity. *Neuroreport*, *5*(7), 844-846.

Tillmann, B., Janata, P., & Bharucha, J. (2003). Activation of the inferior frontal cortex in musical priming. *Cognitive Brain Research*, *16*(2), 145-161.

Tillmann, B., Koelsch, S., Escoffier, N., Bigand, E., Lalitte, P., Friederici, A., & von Cramon, D. (2006). Cognitive priming in sung and instrumental music: Activation of inferior frontal cortex. *Neuroimage*, *31*(4), 1771-1782.

Tomasello, M., & Rakoczy, H. (2003). What Makes Human Cognition Unique? From Individual to Shared to Collective Intentionality. *Mind And Language*, *18*(2), 121-147.

Tomasello, M., Call, J., & Hare, B. (2003). Chimpanzees understand psychological states – the question is which ones and to what extent. *Trends In Cognitive Sciences*, *7*(4), 153-156.

Trainor, L., & Zatorre, R. (2009). The neurobiological basis of musical expectations: From probabilities to emotional meaning. In S. Hallen, I. Cross & M. Thaut, *Oxford Handbook of Music Psychology* (1st ed., pp. 171-182). Oxford University Press.

Trainor, L., McDonald, K., & Alain, C. (2002). Automatic and Controlled Processing of Melodic Contour and Interval Information Measured by Electrical Brain Activity. *Journal Of Cognitive Neuroscience*, *14*(3), 430-442.

Trbovich, P. L. & LeFevre, J. A. (2003). Phonological and visual working memory in mental addition. *Memory & Cognition, 31*(5), 738-745.

Twyman, A., Friedman, A., & Spetch, M. L. (2007). Penetrating the geometric module: Catalyzing children's use of landmarks. *Developmental Psychology, 43*(6), 1523–1530

Van Harskamp, N., & Cipolotti, L. (2001). Selective Impairments for Addition, Subtraction and Multiplication. Implications for the Organisation of Arithmetical Facts. *Cortex, 37*(3), 363-388.

van Zuijen TL, et al. (2004). Grouping of sequential sounds: An event-related potential study comparing musicians and nonmusicians. *Journal of Cognitive Neuroscience, 16*(2), 331-338.

Varley, R., & Siegal, M. (2000). Evidence for cognition without grammar from causal reasoning and 'theory of mind' in an agrammatic aphasic patient. *Current Biology*, *10*(12), 723-726.

Varley, R., Klessinger, N., Romanowski, C., & Siegal, M. (2005). From The Cover: Agrammatic but numerate. *Proceedings Of The National Academy Of Sciences, 102*(9), 3519-3524.

Varley, R., Siegal, M., & Want, S. (2001). Severe Impairment in Grammar Does Not Preclude Theory of Mind. *Neurocase*, *7*(6), 489-493.

Vissers, C. T., Chwilla, D. J., & Kolk, H. H. J. (2006). Monitoring in language perception: The effect of misspellings of words in highly constrained sentences. *Brain Research*, *1106*(1), 150-163.

Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happé, F., & Falkai, P. et al. (2001). Mind Reading: Neural Mechanisms of Theory of Mind and Self-Perspective. *Neuroimage*, *14*(1), 170-181.

Fedorenko, E., & Varley, R. (2016). Language and thought are not the same thing: Evidence from neuroimaging and neurological patients. Annals of the New York Academy of Sciences. 1369, 132-153.*doi:10.1111/nyas.13046*

Vuust, P., Pallesen, K. J., Bailey, C., van Zuijen, T. L., Gjedde, A., Roepstorff, A., & Østergaard, L. (2005). To musicians, the message is in the meter pre-attentive neuronal responses to incongruent rhythm are left-lateralized in musicians. *Neuroimage*, *24*(2), 560-564.

Warrier, C., & Zatorre, R. (2004). Right temporal cortex is critical for utilization of melodic contextual cues in a pitch constancy task. *Brain*, *127*(7), 1616-1625.

Wellman, H., Cross, D., & Watson, J. (2001). Meta-Analysis of Theory-of-Mind Development: The Truth about False Belief. *Child Development*, *72*(3), 655-684.

Whalen, J., Gallistel, C., & Gelman, R. (1999). Nonverbal Counting in Humans: The Psychophysics of Number Representation. *Psychological Science*, *10*(2), 130-137.

Whiten, A. (2011). The scope of culture in chimpanzees, humans and ancestral apes. *Philosophical Transactions Of The Royal Society B: Biological Sciences*, *366*(1567), 997-1007.

Whiteside, S.P., Dyson, L., Cowell, P.E. & Varley, R.A. (2015). The Relationship Between Apraxia of Speech and Oral Apraxia: Association or Dissociation? *Archives of Clinical Neuropsychology*, acv051.

Willems, R., Benn, Y., Hagoort, P., Toni, I., & Varley, R. (2011). Communicating without a functioning language system: Implications for the role of language in mentalizing. *Neuropsychologia*, *49*(11), 3130-3135.

Wilson, S., & Pressing, J. (1999). Neuropsychological assessment and the modeling of musical deficits. In R. Pratt & D. Erdonmez Grocke, *Music Medicine and Music Therapy: Expanding horizons* (1st ed., pp. 47-74). Melbourne: The University of Melbourne.

Wilson, S., Pressing, J., & Wales, R. (2002). Modelling rhythmic function in a musician post-stroke. *Neuropsychologia*, *40*(8), 1494-1505.

Wynn, K. (1990). Children's understanding of counting. *Cognition*, *36*(2), 155-193.

Xu, F., Carey, S., & Quint, N. (2004). The emergence of kind-based object individuation in infancy. *Cognitive psychology*, *49*(2), 155-190.

Young, L., & Saxe, R. (2009). Innocent intentions: A correlation between forgiveness for accidental harm and neural activity. *Neuropsychologia*, *47*(10), 2065-2072.

Young, L., Camprodon, J., Hauser, M., Pascual-Leone, A., & Saxe, R. (2010). Disruption of the right temporoparietal junction with transcranial magnetic stimulation reduces the role of beliefs in moral judgments. *Proceedings Of The National Academy Of Sciences*, *107*(15), 6753-6758.