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Language and thought are not the same thing: evidence from neuroimaging and neurological patients

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Is thought possible without language? Individuals with global aphasia, who have almost no ability to understand or produce language, provide a powerful opportunity to find out. Surprisingly, despite their near-total loss of language, these individuals are nonetheless able to add and subtract, solve logic problems, think about another person's thoughts, appreciate music, and successfully navigate their environments. Further, neuroimaging studies show that healthy adults strongly engage the brain's language areas when they understand a sentence, but not when they perform other nonlinguistic tasks such as arithmetic, storing information in working memory, inhibiting prepotent responses, or listening to music. Together, these two complementary lines of evidence provide a clear answer: many aspects of thought engage distinct brain regions from, and do not depend on, language.

Keywords: language; syntax; semantics; functional specificity; numerical cognition; cognitive control; executive functions; theory of mind; music; navigation; fMRI; neuropsychology; aphasia

My language to describe things in the world is very small, limited. My thoughts when I look at the world are vast, limitless and normal, same as they ever were. My experience of the world is not made less by lack of language but is essentially unchanged.[1]

Introduction

What thinking person has not wondered about the relationship between thought and language? When we express a thought in language, do we start with a fully formed idea and then "translate" it into a string of words? Or is the thought not fully formed until the string of words is assembled? In the former view, it should be possible to think even if we did not have language. In the latter view, thought completely depends on, and is not distinct from, language. Here, we argue that data from human cognitive neuroscience provide a crisp and clear answer to this age-old question about the relationship between thought and language.

One might argue that we already know the answer, from the simple fact that myriad forms of complex cognition and behavior are evident in nonhuman animals who lack language,[a] from chimpanzees[2–7] and bonobos[8,9] to marine mammals[10–12] and birds.[13,14] On the other hand, intuition and evidence suggest that human thought encompasses many cognitive abilities that are not present in animals (in anything like their human form), from arithmetic to music to the ability to infer what another person is thinking. Are these sophisticated cognitive abilities, then, dependent on language? Here, we use two methods from cognitive neuroscience to ask whether complex quintessentially human thought is distinct from, and possible without, language.

The first method is functional magnetic resonance imaging (fMRI), which can be used to ask whether language and thought are distinct in the brain. If a brain region supports both linguistic processing, and, say, musical processing, then it

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[a]Although all animal species exchange information with one another,[15] human language is unparalleled in the animal kingdom in its complexity and generative power.[16–20]

should be active during both. 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 they listen to music. The second method relies on individuals with global aphasia due to brain damage, enabling us to ask whether damage to the language system affects performance on various kinds of thought. If the language system—or some of its components—are critical for performing arithmetic or appreciating music, then damage to these brain regions should lead to deficits in these abilities. If, on the other hand, the language system is not necessary for nonlinguistic forms of thought, then focal damage to the language system should only affect language comprehension and/or production, leaving intact performance on nonlinguistic tasks.

We review evidence from these two methods, 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[18] or complex hierarchical structure.[21–23] In the case of theory of mind, some aspects of linguistic syntax have been argued by some to constitute a critical component of our representations of others' mental states.[24] Language also shares some cognitive requirements with domain-general executive functions like inhibition.[25]

However, in other cases, linguistic representations have been hypothesized to play key roles in domains that share little similarity in representations or computations. In particular, language has been argued to serve as a medium for integrating information across various specialized systems.[26,27] Thus, in addition to enabling communication between people, language may enable communication between

cognitive systems within a person. This kind of relationship is, for example, hypothesized to hold between language and spatial navigation.[26]

We argue, on the basis of 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 that damage to these regions affects an individual's ability to understand and produce language, but not to engage in many forms of complex thought.

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[28] (regions schematically marked in red in Fig. 1, adapted from Ref. 29). We are thus excluding from consideration (1) auditory and visual regions concerned with the perceptual analysis of speech sounds or visual orthography (marked in yellow and green in Fig. 1, respectively), and (2) 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 (i.e., to what extent do they overlap with brain regions that support nonlinguistic abilities?) can be—and has been—asked with respect to lower-level perceptual and motor regions. Briefly, it appears that some degree of specificity characterizes both auditory[30–32] and visual[33,34] perceptual regions. The answer is somewhat equivocal for the motor regions, and the degree of functional specificity of parts of the motor/premotor cortex for speech production over other motor behaviors, such as nonspeech 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—on the basis of patient evidence[35] (but compare with Ref. 36), although findings from fMRI generally do not support this claim.[29,37] However, dissociations between speech production and the production of nonspeech oral movements have been reported.[38] Furthermore, a recent fMRI study[39] has reported selectivity for letters over nonletter symbols in written production. Thus, the question clearly deserves further investigation.
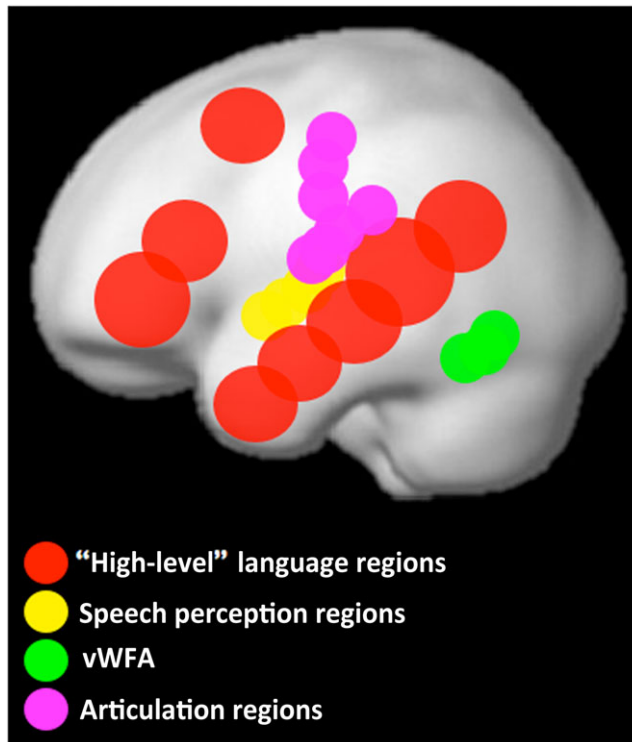
Figure 1. A schematic illustration of the approximate locations of brain regions that support perceptual (yellow, green), motor articulation (pink), and high-level (red) aspects of language processing. Adapted from Ref. 29.

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,[40–42] although the top-down effects of predictive processing are well accepted.[43–50] 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[51] (but compare with Ref. 52). However, no compelling evidence exists, in our opinion, for either (1) a consistent relationship between particular brain regions and particular mental operations in the patient literature or (2) the

spatial separability of different components of high-level language processing in fMRI.[53–55,b] Moreover, the language-processing brain regions form a deeply integrated functional system, as evidenced by both (1) strong anatomical connectivity[56] and (2) high correlations in neural activity over time during both rest and naturalistic cognition.[57,58] Thus here, we 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 complex thought.

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[b]Of course, it is possible that evidence may come along in the future revealing clear relationships between different aspects of language processing and particular brain regions, but repeated efforts to find such evidence have failed to date.

Review of the evidence

Language versus arithmetic processing

Previous work in numerical cognition has identified two distinct core systems underlying different aspects of numerical competence: (1) 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;[63–65] and (2) a large approximate number system (sometimes referred to as the analog magnitude-estimation system), which provides noisy estimates of large sets.[66] These core abilities are shared across species[67,68] and are present in prelinguistic infants.[65] 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,[69–71] 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.[72] Indeed, neuroimaging studies and studies in bilingual speakers provided some evidence in support of this view.[73–77] For example, Dehaene *et al.*[74] had participants perform an exact versus 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.*[74] 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.[78] 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,[28] because interindividual variability can give rise to apparent overlap at the group level even when the activations are entirely nonoverlapping in any given individual.[59]

A neuropsychological investigation that is characterized by a similar problematic inference was reported by Baldo and Dronkers,[79] who examined a large set of individuals with left hemisphere strokes and found (1) a correlation in performance between a language comprehension task and an arithmetic task and (2) overlap in brain regions whose damage was associated with linguistic and arithmetic deficits (including in the left inferior frontal gyrus). As discussed extensively in the literature in the 1980s and 1990s,[80,81] however, dissociations are more powerful than associations because an association can arise from damage to nearby but distinct regions. Curiously, Baldo and Dronkers[79] actually observed 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 took 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.[82] In particular, three such patients were able to solve a variety of mathematical problems that involved addition, subtraction, multiplication, division; small and large numbers; whole numbers and fractions; and expressions with brackets. Particularly surprising in these patients was the dissociation between their lack of sensitivity to structural information in language and 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 noncommutative math
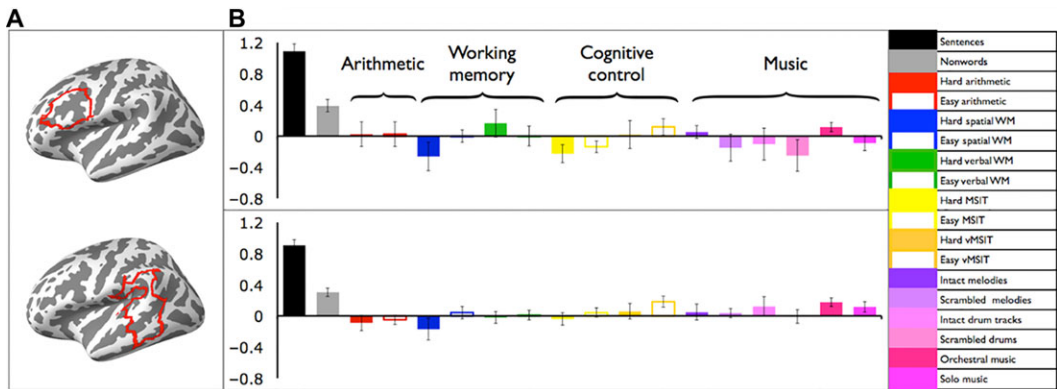
Figure 2. Functional response profiles of two high-level language processing brain regions. (A) Two functional "parcels" derived from a group-level representation of language activations (the LIFG and the LMidPostTemp parcels from Ref. 28) and used to constrain the selection of subject-specific regions of interest (ROIs). Individual ROIs were functionally defined: each parcel was intersected with the individual activation map for the language-localizer contrast (sentences > nonword lists[28]), and the top 10% of voxels were taken to be that participant's ROI. (B) Responses to the language-localizer conditions and a broad range of nonlinguistic tasks. Responses to the sentences and nonword conditions were estimated using across-runs cross validation,[59] 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 ((v) MSIT; (verbal) multisource interference task) tasks were reported in Ref. 60, and the data for the music conditions come from Ref. 61; see also Refs. 60 and 62.

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 positron emission tomography study[83] 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 *et al.*[60] evaluated this question more directly. Participants performed a language-understanding task in fMRI, which was used to localize language-responsive regions of interest in each participant individually. The responses of these brain regions were then examined while participants engaged in solving easier (with smaller numbers) or harder (with larger numbers) arithmetic addition problems. The language regions responded during the arithmetic conditions at the same level as, or below, a low-level fixation baseline condition (Fig. 2), strongly suggesting that the language system is not active when individuals engage in exact arithmetic. Similarly, Monti *et al.*[84] found that linguistic, but not algebraic, syntax produced activation in the inferior frontal cortex. Algebraic syntax produced instead responses in bilateral parietal

brain regions. Finally, Maruyama *et al.*[23] manipulated the syntactic complexity of algebraic operations and found activation in parietal (and occipital) regions, but not within the frontotemporal language system.

In summary, it appears that brain regions that respond robustly during linguistic processing are not generally (but see Ref. 85) active when arithmetic problems are solved. Furthermore, damage—even extensive damage—to the language regions appears to leave arithmetic abilities intact. We therefore conclude that linguistic processing occurs in brain circuits distinct from those that support arithmetic processing.

Language versus logical reasoning and other executive functions

In addition to the ability to exchange thoughts with one another via language, humans differ from other animals in the complexity of their thought processes.[86] In particular, humans are experts in organizing thoughts and actions according to internal goals. This structured behavior has been linked to a large number of theoretical constructs, including working memory, cognitive control, attention, and fluid intelligence.[87–89] 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 concerns the anatomical substrates of executive control. In particular, the prefrontal cortex has long been argued to be important.[87] Although, over the years, additional brain regions have been incorporated into the cognitive control network, including regions in the parietal cortices, the frontal lobes continue to figure prominently in accounts 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, therefore, is that language processing at least partially relies on domain-general circuits in the left frontal lobe.[25,90]

The second reason concerns the functional importance of cognitive control and working memory for language. It has been long known that these domain-general mechanisms play a role in language processing (e.g., see Ref. 91 for a recent review). For example, superadditive processing difficulties have been reported when participants perform a language task at the same time as a demanding working memory or inhibitory task.[69,92] 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.[93–95] These findings suggest that cognitive control mechanisms can and do sometimes support language processing, much as they support the processing of information in other domains.

So, how is the 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,[60] 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 and 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 the left frontal cortex in close proximity to the language-responsive regions.[96]

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.[97,98] examined the relationship between linguistic processing and logical reasoning—another ability that strongly draws on domain-general cognitive control resources[99]—and found largely nonoverlapping responses, with the language regions responding strongly during the processing of language stimuli but 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 and Siegal[100a] 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.[100b] Chess is perhaps the epitome of human intelligence/reasoning, with high demands on attention, working memory, planning, deductive reasoning, inhibition, and other faculties. Conversely, Reverberi et al.[101] found that patients with extensive lesions in the 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 concluded that language is, in fact, necessary for complex reasoning. In particular, using the Wisconsin Card Sorting Task,[102] Baldo et al.[103] reported impairments in aphasic individuals, but not in patients with left-hemisphere damage 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,[96] but also in the left temporoparietal 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,[80,81] so the fact that there exist severely aphasic individuals who have intact executive functions is strong evidence for the language system not being critical to those functions.
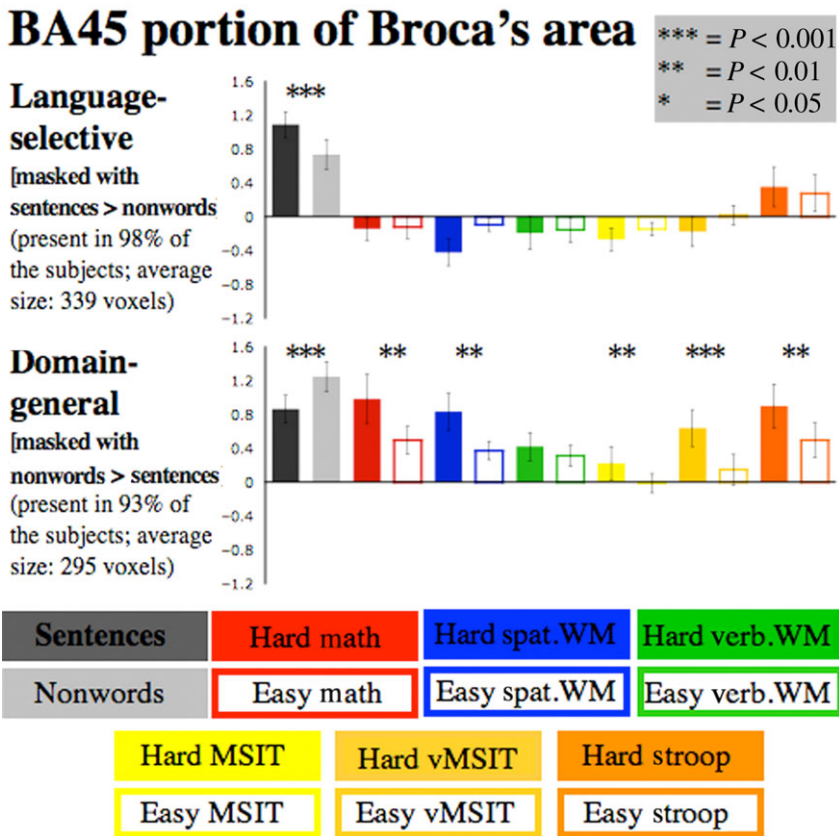
Figure 3. Functional response profiles of language-selective and domain-general regions within Broca's area (adapted from Ref. 96). Language-selective regions were defined by intersecting the anatomical parcel for BA45 with the individual activation maps for the language-localizer contrast (sentences > nonword lists[28]). Domain-general regions were defined by intersecting the same parcel with the individual activation maps for the nonword lists > sentences contrast. All magnitudes shown are estimated from data independent of those used to define the regions; responses to the sentences and nonwords are estimated using a left-out run.

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 (Fig. 3), as evidenced by clear dissociations observed in fMRI studies and the preserved abilities of at least some severely aphasic individuals to engage in complex nonlinguistic reasoning tasks.

Language versus theory of mind

A sophisticated ability to consider the subtleties of another's mental states when acting in the world, theory of mind (ToM) is yet another defining characteristic of humans.[104] Some have argued that certain linguistic (specifically, grammatical) representations are necessary for thinking about others'

minds.[24,105] 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.[106–110] Furthermore, training children with no understanding of false beliefs on certain linguistic constructions allows them to pass the false-belief task.[111–114] However, we are concerned here 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.

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.[115–121] These

regions include the right and left temporoparietal junction (TPJ), the precuneus, and regions in the medial prefrontal cortex. The right TPJ, in particular, is highly selective for thinking about someone else's thoughts and beliefs,[122–127] in line with both (1) early patient studies showing that damage to this region led to deficits in ToM reasoning[128,129] and (2) recent virtual lesion transcranial magnetic stimulation experiments.[130,131]

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,[132] and a recent study reported overlap between the left TPJ and the language regions.[133] 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.[100a,134–137] 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.[100a] Willems *et al.*[137] extended these observations to people with global aphasia. They employed a nonlinguistic 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 naive "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 interpret the intentions behind movement of a token in order to correctly locate and orient their tokens. Thus, although the potential theoretical significance of the overlap observed between

language comprehension and ToM 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.

Language versus music processing

Language and music—two universal cognitive abilities unique to humans[138]—share multiple features. Apart from the obvious surface-level similarity, with both involving temporally unfolding sequences of sounds with a salient rhythmic and melodic structure,[139,140] there is a deeper parallel: language and music exhibit similar structural properties, as has been noted for many years (e.g., Riemann[141] and Refs. 142–150). 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 human adults 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[151–153] (and see Refs. 154 and 155 for original reports of the P600 response to syntactic violations in language) and the early anterior negativity, present more strongly in the right hemisphere (early right anterior negativity (eRAN);[152,156–158] see Refs. 159 and 160 for the original reports of the early left anterior negativity (eLAN) in response to syntactic violations in language; see Ref. 161 for a recent critical evaluation of the eLAN findings). Later studies observed a similar effect in magnetoencephalography and suggested that it originates in or around Broca's area and its right hemisphere homologue.[21] Subsequently, fMRI studies also identified parts of Broca's area among the generators of the effect[162] (see Ref. 165 for similar evidence from rhythmic violations), although other regions were also implicated,

including the ventrolateral premotor cortex,[166] the insular cortex, parietal regions,[162,163] and superior temporal regions[162] (see also Refs. 167 and 168 for evidence from intracranial electroencephalography recordings).

A number of behavioral dual-task studies have also argued for language/music overlap on the basis of superadditive processing difficulty when musical violations coincided with syntactic violations in language[169–171] (compare to Ref. 172). 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.[173] found subtle deficits in processing musical structure, which—as the authors acknowledge—could also be attributed to lower-level auditory processing deficits. Sammler et al.[174] observed an abnormal scalp distribution of the eRAN component and subtle behavioral deficits in patients with inferior frontal gyrus (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.[164] 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 (1) applies equally to language, music, and other nonmusical and nonlinguistic domains and (2) 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[175,176] and sequential learning of complex structured sequences.[177] For example, Niedeggen and Rosler[175] observed a P600 in response to violations of multiplication rules, and Núñez-Peña and Honrubia-Serrano[176] 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 structures in language argued that structural processing in music selectively interferes with syntac-

tic processing in language,[170,178] more recent studies suggest that structural processing in music can interfere with both syntactic and semantic processing in language,[171,179] 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 et al.[180,181] 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.[182] Kolk et al.[183] have also argued for a domain-general interpretation of the P600 component. For example, Vissers et al.[184] observed a P600 for spelling errors ("fone" instead of "phone"), which seems unlikely to involve anything that might be called abstract structural processing.

Some uncertainty also exists with respect to the relationship between the eRAN component[156] 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[185] (see Refs. 186 and 187 for recent overviews). Most of the work on the MMN has focused on the auditory domain (e.g., see Ref. 188 for a review), but several studies have reported a visual MMN.[189–191] In the auditory domain, although early studies employed relatively low-level manipulations (e.g., a repeated tone in a sequence of ascending tones[192] or a switch in the direction of a within-pair frequency change[193]), later studies observed the MMN component for more abstract manipulations, such as violations of tonal[194–196] or rhythmic[197,198] 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[199] (compare with Ref. 200, which reports 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[201]). However, a number of other studies have reported multiple sources for the MMN, including both temporal and frontal components
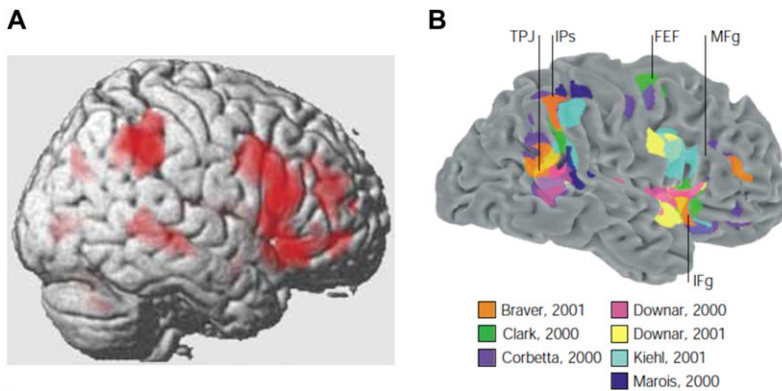
Figure 4. The similarity between activations for violations of musical structure and low-level unexpected events. (A) The functional magnetic resonance imaging activation map for a contrast of structural violation versus no structural violations in music from Ref. 208. (B) The results of a meta-analysis of brain imaging studies examining low-level unexpected events from Ref. 211.

(see Ref. 202 for the patient evidence implicating the frontal source). According to one proposal[203] (see also Refs. 204 and 205), two mental processes contribute to the MMN: (1) a sensory memory mechanism (located in the temporal lobe[206]) and (2) an attention-switching process (located in the frontal lobes), which has been shown to peak later than the temporal component.[207]

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.*[208] 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 Refs. 163, 209, and 210). Furthermore, a meta-analysis of activation peaks from fMRI studies investigating brain responses to unexpected sensory events[211] revealed a set of brain regions that closely resemble those activated by structural violations in music (Fig. 4).

The frontal regions (including parts of Broca's area[96]) and parietal regions that are present in both

the activation map for the presence versus absence of a structural violation in music and Corbetta and Shulman's[211] meta-analysis of activation peaks for unexpected events have long been implicated in a wide range of cognitive demands, as discussed above.[88,89]

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 (compare with Ref. 212), 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 and Menon[213,214] 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 versus scrambled music. Based on previous reports of high-level linguistic manipulations activating parts of BA47,[215–217] Levitin and 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 nonoverlapping regions in the anterior parts of the inferior frontal gyrus.

Later studies that directly compared structured and unstructured language and music stimuli[60,218] 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[60,61] (Fig. 2). Furthermore, in our recent work[62] (see also Ref. 32), we reported several brain regions in the temporal cortices that respond more strongly to structured than unstructured musical stimuli (we randomly reordered 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 versus music processing.

This nonoverlap is consistent with the dissociation between linguistic and musical abilities that has frequently been reported in the neuropsychological literature. In particular, patients who 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[219–234] (see Refs. 235 and 236 for reviews). And conversely, aphasic patients—even those with severe language deficits—appear to have little or no difficulties with music perception.[29,220,237–239] 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 strokes that was deemed to be comparable in quality to the music he composed before sustaining brain damage.[240]

In summary, recent brain imaging studies suggest that nonoverlapping sets of brain regions are sensitive to the presence of structure in language versus music.[60,62,218] 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.

Language versus spatial navigation

The claim for a role for language in cross-domain integration has been explored in the areas 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 visuospatial processing and object recognition), it might be that only in the presence of relevant language forms can the two informational streams be integrated, creating a capacity for flexible reorienting behavior. Initial experimental findings supported this claim. Cheng[241] 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 rely on the geometry of the environment.[242] Furthermore, in a striking demonstration of the possible role of language, healthy adults engaged in verbal shadowing fail to combine available landmark and geometric cues and attempt to reorient on the basis of geometric information alone.[26] The capacity to incorporate landmark information into reorientation performance appeared to require linguistic resources.

Subsequent experiments have not always replicated these findings, however. For example, investigations with nonhuman species, such as monkeys and fish, revealed the capacity to combine landmarks and geometry.[243,244] Learmonth et al.[245] 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 the use of spatial terms, both in isolation and in sentences, were indistinguishable in reorientation performance from healthy controls.[246] 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 to 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 et al.[247] 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 nonspatial 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 being a mandatory resource for informational integration, language representations provide more general scaffolding to learning. Furthermore, language is not the only resource to support attention to significant cues. Twyman et al.[248] report that nonlinguistic 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 et al.[249] 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.[249] 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 used by healthy adults under conditions of cognitive challenge in order to support performance in intrinsically nonlinguistic domains. For example, through encoding into linguistic form, subelements 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 et al.[250] provide a similar demonstration of the use of language resources in support of calculation in healthy adults. Whereas competent calculators showed little evidence of phonological mediation in solving two-digit plus two-digit addition problems, less competent calculators displayed phonological length effects (i.e., longer calculation times on prob-lems with phonologically long versus short numbers). Thus, across a range of cognitive domains, language representations might be used in support of reasoning, particularly under conditions of high demand.

Functional specificity places constraints on possible mechanisms

The key motivation for investigating the degree of functional specialization in the human brain (and mind) is that such investigations critically constrain the hypothesis space of possible computations of each relevant brain region.[251] If only a particular stimulus or class of stimuli elicit a response in some brain region, fundamentally different hypotheses about what this region does, compared to a case where diverse stimuli produce similarly robust responses, could be entertained. For example, were a brain region to be found within the high-level processing system that responded with similar strength[c] during the processing of linguistic and musical stimuli, one could hypothesize that this region is sensitive to some abstract features of the structure present in *both* kinds of stimuli (e.g., dependencies among the relevant elements—words in language, tones and chords in music—or perhaps the engagement of a recursive operation). Such a finding would indicate that, at some level, humans extract these highly abstract representations from very different 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 nonlinguistic tasks suggests that these regions

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[c]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.

respond to some features that are only present in linguistic stimuli. We hypothesize that the language system stores 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[252–260] (compare with earlier proposals like Refs. 261 and 262). Whatever their nature, 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.

Issues that often get conflated with the question of functional specialization

The question of whether in a mature 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 Ref. 263 for earlier discussions). We attempt to briefly clarify a few such issues below.

First, the existence of specialized language machinery does not imply the innateness of such machinery (e.g., see Refs. 263 and 264 for discussion). Functional specialization can develop as a function of our experience with the world. A clear example is the visual word-form area, a region in the inferior temporal cortex that responds selectively to letters in one's native script.[33] Recent experiments with macaques have also suggested that specialized circuits can develop via an experiential route.[265] 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, if our language system stores linguistic knowledge representations, as we hypothesize above, it would be difficult to argue that this system is present at birth, given that the representations we learn are highly dependent on experience.

What do brain regions selective for high-level language processing in the adult brain do before or at birth? This remains an important open question. A number of studies have reported responses to

human speech in young infants characterized by at least some degree of selectivity over nonspeech sounds and, in some cases, selectivity for native language over other languages[266–269] (compare with Ref. 270). 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.[32] In any case, as noted above, infants have exposure to speech in the womb,[271] and some studies have shown sensitivity to sounds experienced prenatally shortly after birth.[272] 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 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 nonhuman primates,[274,275] many others have argued for homologies between human neocortical brain regions and those in nonhuman primates, including Broca's area encompassing Brodmann areas 44 and 45.[276–278] Some have further suggested that a human brain is simply a scaled-up version of a nonhuman primate brain.[279] Regardless of whether or not the human brain includes any species-specific neural circuitry, relative to the brains of our primate relatives, humans possess massively expanded association cortices in the frontal, temporal, and parietal regions.[280] However, these association cortices house at least three spatially and functionally distinct large-scale networks: (1) the frontotemporal language system that we have focused on here, (2) the frontoparietal domain-general cognitive control system,[88] and (3) the so-called default mode network[281] that overlaps with the ToM network[104] and has also been implicated in introspection and creative thinking. The latter two systems are present in nonhuman primates and appear to be structurally

and functionally similar.[88,282] 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.

Third, the question of the existence of specialized language machinery is orthogonal to whether and how this system interacts with other cognitive and neural systems. Most researchers today—ourselves included—do not find plausible the idea that the language system is in some way encapsulated (but see Ref. 273). However, how the language system exchanges information with other large-scale neural networks and what the precise nature and scope of such interactions are remain important questions for future research. With respect to the latter, it is important to consider both the role of language in other cognitive abilities and the role of other cognitive abilities in language processing.

For example, above we have discussed a couple of possible roles that language may play in nonlinguistic cognition, including the development of certain capacities (such as our ability to explicitly represent others' mental states), and as a kind of a mental scratchpad that can be used to store and manipulate information in a linguistic format, which may be especially helpful when the task at hand is demanding and additional representational formats can ease the cognitive load. To further investigate the role of language in the development of nonlinguistic human capacities, one can (1) look at the developmental time courses of the relevant abilities to see if mastering particular linguistic devices leads to the emergence of the relevant nonlinguistic ability or (2) examine the nonlinguistic 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.[134,283]

Regarding the role of nonlinguistic capacities in language processing, a number of linguistic manipulations have been shown to recruit the regions of the frontoparietal executive system (see Ref. 91 for additional discussion), suggesting that domain-general resources can aid language comprehension/production. That said, it remains unclear how frequently, and under what precise circumstances, these domain-general mechanisms get engaged when we understand and produce language, as well as whether these mechanisms are causally necessary for language processing.[91]

Conclusions

Evidence from brain imaging investigations and studies of patients with severe aphasia show 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 many forms of complex thought, including arithmetic, solving complex problems, listening to music, thinking about other people's mental states, or navigating in the world. Furthermore, all these nonlinguistic abilities further appear to remain intact following damage to the language system, suggesting that linguistic representations are not critical for much of human thought.

Researchers may someday discover aspects of thought that do in fact depend critically on the language system, but repeated efforts to test the candidates that seemed most likely have shown that none of these produce much activation of the language system, and none of these abilities are absent in people who are globally aphasic.

The evidence that the language regions are selectively engaged in language per se suggests 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 their activity as a functional marker of the activation of linguistic representations, thus enabling us to test the role of language processing in a broader space of cognitive tasks. Most importantly, the research reviewed here provides a definitive answer to the age-old question: language and thought are not the same thing.

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Conflicts of interest

The authors declare no conflicts of interest.

References

1. The Guardian. 2016. Tom Lubbock: a memoir of living with a brain tumour. November 6, 2010. Accessed February 15, 2016. http://www.theguardian.com/books/2010/nov/07/tom-lubbock-brain-tumour-language.
2. Call, J. 2001. Chimpanzee social cognition. *Trends Cogn. Sci.* **5:** 388–393.
3. Tomasello, M., J. Call & B. Hare. 2003. Chimpanzees understand psychological states—the question is which ones and to what extent. *Trends Cogn. Sci.* **7:** 153–156.
4. Hurley, S. & M. Nudds. 2006. *Rational Animals?* Oxford: Oxford University Press.
5. Penn, D. & D. Povinelli. 2007. Causal cognition in human and nonhuman animals: a comparative, critical review. *Annu. Rev. Psychol.* **58:** 97–118.
6. Matsuzawa, T. 2009. The chimpanzee mind: in search of the evolutionary roots of the human mind. *Anim. Cogn.* **12:** 1–9.
7. Whiten, A. 2011. The scope of culture in chimpanzees, humans and ancestral apes. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **366:** 997–1007.
8. Hare, B. & S. Yamamoto. 2015. *Bonobo Cognition and Behaviour.* Leiden: Brill Academic Publishers.
9. Roffman, I., S. Savage-Rumbaugh, E. Rubert-Pugh, *et al.* 2015. Preparation and use of varied natural tools for extractive foraging by bonobos (*Pan paniscus*). *Am. J. Phys. Anthropol.* **158:** 78–91.
10. Herman, L., A. Pack & P. Morrel-Samuels. 1993. *Language and Communication: Comparative Perspectives.* H. Roitblat, L. Herman & P. Nachtigall, Eds.: 273–298. Hillside, NJ: Lawrence Erlbaum.
11. Reiss, D. & L. Marino. 2001. Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. *Proc. Natl. Acad. Sci. U.S.A.* **98:** 5937–5942.
12. Schusterman, R., J. Thomas & F. Wood. 2013. *Dolphin Cognition and Behavior: A Comparative Approach.* Hillsdale, NJ: Taylor & Francis Group.
13. Bluff, L., A. Weir, C. Rutz, *et al.* 2007. Tool-related cognition in new Caledonian crows. *Comp. Cogn. Behav. Rev.* **2:** 1–25.
14. Taylor, A., G. Hunt, J. Holzhaider, *et al.* 2007. Spontaneous metatool use by new Caledonian crows. *Curr. Biol.* **17:** 1504–1507.
15. Kaplan, G. 2014. Animal communication. *Wiley Interdiscip. Rev. Cogn. Sci.* **5:** 661–677.
16. Snowdon, C. 1990. Language capacities of nonhuman animals. *Am. J. Phys. Anthropol.* **33:** 215–243.
17. Deacon, T.W. 1997. *The Symbolic Species.* New York: W.W. Norton.
18. Hauser, M., N. Chomsky & W. Fitch. 2002. The faculty of language: what is it, who has it, and how did it evolve? *Science* **298:** 1569–1579.
19. Premack, D. 2007. Human and animal cognition: continuity and discontinuity. *Proc. Natl. Acad. Sci. U.S.A.* **104:** 13861–13867.
20. Kinsella, A. 2009. *Language Evolution and Syntactic Theory.* Cambridge, MA: Cambridge University Press.
21. Maess, B., S. Koelsch, T.C. Gunter, *et al.* 2001. Musical syntax is processed in Broca's area: an MEG study. *Nat. Neurosci.* **4:** 540–545.
22. Patel, A. 2003. Language, music, syntax and the brain. *Nat. Neurosci.* **6:** 674–681.
23. Maruyama, M., C. Pallier, A. Jobert, *et al.* 2012. The cortical representation of simple mathematical expressions. *Neuroimage* **61:** 1444–1460.
24. de Villiers, J. & P. de Villiers. 2000. "Linguistic determinism and the understanding of false beliefs." In *Children's Reasoning and the Mind.* P. Mitchell & K.J. Riggs, Eds.: 191–228. Hove: Psychology Press.
25. Novick, J.M., J.C. Trueswell & S.L. Thompson-Schill. 2005. Cognitive control and parsing: reexamining the role of Broca's area in sentence comprehension. *Cogn. Affect. Behav. Neurosci.* **5:** 263–281.
26. Hermer-Vazquez, L., E.S. Spelke & A.S. Katsnelson. 1999. Sources of flexibility in human cognition: dual-task studies of space and language. *Cogn. Psychol.* **39:** 3–36.
27. Carruthers, P. 2005. *Distinctively Human Thinking: Modular Precursors and Components.* P. Carruthers, S. Laurence & S. Stitch, Eds.: 69–88. Oxford: Oxford University Press.
28. Fedorenko, E., P.-J. Hsieh, A. Nieto-Castañón, *et al.* 2010. A new method for fMRI investigations of language: defining ROIs functionally in individual subjects. *J. Neurophysiol.* **104:** 1177–1194.
29. Fedorenko, E. & S. Thompson-Schill. 2014. Reworking the language network. *Trends Cogn. Sci.* **18:** 120–126.
30. Overath, T., J. McDermott, J. Zarate, *et al.* 2015. The cortical analysis of speech-specific temporal structure revealed by responses to sound quilts. *Nat. Neurosci.* **18:** 903–911.
31. Peretz, I., D. Vuvan, M. Lagrois, *et al.* 2015. Neural overlap in processing music and speech. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **370:** 20140090.
32. Norman-Haignere, S., N. Kanwisher & J. McDermott. 2015. Distinct cortical pathways for music and speech revealed by hypothesis-free voxel decomposition. *Neuron* **88:** 1281–1296.
33. Baker, C.I., J. Liu, L.L. Wald, *et al.* 2007. Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. *Proc. Natl. Acad. Sci. U.S.A.* **104:** 9087–9092.
34. Hamame, C.M., M. Szwed, M. Sharman, *et al.* 2013. Dejerine's reading area revisited with intracranial EEG: selective responses to letter strings. *Neurology* **80:** 602–603.
35. Dronkers, N. 1996. A new brain region for coordinating speech articulation. *Nature* **384:** 159–161.
36. Hillis, A., M. Work, P. Barker, *et al.* 2004. Re-examining the brain regions crucial for orchestrating speech articulation. *Brain* **127:** 1479–1487.

37. Bonilha, L., C. Rorden, S. Appenzeller, *et al.* 2006. Gray matter atrophy associated with duration of temporal lobe epilepsy. *Neuroimage* **32:** 1070–1079.

38. Whiteside, S.P., L. Dyson, P.E. Cowell, *et al.* 2015. The relationship between apraxia of speech and oral apraxia: association or dissociation? *Arch. Clin. Neuropsychol.* **30:** 670–682.

39. Longcamp, M., A. Lagarrigue, B. Nazarian, *et al.* 2014. Functional specificity in the motor system: evidence from coupled fMRI and kinematic recordings during letter and digit writing. *Hum. Brain Mapp.* **35:** 6077–6087.

40. Swinney, D.A. 1979. Lexical access during sentence comprehension: (re)consideration of context effects. *J. Verb. Learn. Verb. Behav.* **18:** 645–659.

41. Fodor, J. 1983. *The Modularity of Mind.* Cambridge, MA: MIT Press.

42. Marslen-Wilson, W.D. 1987. Functional parallelism in spoken word-recognition. *Cognition* **25:** 71–102.

43. Marslen-Wilson, W.D. 1975. Sentence perception as an interactive parallel process. *Science* **189:** 226–228.

44. Altman, G.T. & Y. Kamide. 1999. Incremental interpretation at verbs: restricting the domain of subsequent reference. *Cognition* **73:** 247–264.

45. Hale, J. 2001. *A* probabilistic Earley parser as a psycholinguistic model. In *Proceedings of the Second Meeting of the North American Chapter of the Association for Computational Linguistics.*

46. DeLong, K.A., T.P. Urbach & M. Kutas. 2005. Probabilistic word pre-activation during language comprehension inferred from electrical brain activity. *Nat. Neurosci.* **8:** 1117–1121.

47. Van Berkum, J.J.A., C.M. Brown, P. Zwitserlood, *et al.* 2005. Anticipating upcoming words in discourse: evidence from ERPs and reading times. *J. Exp. Psychol. Learn. Mem. Cogn.* **31:** 443.

48. Dikker, S., H. Rabagliati, T.A. Farmer & L. Pylkkänen. 2010. Early occipital sensitivity to syntactic category is based on form typicality. *Psychol. Sci.* **21:** 629–634.

49. Levy, R. 2008. Expectation-based syntactic comprehension. *Cognition* **106:** 1126–1177.

50. Smith, N.J. & R. Levy. 2013. The effect of word predictability on reading time is logarithmic. *Cognition* **128:** 302–319.

51. Caramazza, A. & A.E. Hillis. 1990. Spatial representation of words in the brain implied by studies of a unilateral neglect patient. *Nature* **346:** 267–269.

52. Plaut, D.C. 1995. Double dissociation without modularity: evidence from connectionist neuropsychology. *J. Clin. Exp. Neuropsychol.* **17:** 291–321.

53. Fedorenko E., A. Nieto-Castañon & N. Kanwisher. 2012. Lexical and syntactic representations in the brain: an fMRI investigation with multi-voxel pattern analyses. *Neuropsychologia* **50:** 499–513.

54. Blank, I., Z. Balewski, K. Mahowald, *et al.* 2016. Syntactic processing is distributed across the language system. *Neuroimage* **127:** 307–323.

55. Bautista, A. & A.M. Wilson. 2016. Neural responses to grammatically and lexically degraded speech. *Lang. Cogn. Neurosci.* **31:** 1–8.

56. Saur D., B.W. Kreher, S. Schnell, *et al.* 2008. Ventral and dorsal pathways for language. *Proc. Natl. Acad. Sci. U.S.A.* **105:** 18035–18040.

57. Blank, I., N. Kanwisher & E. Fedorenko. 2015. A functional dissociation between language and multiple-demand systems revealed in patterns of BOLD signal fluctuations. *J. Neurophysiol.* **112:** 1105–1118.

58. Tie, Y., L. Rigolo, I.H. Norton, *et al.* 2013. Defining language networks from resting-state fMRI for surgical planning—a feasibility study. *Hum. Brain Mapp.* **35:** 1018–1030.

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

60. Fedorenko, E., M. Behr & N. Kanwisher. 2011. Functional specificity for high-level linguistic processing in the human brain. *Proc. Natl. Acad. Sci. U.S.A.* **108:** 16428–16433.

61. Norman-Haignere, S., N. Kanwisher & J. McDermott. 2015. Hypothesis-free decomposition of voxel responses to natural sounds reveals distinct cortical pathways for music and speech. *Neuron* **88:** 1281–1296.

62. Fedorenko, E., J. McDermott, S. Norman-Haignere, *et al.* 2012. Sensitivity to musical structure in the human brain. *J. Neurophysiol.* **108:** 3289–3300.

63. Wynn, K. 1990. Children's understanding of counting. *Cognition* **36:** 155–193.

64. Xu, F., S. Carey & N. Quint. 2004. The emergence of kind-based object individuation in infancy. *Cogn. Psychol.* **49:** 155–190.

65. Feigenson, L., S. Dehaene & E. Spelke. 2004. Core systems of number. *Trends Cogn. Sci.* **8:** 307–314.

66. Whalen, J., C. Gallistel & R. Gelman. 1999. Nonverbal counting in humans: the psychophysics of number representation. *Psychol. Sci.* **10:** 130–137.

67. Gallistel, C. 1990. *The Organization of Learning.* Cambridge, MA: MIT Press.

68. Hauser, M. & S. Carey. 2003. Spontaneous representations of small numbers of objects by rhesus macaques: examinations of content and format. *Cogn. Psychol.* **47:** 367–401.

69. Gordon, P.C., R. Hendrik & W.H. Levine. 2002. Memory-load interference in syntactic processing. *Psychol. Sci.* **13:** 425–430.

70. Pica, P., C. Leme, V. Izard, *et al.* 2004. Exact and approximate arithmetic in an Amazonian indigene group. *Science* **306:** 499–503.

71. Frank, M., D. Everett, E. Fedorenko, *et al.* 2008. Number as a cognitive technology: evidence from Pirahã language and cognition. *Cognition* **108:** 819–824.

72. Dehaene, S. 2003. The neural basis of the Weber–Fechner law: a logarithmic mental number line. *Trends Cogn. Sci.* **7:** 145–147.

73. Dehaene, S. & L. Cohen. 1997. Cerebral pathways for calculation: double dissociation between rote verbal and quantitative knowledge of arithmetic. *Cortex* **33:** 219–250.

74. Dehaene, A., E. Spelke & P. Pinel. 1999. Sources of mathematical thinking: behavioral and brain-imaging evidence. *Science* **284:** 970–974.

75. Stanescu-Cosson, R., P. Pinel, P. van de Moortele, *et al.* 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:** 2240–2255.

76. Van Harskamp, N. & L. Cipolotti. 2001. Selective impairments for addition, subtraction and multiplication. Implications for the organisation of arithmetical facts. *Cortex* **37:** 363–388.

77. Delazer, M., L. Girelli, A. Granà, *et al.* 2003. Number processing and calculation—normative data from healthy adults. *Clin. Neuropsychol.* **17:** 331–350.

78. Schwarzlose, R., C. Baker & N. Kanwisher. 2005. Separate face and body selectivity on the fusiform gyrus. *J. Neurosci.* **25:** 11055–11059.

79. Baldo, J.V. & N.F. Dronkers. 2007. Neural correlates of arithmetic and language comprehension: a common substrate? *Neuropsychologia* **45:** 229–235.

80. Coltheart, M. 1985. *Cognitive Neuropsychology and the Study of Reading.* M.I. Posner & O.S.M. Marin, Eds.: 3–37. Hillsdale, NJ: Lawrence Erlbaum Associates.

81. Shallice, T. 1988. *From Neuropsychology to Mental Structure.* Cambridge, MA: Cambridge University Press.

82. Varley, R., N. Klessinger, C. Romanowski, *et al.* 2005. From the cover: agrammatic but numerate. *Proc. Natl. Acad. Sci. U.S.A.* **102:** 3519–3524.

83. Zago L., M. Pesenti, E. Mellet, *et al.* 2001. Neural correlates of simple and complex mental calculation. *Neuroimage* **13:** 314–327.

84. Monti, M., L. Parsons & D. Osherson. 2012. Thought beyond language: neural dissociation of algebra and natural language. *Psychol. Sci.* **23:** 914–922.

85. Trbovich, P.L. & J.A. LeFevre. 2003. Phonological and visual working memory in mental addition. *Mem. Cognit.* **31:** 738–745.

86. Gray, J. & P. Thompson. 2004. Neurobiology of intelligence: science and ethics. *Nat. Rev. Neurosci.* **5:** 471–482.

87. Miller, E. & J. Cohen. 2001. An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.* **24:** 167–202.

88. Duncan, J. 2010. The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends Cogn. Sci.* **14:** 172–179.

89. Duncan, J., M. Schramm, R. Thompson, *et al.* 2012. Task rules, working memory, and fluid intelligence. *Psychon. Bull. Rev.* **19:** 864–870.

90. Kaan, E. & T.Y. Swaab. 2002. The brain circuitry of syntactic comprehension. *Trends Cogn. Sci.* **6:** 350–356.

91. Fedorenko, E. 2014. The role of domain-general cognitive control in language comprehension. *Front. Psychol.* **5:** 335.

92. Fedorenko, E., E. Gibson & D. Rohde. 2006. The nature of working memory capacity in sentence comprehension: evidence against domain-specific working memory resources. *J. Mem. Lang.* **54:** 541–553.

93. Rodd, J.M., M.H. Davis & I.S. Johnsrude. 2005. The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. *Cereb. Cortex* **15:** 1261–1269.

94. Novais-Santos, S., J. Gee, M. Shah, *et al.* 2007. Resolving sentence ambiguity with planning and working memory resources: evidence from fMRI. *Neuroimage* **37:** 361–378.

95. January, D., J.C. Trueswell & S.L. Thompson-Schill. 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:** 2434–2444.

96. Fedorenko, E., J. Duncan & N. Kanwisher. 2012. Language-selective and domain-general regions lie side by side within Broca's area. *Curr. Biol.* **22:** 2059–2062.

97. Monti, M.M., D. Osherson, M. Martinez, *et al.* 2007. Functional neuroanatomy of deductive inference: a language-independent distributed network. *Neuroimage* **37:** 1005–1016.

98. Monti, M., L. Parsons & D. Osherson. 2009. The boundaries of language and thought in deductive inference. *Proc. Natl. Acad. Sci. U.S.A.* **106:** 12554–12559.

99. Goel, V. 2007. Anatomy of deductive reasoning. *Trends Cogn. Sci.* **11:** 435–441.

100a. Varley, R. & M. Siegal. 2000. Evidence for cognition without grammar from causal reasoning and 'theory of mind' in an agrammatic aphasic patient. *Curr. Biol.* **10:** 723–726.

100b. Varley, R. 2002. "Science without grammar: scientific reasoning in severe agrammatic aphasia." In *The Cognitive Basis of Science.* P. Carruthers, S. Stich & M. Siegal, Eds.: 99–116. Cambridge: Cambridge University Press.

101. Reverberi, C., T. Shallice, S. D'Agostini, *et al.* 2009. Cortical bases of elementary deductive reasoning: inference, memory, and metadeduction. *Neuropsychologia* **47:** 1107–1116.

102. Berg, E. 1948. A simple objective technique for measuring flexibility in thinking. *J. Gen. Psychol.* **39:** 15–22.

103. Baldo, J., N. Dronkers, D. Wilkins, *et al.* 2005. Is problem solving dependent on language? *Brain Lang.* **92:** 240–250.

104. Saxe, R. 2006. Uniquely human social cognition. *Curr. Opin. Neurobiol.* **16:** 235–239.

105. de Villiers, J. 2000. "Language and theory of mind: What are the developmental relationships." In *Understanding Other Minds: Perspectives from Autism and Developmental Cognitive Neuroscience.* S. Baron-Cohen, H. Tager-Flusberg & D. Cohen, Eds.: 88–123. Cambridge, MA: Cambridge University Press.

106. Astington, J.W. & J.M. Jenkins. 1999. A longitudinal study of the relation between language and theory-of-mind development. *Dev. Psychol.* **35:** 1311–1320.

107. Dunn, J., J. Brown, C. Slomkowski, *et al.* 1991. Young children's understanding of other people's feelings and beliefs: individual differences and their antecedents. *Child Dev.* **62:** 1352.

108. Astington, J. & J. Baird. 2005. *Why Language Matters for Theory of Mind.* Oxford: Oxford University Press.

109. Milligan, K., J. Astington & L. Dack. 2007. Language and theory of mind: meta-analysis of the relation between language ability and false-belief understanding. *Child Dev.* **78:** 622–646.

110. Wellman, H., D. Cross & J. Watson. 2001. Meta-analysis of theory-of-mind development: the truth about false belief. *Child Dev.* **72:** 655–684.

111. Appleton, M. & V. Reddy. 1996. Teaching three year-olds to pass false belief tests: a conversational approach. *Soc. Dev.* **5:** 275–291.

112. Clements, W., C. Rustin & S. McCallum. 2000. Promoting the transition from implicit to explicit understanding: a training study of false belief. *Dev. Sci.* **3:** 81–92.

113. Hale, C. & H. Tager-Flusberg. 2003. The influence of language on theory of mind: a training study. *Dev. Sci.* **6:** 346–359.

114. Slaughter, V. & A. Gopnik. 1996. Conceptual coherence in the child's theory of mind: training children to understand belief. *Child Dev.* **67:** 2967–2988.

115. Fletcher, P., F. Happé, U. Frith, *et al.* 1995. Other minds in the brain: a functional imaging study of "theory of mind" in story comprehension. *Cognition* **57:** 109–128.

116. Gallagher, H., F. Happé, N. Brunswick, *et al.* 2000. Reading the mind in cartoons and stories: an fMRI study of 'theory of mind' in verbal and nonverbal tasks. *Neuropsychologia* **38:** 11–21.

117. Vogeley, K., P. Bussfeld, A. Newen, *et al.* 2001. Mind reading: neural mechanisms of theory of mind and self-perspective. *Neuroimage* **14:** 170–181.

118. Ruby, P. & J. Decety. 2003. What you believe versus what you think they believe: a neuroimaging study of conceptual perspective-taking. *Eur. J. Neurosci.* **17:** 2475–2480.

119. Saxe, R. & N. Kanwisher. 2003. People thinking about thinking people. The role of the temporo-parietal junction in "theory of mind." *Neuroimage* **19:** 1835–1842.

120. Ciaramidaro, A., M. Adenzato, I. Enrici, *et al.* 2007. The intentional network: how the brain reads varieties of intentions. *Neuropsychologia* **45:** 3105–3113.

121. Gobbini, M., A. Koralek, R. Bryan, *et al.* 2007. Two takes on the social brain: a comparison of theory of mind tasks. *J. Cogn. Neurosci.* **19:** 1803–1814.

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

123. Saxe, R. & L. Powell. 2006. It's the thought that counts: specific brain regions for one component of theory of mind. *Psychol. Sci.* **17:** 692–699.

124. Perner, J., M. Aichhorn, M. Kronbichler, *et al.* 2006. Thinking of mental and other representations: the roles of left and right temporo-parietal junction. *Soc. Neurosci.* **1:** 245–258.

125. Young, L. & R. Saxe. 2009. Innocent intentions: a correlation between forgiveness for accidental harm and neural activity. *Neuropsychologia* **47:** 2065–2072.

126. Jenkins, A. & J. Mitchell. 2009. Mentalizing under uncertainty: dissociated neural responses to ambiguous and unambiguous mental state inferences. *Cereb. Cortex* **20:** 404–410.

127. Bedny, M., A. Pascual-Leone & R. Saxe. 2009. Growing up blind does not change the neural bases of Theory of Mind. *Proc. Natl. Acad. Sci. U.S.A.* **106:** 11312–11317.

128. Siegal, M., J. Carrington & M. Radel. 1996. Theory of mind and pragmatic understanding following right hemisphere damage. *Brain Lang.* **53:** 40–50.

129. Happé, F., H. Brownell & E. Winner. 1999. Acquired 'theory of mind' impairments following stroke. *Cognition* **70:** 211–240.

130. Kalbe, E., M. Schlegel, A. Sack, *et al.* 2010. Dissociating cognitive from affective theory of mind: a TMS study. *Cortex* **46:** 769–780.

131. Young, L., J. Camprodon, M. Hauser, *et al.* 2010. Disruption of the right temporoparietal junction with transcranial magnetic stimulation reduces the role of beliefs in moral judgments. *Proc. Natl. Acad. Sci. U.S.A.* **107:** 6753–6758.

132. Samson, D., I. Apperly, C. Chiavarino, *et al.* 2004. Left temporoparietal junction is necessary for representing someone else's belief. *Nat. Neurosci.* **7:** 499–500.

133. Deen, B., K. Koldewyn & N. Kanwisher. 2015. Functional organization of social perception and cognition in the superior temporal sulcus. *Cereb. Cortex* **25:** 4596–4609.

134. Dronkers, N., C. Ludy & B. Redfern. 1998. Pragmatics in the absence of verbal language: descriptions of a severe aphasic and a language-deprived adult. *J. Neurolinguist* **11:** 179–190.

135. Varley, R., M. Siegal & S. Want. 2001. Severe impairment in grammar does not preclude theory of mind. *Neurocase* **7:** 489–493.

136. Apperly, I., D. Samson, N. Carroll, *et al.* 2006. Intact first- and second-order false belief reasoning in a patient with severely impaired grammar. *Soc. Neurosci.* **1:** 334–348.

137. Willems, R., Y. Benn, P. Hagoort, *et al.* 2011. Communicating without a functioning language system: implications for the role of language in mentalizing. *Neuropsychologia* **49:** 3130–3135.

138. McDermott, J. & M. Hauser. 2005. The origins of music: innateness, uniqueness, and evolution. *Music Percept.* **23:** 29–59.

139. Handel, S. 1989. *Listening: An Introduction to the Perception of Auditory Events.* Cambridge, MA: MIT Press.

140. Patel, A., J. Iversen, M. Wassenaar, *et al.* 2008. Musical syntactic processing in agrammatic Broca's aphasia. *Aphasiology* **22:** 776–789.

141. Riemann, H. 1877. *Musikalische Syntaxis.* Leipzig: Breitkopf & Hartel.

142. Swain, J.P. 1995. The concept of musical syntax. *Music Quart.* **79:** 281–308.

143. Lindblom, B. & J. Sundberg. 1969. Towards a generative theory of melody. *STL-QPSR* **10:** 53–68.

144. Fay, T. 1971. Perceived hierarchic structure in language and music. *J. Music Theory* **15:** 112.

145. Bernstein, L. 1976. *The Unanswered Question.* Cambridge, MA: Harvard University Press.

146. Sundberg, J. & B. Lindblom. 1976. Generative theories in language and music descriptions. *Cognition* **4:** 99–122.

147. Lerdahl, F. & R. Jackendoff. 1977. Toward a formal theory of tonal music. *J. Music Theory* **21:** 111.

148. Lerdahl, F. & R. Jackendoff . 1983. *A Generative Grammar of Tonal Music.* Cambridge, MA: MIT Press.

149. Roads, C. 1979. Grammars as representations for music. *Comput. Music J.* **3:** 48.

150. Krumhansl, C. & F. Keil. 1982. Acquisition of the hierarchy of tonal functions in music. *Mem. Cognit.* **10:** 243–251.

151. Janata, P. 1995. ERP measures assay the degree of expectancy violation of harmonic contexts in music. *J. Cogn. Neurosci.* **7:** 153–164.

152. Patel, A., I. Peretz, M. Tramo, *et al.* 1998. Processing prosodic and musical patterns: a neuropsychological investigation. *Brain Lang.* **61:** 123–144.

153. Fitzroy, A. & L. Sanders. 2013. Musical expertise modulates early processing of syntactic violations in language. *Front. Psychol.* **3:** 603.

154. Osterhout, L. & P. Holcomb. 1993. Event-related potentials and syntactic anomaly: evidence of anomaly detection during the perception of continuous speech. *Lang. Cogn. Process* **8:** 413–437.

155. Hagoort, P., C. Brown & J. Groothusen. 1993. The syntactic positive shift (SPS) as an ERP measure of syntactic processing. *Lang. Cogn. Process* **8:** 439–483.

156. Koelsch, S., T. Gunter, A. Friederici, *et al.* 2000. Brain indices of music processing: "nonmusicians" are musical. *J. Cogn. Neurosci.* **12:** 520–541.

157. Loui, P., T. Grent-'t-Jong, D. Torpey, *et al.* 2005. Effects of attention on the neural processing of harmonic syntax in Western music. *Brain Res. Cogn. Brain Res.* **25:** 678–687.

158. Miranda, R. & M. Ullman. 2007. Double dissociation between rules and memory in music: an event-related potential study. *Neuroimage* **38:** 331–345.

159. Neville, H., J. Nicol, A. Barss, *et al.* 1991. Syntactically based sentence processing classes: evidence from event-related brain potentials. *J. Cogn. Neurosci.* **3:** 151–165.

160. Friederici, A.D., E. Pfeifer & A. Hahne. 1993. Event-related brain potentials during natural speech processing: effects of semantic, morphological and syntactic violations. *Brain Res. Cogn. Brain Res.* **1:** 183–192.

161. Steinhauer, K. & J.E. Drury. 2012. On the early left-anterior negativity (ELAN) in syntax studies. *Brain Lang.* **120:** 135–162.

162. Koelsch, S., T.C. Gunter, D.Y. von Cramon, *et al.* 2002. Bach speaks: a cortical "language-network" serves the processing of music. *Neuroimage* **17:** 956–966.

163. Tillmann, B., P. Janata & J. Bharucha. 2003. Activation of the inferior frontal cortex in musical priming. *Cogn. Brain Res.* **16:** 145–161.

164. Tillmann, B., S. Koelsch, N. Escoffier, *et al.* 2006. Cognitive priming in sung and instrumental music: activation of inferior frontal cortex. *Neuroimage* **31:** 1771–1782.

165. Herdener, M., T. Humbel, F. Esposito, *et al.* 2012. Jazz drummers recruit language-specific areas for the processing of rhythmic structure. *Cereb. Cortex* **24:** 836–843.

166. Koelsch, S. 2006. Significance of Broca's area and ventral premotor cortex for music-syntactic processing. *Cortex* **42:** 518–520.

167. Sammler D., S. Koelsch, T. Ball, *et al.* 2009. Overlap of musical and linguistic syntax processing: intracranial ERP evidence. *Ann. N.Y. Acad. Sci.* **1169:** 494–498.

168. Sammler, D., S. Koelsch, T. Ball, *et al.* 2013. Co-localizing linguistic and musical syntax with intracranial EEG. *Neuroimage* **64:** 134–146.

169. Fedoernko, E., A. Patel, D. Casasanto, *et al.* 2009. Structural integration in language and music: evidence for a shared system. *Mem. Cognit.* **37:** 1–9.

170. Slevc, L., J. Rosenberg & A. Patel. 2009. Making psycholinguistics musical: self-paced reading time evidence for shared processing of linguistic and musical syntax. *Psychon. Bull. Rev.* **16:** 374–381.

171. Hoch, L., B. Poulin-Charronnat & B. Tillmann. 2011. The influence of task-irrelevant music on language processing: syntactic and semantic structures. *Front. Psychol.* **2:** 112.

172. Bonnel, A., F. Faita, I. Peretz, *et al.* 2001. Divided attention between lyrics and tunes of operatic songs: evidence for independent processing. *Percept. Psychophys.* **63:** 1201–1213.

173. Patel, A., J. Iversen, M. Wassenaar, *et al.* 2008. Musical syntactic processing in agrammatic Broca's aphasia. *Aphasiology* **22:** 776–789.

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

175. Niedeggen, M. & F. Rosler. 1999. N400 effects reflect activation spread during retrieval of arithmetic facts. *Psychol. Sci.* **10:** 271–276.

176. Núñez-Peña, M.I. & M.L. Honrubia-Serrano. 2004. P600 related to rule violation in an arithmetic task. *Brain Res. Cogn. Brain Res.* **18:** 130–141.

177. Christiansen, M., C. Conway & L. Onnis. 2012. Similar neural correlates for language and sequential learning: evidence from event-related brain potentials. *Lang. Cogn. Process* **27:** 231–256.

178. Besson, M. & D. Schön. 2001. *The Biological Foundations of Music.* R. Zatorre & I. Peretz, Eds.: 232–259. New York: New York Academy of Sciences.

179. Perruchet, P. & B. Poulin-Charronnat. 2013. Challenging prior evidence for a shared syntactic processor for language and music. *Psychon. Bull. Rev.* **20:** 310–317.

180. Coulson, S., J.W. King & M. Kutas. 1998. Expect the unexpected: event-related brain response to morphosyntactic violations. *Lang. Cogn. Process* **13:** 21–58.

181. Coulson, S., J.W. King & M. Kutas. 1998. ERPs and domain specificity: beating a straw horse. *Lang. Cogn. Process* **13:** 653–672.

182. Pritchard, W. 1981. Psychophysiology of P300. *Psychol. Bull.* **89:** 506–540.

183. Kolk, H.H. & D.J. Chwilla. 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 Lang.* **100:** 257–262.

184. Vissers, C.T., D.J. Chwilla & H.H.J. Kolk. 2006. Monitoring in language perception: the effect of misspellings of words in highly constrained sentences. *Brain Res.* **1106:** 150–163.

185. Näätänen, R., A.W. Gaillard & S. Mäntysalo. 1978. Early selective-attention effect on evoked potential reinterpreted. *Acta Psychol.* **42:** 313–329.

186. Garrido, M., J. Kilner, K. Stephan, *et al.* 2009. The mismatch negativity: a review of underlying mechanisms. *Clin. Neurophysiol.* **120:** 453–463.

187. Trainor L.J. & R. Zatorre. 2009. *The Neurobiological Basis of Musical Expectations: From Probabilities to Emotional Meaning.* S. Hallam, I. Cross & M. Thaut, Eds.: 171–183. Oxford: Oxford University Press.

188. Näätänen, R., P. Paavilainen, T. Rinne, *et al.* 2007. The mismatch negativity (MMN) in basic research of central auditory processing: a review. *Clin. Neurophysiol.* **118:** 2544–2590.

189. Cammann, R. 1990. Is there a mismatch negativity (MMN) in visual modality? *Behav. Brain Sci.* **13:** 2.

190. Astikainen, P., T. Ruusuvirta, J. Wikgren, *et al.* 2004. The human brain processes visual changes that are not cued by attended auditory stimulation. *Neurosci. Lett.* **368:** 231–234.

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

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

193. Saarinen, J., P. Paavilainen, E. Schöger, *et al.* 1992. Representation of abstract attributes of auditory stimuli in the human brain. *Neuroreport* **3:** 1149–1151.

194. Trainor, L., K. McDonald & C. Alain. 2002. Automatic and controlled processing of melodic contour and interval information measured by electrical brain activity. *J. Cogn. Neurosci.* **14:** 430–442.

195. Neuloh, G. & G. Curio. 2004. Does familiarity facilitate the cortical processing of music sounds? *Neuroreport* **15:** 2471–2475.

196. Fujioka, T., L. Trainor, B. Ross, *et al.* 2005. Automatic encoding of polyphonic melodies in musicians and nonmusicians. *J. Cogn. Neurosci.* **17:** 1578–1592.

197. Vuust, P., K.J. Pallesen, C. Bailey, *et al.* 2005. To musicians, the message is in the meter pre-attentive neuronal responses to incongruent rhythm are left-lateralized in musicians. *Neuroimage* **24:** 560–564.

198. van Zuijen, T.L., E. Sussman, I. Winkler, *et al.* 2004. Grouping of sequential sounds: an event-related potential study comparing musicians and nonmusicians. *J. Cogn. Neurosci.* **16:** 331–338.

199. Koelsch, S., T.C. Gunter, E. Schroger, *et al.* 2001. Differentiating ERAN and MMN: an ERP study. *Neuroreport* **12:** 1385–1389.

200. Leino, S., E. Brattico, M. Tervaniemi, *et al.* 2007. Representation of harmony rules in the human brain: further evidence from event-related potentials. *Brain Res.* **1142:** 169–177.

201. Garza Villarreal, E., E. Brattico, S. Leino, *et al.* 2011. Distinct neural responses to chord violations: a multiple source analysis study. *Brain Res.* **1389:** 103–114.

202. Alain, C., D. Woods & R. Knight. 1998. A distributed cortical network for auditory sensory memory in humans. *Brain Res.* **812:** 23–37.

203. Giard, M., F. Perrin, J. Pernier, *et al.* 1990. Brain generators implicated in the processing of auditory stimulus deviance: a topographic event-related potential study. *Psychophysiology* **27:** 627–640.

204. Gomot, M., M. Giard, S. Roux, *et al.* 2000. Maturation of frontal and temporal components of mismatch negativity (MMN) in children. *Neuroreport* **11:** 3109–3112.

205. Maess, B., T. Jacobsen, E. Schröger, *et al.* 2007. Localizing pre-attentive auditory memory-based comparison: magnetic mismatch negativity to pitch change. *Neuroimage* **37:** 561–571.

206. Schonwiesner, M., K. Krumbholz, R. Rubsamen, *et al.* 2007. Hemispheric asymmetry for auditory processing in the human auditory brain stem, thalamus, and cortex. *Cereb. Cortex* **17:** 492–499.

207. Rinne, T., K. Alho, R. Ilmoniemi, *et al.* 2000. Separate time behaviors of the temporal and frontal mismatch negativity sources. *Neuroimage* **12:** 14–19.

208. Koelsch, S., T. Fritz, K. Schulze, *et al.* 2005. Adults and children processing music: an fMRI study. *Neuroimage* **25:** 1068–1076.

209. Doeller, C., B. Opitz, A. Mecklinger, *et al.* 2003. Prefrontal cortex involvement in preattentive auditory deviance detection. *Neuroimage* **20:** 1270–1282.

210. Opitz, B., T. Rinne, A. Mecklinger, *et al.* 2002. Differential contribution of frontal and temporal cortices to auditory change detection: fMRI and ERP results. *Neuroimage* **15:** 167–174.

211. Corbetta, M. & G. Shulman. 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* **3:** 215–229.

212. Wang, L., L. Uhrig, B. Jarraya, *et al.* 2015. Representation of numerical and sequential patterns in macaque and human brains. *Curr. Biol.* **25:** 1966–1974.

213. Levitin, D.J. & V. Menon. 2003. Musical structure is processed in "language" areas of the brain: a possible role for Brodmann area 47 in temporal coherence. *Neuroimage* **20:** 2142–2152.

214. Levitin, D.J. & V. Menon. 2005. The neural locus of temporal structure and expectancies in music: evidence from functional neuroimaging at 3 Tesla. *Music Percept.* **22:** 563–575.

215. Fiez, J., M. Raichle, F. Miezin, *et al.* 1995. PET studies of auditory and phonological processing: effects of stimulus characteristics and task demands. *J. Cogn. Neurosci.* **7:** 357–375.

216. Binder, J., J. Frost, T. Hammeke, *et al.* 1997. Human brain language areas identified by functional magnetic resonance imaging. *Neuroscience* **17:** 353–362.

217. Dapretto, M. & S. Bookheimer. 1999. Form and content: dissociating syntax and semantics in sentence comprehension. *Neuron* **24:** 427–432.

218. Rogalsky, C., F. Rong, K. Saberi, *et al.* 2011. Functional anatomy of language and music perception: temporal and

structural factors investigated using fMRI. *J. Neurosci.* **31:** 3843–3852.

219. Allen, G. 1878. Note-deafness. *Mind* **10:** 157–167.

220. Polk, M. & A. Kertesz. 1993. Music and language in degenerative disease of the brain. *Brain Cogn.* **22:** 98–117.

221. Peretz, I. 1993. Auditory atonalia for melodies. *Cogn. Neuropsychol.* **10:** 21–56.

222. Peretz, I., R. Kolinsky, M. Tramo, *et al.* 1994. Functional dissociations following bilateral lesions of auditory cortex. *Brain* **117:** 1283–1301.

223. Samson, S. & R. Zatorre. 1994. Contribution of the right temporal lobe to musical timbre discrimination. *Neuropsychologia* **32:** 231–240.

224. Steinke, W.R, Cuddy, L.L. & R.R. Holden. 1997. Dissociation of musical tonality and pitch memory from nonmusical cognitive abilities. *Can. J. Exp. Psychol.* **51:** 316–334.

225. Griffiths, T.D., A. Rees, C. Witton, *et al.* 1997. Spatial and temporal auditory processing deficits following right hemisphere infarction. A psychophysical study. *Brain* **120:** 785–794.

226. Liegeois-Chauvel, C., I. Peretz, M. Babai, *et al.* 1998. Contribution of different cortical areas in the temporal lobes to music processing. *Brain* **121:** 1853–1867.

227. Wilson, S. & J. Pressing. 1999. *Neuropsychological Assessment and the Modeling of Musical Deficits.* R. Pratt & D. Erdonmez Grocke, Eds.: 47–74. Melbourne: The University of Melbourne.

228. Piccirilli, M., T. Sciarma & S. Luzzi. 2000. Modularity of music: evidence from a case of pure amusia. *J. Neurol. Neurosurg. Psychiatry* **69:** 541–545.

229. Steinke, W., L. Cuddy & L. Jakobson. 2001. Dissociations among functional subsystems governing melody recognition after right-hemisphere damage. *Cogn. Neuropsychol.* **18:** 411–437.

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

231. Di Pietro, M., M. Laganaro, B. Leemann, *et al.* 2004. Receptive amusia: temporal auditory processing deficit in a professional musician following a left temporo-parietal lesion. *Neuropsychologia* **42:** 868–877.

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

233. Stewart, L. 2006. Music and the brain: disorders of musical listening. *Brain* **129:** 2533–2553.

234. Phillips-Silver, J., P. Toiviainen, N. Gosselin, *et al.* 2011. Born to dance but beat deaf: a new form of congenital amusia. *Neuropsychologia* **49:** 961–969.

235. Peretz, I. & M. Coltheart. 2003. Modularity of music processing. *Nat. Neurosci.* **6:** 688–691.

236. Peretz, I. & K. Hyde. 2003. What is specific to music processing? Insights from congenital amusia. *Trends Cogn. Sci.* **7:** 362–367.

237. Brust, J. 1980. Music and language: musical alexia and agraphia. *Brain* **103:** 367–392.

238. Marin, O.S.M. 1982. *Neurological Aspects of Music Perception and Performance.* New York: Academic Press.

239. Basso, A. & E. Capitani. 1985. Spared musical abilities in a conductor with global aphasia and ideomotor apraxia. *J. Neurol. Neurosurg. Psychiatry* **48:** 407–412.

240. Luria, A., L. Tsvetkova & D. Futer. 1965. Aphasia in a composer. *J. Neurol. Sci.* **2:** 288–292.

241. Cheng, K. 1986. A purely geometric module in the rat's spatial representation. *Cognition* **23:** 149–178.

242. Hermer, L. & E. Spelke. 1996. Modularity and development: the case of spatial reorientation. *Cognition* **61:** 195–232.

243. Gouteux, S., C. Thinus-Blanc & J. Vauclair. 2001. Rhesus monkeys use geometric and nongeometric information during a reorientation task. *J. Exp. Psychol. Gen.* **130:** 505–519.

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

245. Learmonth, A.E., N.S. Newcombe & J. Huttenlocher. 2001. Toddler's use of metric information and landmarks to reorient. *J. Exp. Child. Psychol.* **80:** 225–244.

246. Bek, J., M. Blades, M. Siegal, *et al.* 2010. Language and spatial reorientation: evidence from severe aphasia. *J. Exp. Psychol. Learn.* **36:** 646–658.

247. Shusterman, A., A. Ah Lee & E. Spelke. 2011. Cognitive effects of language on human navigation. *Cognition* **120:** 186–201.

248. Twyman, A., A. Friedman & M.L. Spetch. 2007. Penetrating the geometric module: catalyzing children's use of landmarks. *Dev. Psychol.* **43:** 1523–1530.

249. Sutton, J.E., A.D. Twyman, M.F. Joanisse, *et al.* 2012. Geometry three ways: an fMRI investigation of geometric information processing during reorientation. *J. Exp. Psychol. Learn.* **38:** 1530–1541.

250. Klessinger, N., M. Szczerbinski & R. Varley. 2012. The role of number words: the phonological length effect in multidigit addition. *Mem. Cognit.* **40:** 1289–1302.

251. Kanwisher, N. 2010. Functional specificity in the human brain: a window into the functional architecture of the mind. *Proc. Natl. Acad. Sci. U.S.A.* **107:** 11163–11170.

252. Joshi, A., L. Levy & M. Takahashi. 1975. Tree adjunct grammars. *J. Comput. Syst. Sci.* **10:** 136–163.

253. Bresnan, J. 1982. *The Mental Representation of Grammatical Relations.* Cambridge, MA: MIT Press.

254. Schabes Y., A. Abeill & A.K. Joshi. 1988. Parsing strategies with 'lexicalized' grammars: application to tree adjoining grammars. In *Proceedings of the 12th International Conference on Computational Linguistics.* pp. 578–583. Stroudsburg, PA: Association for Computational Linguistics.

255. Pollard, C. & I.A. Sag. 1994. *Head-Driven Phrase Structure Grammar.* Chicago, IL: University of Chicago Press.

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

257. Bybee, J. 1998. A functionalist approach to grammar and its evolution. *Evol. Commun.* **2:** 249–278.

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

259. Jackendoff, R. 2007. A parallel architecture perspective on language processing. *Brain Res.* **1146:** 2.

260. Culicover, P.W. & R. Jackendoff. 2005. *Simpler Syntax.* Oxford: Oxford University Press.

261. Jackendoff, R. 1977. *X-Bar-Syntax: A Study of Phrase Structure.* Cambridge, MA: MIT Press.

262. Chomsky, N. 1981. *Lectures on Government and Binding: The Pisa Lectures.* New York: Mouton de Gruyter.

263. Elman, J.L., E.A. Bates, M.H. Johnson, *et al.* 1996. *Rethinking Innateness.* Cambridge, MA: MIT Press.

264. Karmiloff-Smith, A. 1992. *Beyond Modularity: A Developmental Perspective on Cognitive Science.* Cambridge, MA: MIT Press.

265. Srihasam, K. & M. Livingstone. 2011. Anatomical correlates of early vs. late symbol training. *J. Vision* **11:** 1009–1009.

266. Dehaene-Lambertz, G., S. Dehaene & L. Hertz-Pannier. 2002. Functional neuroimaging of speech perception in infants. *Science* **298:** 2013–2015.

267. Dehaene-Lambertz, G., A. Montavont, A. Jobert, *et al.* 2010. Language or music, mother or Mozart? Structural and environmental influences on infants' language networks. *Brain Lang.* **114:** 53–65.

268. Kuhl, P.K., R.R. Ramírez, A. Bosseler, *et al.* 2014. Infants' brain responses to speech suggest analysis by synthesis. *Proc. Natl. Acad. Sci. U.S.A.* **111:** 11238–11245.

269. Shultz, S., V. Athena, R.H. Bennett, *et al.* 2014. Neural specialization for speech in the first months of life. *Dev. Sci.* **17:** 766–774.

270. Cristia A., Y. Minagawa & E. Dupoux. 2014. Responses to vocalizations and auditory controls in the human newborn brain. *PLoS One* **9:** e11516.

271. Moon, C.M. & W.P. Fifer. 2000. Evidence of transnatal auditory learning. *J. Perinatol.* **20:** S37–S44.

272. Partanena, E., T Kujalaa, R. Näätänena, *et al.* 2013. Learning-induced neural plasticity of speech processing before birth. *Proc. Natl. Acad. Sci. U.S.A.* **110:** 15145–15150.

273. Fodor, J. 1981. The mind–body problem. *Sci. Am.* **244:** 114–125.

274. Karnath H.-O. 2001. New insights into the functions of the superior temporal cortex. *Nat. Rev. Neurosci.* **2:** 568–576.

275. Neubert F.X., R.B. Mars, A.G. Thomas, *et al.* 2014. Comparison of human ventral frontal cortex areas for cognitive control and language with areas in monkey frontal cortex. *Neuron* **81:** 700–713.

276. Preuss, T.M. & P.S. Goldman-Rakic. 1991. Architectonics of the parietal and temporal association cortex in the strepsirhine primate *Galago* compared to the anthropoid primate *Macaca. J. Comp. Neurol.* **310:** 475–506.

277. Petrides, M. & D.N. Pandya. 1999. Dorsolateral prefrontal cortex: comparative cytoarchitectonic analysis in the human and the macaque brain and corticocortical connection patterns. *Eur. J. Neurosci.* **11:** 1011–1036.

278. Petrides, M. & D.N. Pandya. 2002. Comparative cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and corticocortical connection patterns in the monkey. *Eur. J. Neurosci.* **16:** 291–310.

279. Herculano-Houzel, S. 2012. The remarkable, yet not extraordinary, human brain as a scaled-up primate brain and its associated cost. *Proc. Natl. Acad. Sci. U.S.A.* **109:** 10661–10668.

280. Buckner, R.L. & F.M. Krienen. 2013. The evolution of distributed association networks in the human brain. *Trends Cogn. Sci.* **17:** 648–665.

281. Buckner, R.L., J.R. Andrews-Hannah & D.L. Schacter. 2008. The brain's default network: anatomy, function, and relevance to disease. *Ann. N.Y. Acad. Sci.* **1124:** 1–38.

282. Mantini, D., A. Gerits, K. Nelissen, *et al.* 2011. Default mode of brain function in monkeys. *J. Neurosci.* **31:** 12954–12962.

283. Curtiss, S. 1977. *Genie: A Psycholinguistic Study of a Modern-Day Wild Child.* New York: Academic Press.