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_anguage, music, syntax and the brain

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The comparative study of music and language is drawing an increasing amount of research interest. Like language, music is a human universal involving perceptually discrete elements organized into hierarchically structured sequences. Music and language can thus serve as foils for each other in the study of brain mechanisms underlying complex sound processing, and comparative research can provide novel insights into the functional and neural architecture of both domains. This review focuses on syntax, using recent neuroimaging data and cognitive theory to propose a specific point of convergence between syntactic processing in language and music. This leads to testable predictions, including the prediction that that syntactic comprehension problems in Broca's aphasia are not selective to language but influence music perception as well.

Language is a prime example of the special abilities of the human brain, and its neural foundations have long been of interest to both basic and applied neuroscience¹. More recently, there has been growing interest in the brain basis of music². Like language, music is a human universal in which perceptually discrete elements are organized into hierarchically structured sequences according to syntactic principles³. What is the cognitive and neural relationship of language and music? Are they largely separate, 'modular' brain systems that operate in fundamentally different ways (see accompanying review by Peretz & Coltheart⁴ in this issue), or is there significant overlap? The central thesis of this article is that language and music overlap in important ways in the brain, and thus studying the nature of this overlap can help illuminate interesting features about the functional and neural architecture of both domains.

Comparative neural research on language and music can focus on a number of different levels, such as the level of individual speech and musical sounds⁵, or of melodic and rhythmic patterns⁶. This article focuses on syntax, a topic of central concern in the neuroscience of language. An interesting paradox has emerged from comparative language-music research in this area. Recent neuroimaging data suggests an overlap in the processing of syntactic relations in language and music⁷⁻¹⁰. Yet these findings stand in direct contrast to evidence from neuropsychology that linguistic and musical syntax can be dissociated¹¹⁻¹⁶. How can this apparent contradiction can be resolved, and what can we learn about the brain as a result? A possible resolution based on modern cognitive theories of linguistic and musical syntactic processing is proposed in this review. A specific point of convergence between these theories leads to the hypothesis that syntax in language and music share a common set of processes (instantiated in frontal brain areas) that operate on different structural representations (in posterior brain areas). This hypothesis leads to testable predictions, including the prediction that syntactic comprehension problems in Broca's aphasia are not selective to language, but influence music perception as well.

Since music takes a wide variety of forms in different cultures and eras¹⁷, empirical comparison with language requires a focus on the music of a particular period and style¹⁸. This review focuses on Western European music of the tonal period (approximately 1600–1900), as there is a large body of theoretical and empirical research on its structure and perception¹⁹; and perception is emphasized above production, reflecting the greater amount of research in the former area.

What is syntax?

Syntax may be defined as a set of principles governing the combination of discrete structural elements (such as words or musical tones) into sequences²⁰. Linguistic and musical sequences are not created by the haphazard juxtaposition of basic elements. Instead, combinatorial principles operate at multiple levels, such as in the formation of words, phrases and sentences in language, and of chords, chord progressions and keys in music (i.e., 'harmonic structure'; Supplementary Audio 1 and Audio 2 online). Experienced perceivers show implicit knowledge of these principles in a variety of ways, including the ability to detect structural incongruities in novel sequences, such as agreement errors in language ("our baby love his books") and 'sour notes' in music (Supplementary Audio 3 online)²¹. Together with other types of information, syntactic knowledge allows the mind to accomplish a remarkable transformation of the input: a linear sequence of elements is perceived in terms of hierarchical relations that convey organized patterns of meaning. In language, one meaning supported by syntax is 'who did what to whom', that is, the conceptual structure of reference and predication in sentences²². In music, one meaning supported by syntax is the pattern of tension and resolution experienced as the music unfolds in time^{3,23}. Figure 1 shows examples of hierarchical analyses of language and music and discusses how these analyses illuminate the perceived structure of these sequences.

Syntactic overlap between language and music?

The existence of two distinct syntactic systems in the human mind raises the following question: does the processing of syntactic

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Syntactic structure in music: hierarchical patterns of tension & relaxation



Christus, der ist mein Leben 1st phrase (J.S. Bach) F. Lerdahl, Tonal Pitch Space (2001, OUP)

Ivelisse Robles

(harmonic) relations in music have anything in common with the syntactic processing of language? This question addresses the muchdebated issue of modularity in language processing^{24,25}: whether or not the neural operations underlying syntactic processing in language are unique to that domain.

The neuroscientific evidence on this question seems paradoxical. On the one hand, neuropsychology has provided well-documented cases of dissociations between musical and linguistic syntactic processing. For example, individuals with normal hearing may show impaired perception of harmonic relations in music, either following brain damage (acquired amusia) or due to a lifelong condition (congenital amusia), and yet show no signs of aphasia^{12–16}. Furthermore, the reverse pattern has also been reported: the composer Shebalin is often cited as a famous case of 'aphasia without amusia', or language impairment but spared musical abilities after brain damage¹¹.

On the other hand, a growing body of evidence from neuroimaging

Figure 1 Hierarchical structures in language and music. (a) The hierarchical structure of an English sentence. This sentence contains the words "the boy opened the door," yet a listener familiar with English knows that the boy did not do the opening. This is because words are not interpreted in a simple left to right fashion, but rather via their combination into phrases and then via the combination of phrases into sentences. This pattern is shown in the syntactic tree above the sentence (S, sentence; NP, noun phrase; VP, verb phrase; S', sentence modifier [relative clause]; N, noun; V, verb; Det, determiner; Rel-Pro, relative pronoun). Within the relative clause, the relative pronoun "who" is referred to as a filler and is interpreted as the actor for the verb "kissed." This relationship is identified by the presence of a coindexed empty element e_i in the subject position of the relative clause. (b) A phrase from a composition by Johan Sebastian Bach (Supplementary Audio 4 online), together with a syntactic tree indicating the hierarchical patterning of tension and relaxation in this passage according to Tonal Pitch Space Theory (TPS)³⁹. Right-branching indicates an increase in tension, and left-branching a decrease (i.e., relaxation). The tree shows how local tensing and relaxing motions are embedded in larger scale ones. Such patterns arise from the perception of chords with reference to a governing harmonic reference point or 'tonic'.

points to overlap in the processing of linguistic and musical syntax. For example, Patel et al.⁷ investigated a neural correlate of language processing, the P600 event-related potential (ERP), a positive brain potential elicited by syntactic (rather than semantic) processing which starts soon after the onset of a word and peaks at about 600 ms^{26,27}. When musicians listened to sentences and musical chord sequences with varying levels of syntactic incongruity (based on phrase structure rules for language and harmonic principles for music), P600s with statistically indistinguishable amplitude and scalp distribution were elicited (Fig. 2a). Subsequent neuroimaging research has supported the case for syntactic overlap by showing that musical syntactic processing activates 'language areas' of the brain. Maess et al.8, using magnetoencephalography (MEG), found an early right anterior negativity (ERAN)^{28,29} associated with harmonic processing in music originates in a left frontal language area known as Broca's area and its right hemisphere homologue (Fig. 2b). One recent functional magnetic resonance imaging (fMRI) study of harmonic processing9 reports activation of these areas, and a second¹⁰ implicates both Broca's and Wernicke's language areas in harmonic processing.

The apparent contradiction of neuroimaging and neurospsychology raises the question of what research should be done next. Simply gathering further evidence for dissociation from neuropsychology or for overlap from neuroimaging will not resolve the issue. The approach taken here is to use cognitive theory to interpret the current findings and to suggest new avenues for hypothesis-driven research.

A possible resolution: syntactic representation vs. processing

Cognitive theories of language and music suggest that the mental representations of linguistic and musical syntax are quite different. For example, all languages have nouns and verbs, grammatical categories which have no analogs in music³. Furthermore, words in sentences can take on grammatical functions such as subject, direct object and indirect object²⁰, which again have no parallels in music. Finally, long-distance syntactic dependencies are ubiquitous in language³⁰, such as between "girl" and "opened" (Fig. 1a), and every normal listener can be assumed to perceive them. In contrast, the long-distance dependencies posited by music theory (Fig. 1b) cannot simply be assumed to be perceived, and are instead better viewed as hypotheses subject to empirical test. Put another way, a particular sequence of chords does not constrain perceived dependencies to the

b



Figure 2 Neural evidence for syntactic overlap in language and music. (a) A positive event-related potential (ERP) associated with syntactic processing in language (the P600) is also elicited by syntactic processing in music⁷. Traces show ERPs to linguistic (black line) and harmonic (red line) syntactic incongruities from three electrodes along the midline of the head (Fz, front; Cz, vertex; Pz, back). The responses are highly similar in the vicinity of 600 ms after the onset of the incongruity. The continued positivity of the linguistic P600 vs. beyond 600 ms is due to the continuing ungrammaticality of the sentence beyond this point (see ref. 7 for details). (b) Localization data from an MEG study of harmonic processing in music⁸. This study focused on a different brain potential than the P600, namely an early right anterior negativity (ERAN) which had been observed in ERP studies of harmonic processing of language known as Broca's area⁸, as well as its right hemisphere homolog. (Yellow dots show dipole solutions for averaged data; blue dots show single subject solutions). This finding is convergent with subsequent fMRI research^{9,10}.

same degree as does a particular sequence of words, suggesting that words have more intricate syntactic features built into their representations than do musical chords³¹.

Observations of this sort suggest that the overlap in linguistic and musical syntax is not at the level of representation. Thus, one way to break the paradox outlined above is to propose a conceptual distinction between syntactic representation and syntactic processing. This can be understood as the distinction between long-term structural knowledge in a domain (*e.g.*, as instantiated in the strength of synaptic connections between neurons) and operations conducted on that knowledge for the purpose of building coherent percepts. A key idea of this approach is that at least some of the processes involved in syntactic comprehension rely on brain areas separate from the those areas where syntactic representations reside. Such 'dual-system' approaches have been proposed by several researchers concerned with the neurolinguistics of syntax. For example, Caplan and Waters³² have suggested that frontal areas of the brain support a special working memory system for syntactic operations, and Ullman³³ has suggested

Figure 3 How Dependency Locality Theory (DLT)³⁶ measures distances between words. Links between dependent words are shown by curved lines, and the distances associated with each link are shown by the integers below the curved lines (see Supplementary Note 2 online for details on how distance was computed). The numbers below each word show the total distance of that word from its prior dependent words. The total distance of each word is used as a measure of the integration cost for that word. Combining integration cost with storage costs (not shown) yields a total processing cost for each word, which can be compared to empirical data from reading time experiments. For this example, note the greater integration cost of the word "sent" in the lower sentence because of its distance from its dependent "who".





that frontal areas contain a symbol-manipulation system for linguistic syntax. The approach taken in the current review is a dual-system approach, but does not propose that that linguistic and musical syntax share a special memory system or symbol manipulation system. Instead, a hypothesis for what is shared by linguistic and musical syntactic processing is derived from comparison of cognitive theories of syntactic processing in the two domains.

Before introducing these theories, two related points should be made. First, there are theoretical approaches to linguistic syntax which reject a separation between representation and processing³⁴, as well as artificial neural-network ('connectionist') models in which syntactic representation and processing occur in the same network³⁵ and thus by implication in the same brain areas. Second, the theories discussed here are by no means the only theories of syntactic processing in language and music; they were chosen because of their strong empirical basis and because they show a remarkable point of convergence.

Syntactic processing in language: Dependency Locality Theory

Gibson's Dependency Locality Theory (DLT)^{36,37} was developed to account for differences in the perceived complexity of grammatical sentences and for preferences in the interpretation of syntactically ambiguous sentences. DLT posits that linguistic sentence comprehension involves two distinct components, each of which consumes neural resources. One component is structural storage: keeping track of predicted syntactic categories as a sentence is perceived in time (*e.g.*, when

Figure 4 The geometry of musical pitch space. (a-c) Spatial representations of empirical data on the perceptual proximity of musical pitch classes (individual tones) within a musical key, chords within a musical key, and of different musical keys, respectively⁴⁰. All three panels are oriented to the key of C-Major. (a) C' represents the pitch class an octave above the tone C. (b) Chords (triads of tones) are identified by roman numerals, with I representing the chord built on the first note of the scale (e.g., C-E-G in C-Major), II representing the chord built on the second note of the scale (e.g., D-F-A in C-Major), and so on. (c) Perceptual data on key relations displayed on a two-dimensional sheet (note how the left and right edges are equivalent, as are the top and bottom edges, reflecting the circular nature of key relations); each Major key is located close to related Major keys (the circle of fifths for keys) and to related Minor keys (the relative minor, which shares its key signature, and the parallel minor, which shares its principal tone or tonic). In each panel, elements which are close together within a map are perceived as being closely related in a perceptual sense. Tonal Pitch Space theory (TPS)³⁹ provides an algebraic method for combining the three types of distances shown in the figure into a single integer value in order to compute the distance between any chord in a key to another chord in the same key or to any chord in a different key. Panels a-c modified from refs. 87-89, respectively.

a noun is encountered, a verb is predicted to form a complete clause). The other component is structural integration: connecting each incoming word to a prior word on which it depends in the sentence structure. A basic premise of this theory is that the cost of inte-

gration is influenced by locality: cost increases with the distance (measured in words; see Supplementary Note 1 online) between the new element and the site of integration. For example, consider the relationship between the words reporter and sent in the following sentences: (i) The reporter who sent the photographer to the editor hoped for a story. (ii) The reporter who the photographer sent to the editor hoped for a story. In (i), when sent is reached, integration with its dependent reporter is relatively easy because the words are nearly adjacent in the sentence. In (ii), however, the integration between sent and reporter (now the object of the verb) is more difficult, because it must cross an intervening noun phrase, the photographer (technically, the integration is between sent and an empty-category object that is coindexed with the pronoun who). A major strength of this theory is its ability to provide numerical predictions of the processing (storage plus integration) cost at each word in a sentence, thus permitting empirical tests such as reading time experiments, in which the amount of time spent viewing each word of a sentence on a computer screen is quantified (Fig. 3). Experiments on a wide range of sentence types have provided support for Gibson's theory in English, Japanese and Chinese⁸⁶. Here, the relevant aspect of the theory is the idea that mentally connecting distant elements requires more resources.

Syntactic processing in music: Tonal Pitch Space Theory

Lerdahl's Tonal Pitch Space theory (TPS)³⁹ concerns the perception of pitch in a musical context. It has long been known that although

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frequency is a unidimensional feature of sound, the perception of pitch is more complex. The simplest example of this is octave equivalence, whereby frequencies related by a 2/1 ratio are perceived as highly similar in pitch (and are thus given the same letter name or pitch class irrespective of the octave in which they occur). In musical contexts, pitch perception is even richer. Krumhansl⁴⁰ reviews a large body of empirical evidence showing that musicians and nonmusicians alike acquire highly structured mental representations of musical pitch via exposure to tonal music. For example, a musical key such as C-major is much more than simply a scale (or set of pitch classes): C,D,E,F,G,A,B. Within this scale there is a hierarchy of importance, such that some pitch classes are perceived as more central or stable than others, with the first (C) being the most stable, followed by the fifth (G) and third (E) pitch class. Furthermore, triadic chords built on this scale are also perceived in a hierarchy of stability, with chords built on the first, fourth and fifth pitch class being the most stable. For both pitch classes and chords, stable elements in a key are perceived as being near each other in perceptual terms, with less stable elements being more distant. Finally, entire musical keys are also perceived in terms of an orderly set of distances from each other, relating to the difference in their number of sharp and flat notes, such as the 'circle of fifths' for musical keys (Fig. 4).

Based on these empirical data, Lerdahl's TPS provides an algebraic model for quantifying the tonal distance between any two musical chords in a sequence, yielding a single-integer value that incorporates the tripartite distances of pitch classes, chords and keys. TPS also provides a method for deriving tree structures, such as that in Fig. 1b, which serve as a hypothesis for the perceived relations between chords. Using the tree structure, one computes the distance of each chord from the chord to which it attaches in the tree, with the added stipulation that a chord 'inherits' distances from the chords under which it is embedded. Thus each chord is associated with a numerical distance value from another chord. This distance plays an important role in predicting the perceived ebb and flow of tension in musical sequences, with the basic idea being that tension increases with tonal distance between chords³⁹. For example, in a 'cadence,' tension drops between two chords as the music comes to a harmonic resting point in a given key. In contrast, when chords temporarily enter a new key area, tension increases. The numerical predictions of TPS can be compared to 'tension profiles' produced by listeners who rate perceived tension over time in musical passages⁴¹⁻⁴⁶. Such experiments provide support for TPS, and suggest that listeners do in fact hear relations between chords in a hierarchical rather than a purely sequential manner.

Crucially, the validity of TPS does not rely on the idea that listeners hear chord relations in terms of the particular tree structures it proposes. Rather, for a given passage the proposed tree serves as a hypothesis which is subject to empirical test via the perceived tension profiles. TPS can also generate predictions based on alternative hypotheses, including a hypothesis of strictly sequential perception in which each chord's distance is computed from the immediately preceding chord. Thus TPS can be used to empirically study the architecture of perceived chord relations in musical passages⁴⁴. For the present review, the relevant feature of TPS is that (no matter what architecture is used to relate chords to one another) the processing of chords is influenced by their distance from one another in a structured cognitive space of pitch classes, chords and keys.

Convergence of syntactic processing in language and music

DLT and TPS share the notion that structural integration is a key part of syntactic processing; that is, mentally connecting each incoming element X to another element Y in the evolving structure. This is not

surprising given that both theories deal with serial information processing. What is remarkable is that both theories posit that integration is influenced by the distance between X and Y in an abstract cognitive space. Furthermore, both theories can be cast in an activation-based framework. In DLT, integration can be understood as activating the representation of an incoming word while also reactivating a prior dependent word whose activation has decayed in proportion to the distance between the words⁴⁷. In TPS, integration can be understood as activating an incoming chord while maintaining activation of another chord which provides the context for the incoming chord's interpretation. The greater the tonal distance between the incoming and context chords the greater the processing cost, presumably because the incoming chord was not predicted and thus had a low activation level (*i.e.*, was not 'primed' by spreading activation⁴⁸). Thus for both DLT and TPS, syntactic processing consumes more resources when it requires accessing elements (words or chords) with low activation levels.

Overlap in the syntactic processing of language and music can thus be conceived of as overlap in the neural areas and operations which provide the resources for syntactic integration. I call this the 'shared syntactic integration resource hypothesis' (SSIRH). According to SSIRH, the brain regions providing the resources for syntactic integration are 'processing regions' that serve to rapidly and selectively bring low-activation items in 'representation regions' up to the activation threshold needed for integration to take place. The integration itself can then take place within the representation regions.

The neural location of the hypothesized overlapping processing regions for language and music is an important question which does not yet have a firm answer. One idea consistent with current research on language processing is that they are in frontal regions, which do not themselves contain syntactic representations but which provide resources for computations in posterior regions where syntactic representations reside49,50. Defining the neural locus of overlap will require within-subjects comparative studies of language and music using techniques which localize brain activity, such as fMRI. For example, if independent linguistic and musical tasks are designed with two distinct levels of syntactic integration demands within them (i.e., via the distance of elements to be integrated in each domain), one could search for brain regions which show increased activation as a function of integration cost in both language and music (see 'cognitive conjunction' neuroimaging⁵¹). These regions would be strong candidates for the overlapping processing regions proposed by SSIRH.

Reconciling SSIRH with evidence from neuroscience

One advantage of SSIRH is that it can reconcile the apparent contradiction between neuroimaging and neuropsychology described earlier in this article. With respect to neuroimaging, SSIRH is consistent with the findings of Patel *et al.*⁷ under the assumption that the P600 reflects syntactic integration processes in posterior 'representation regions'⁵². It is also consistent with localization studies that find that musical harmonic processing activates anterior language areas^{8–10} under the view that these anterior loci are shared 'processing regions' that help to activate representations in posterior regions. (It should be noted, however, that the precise localization of overlapping processing regions requires a withinsubjects design comparing language and music, as stated above.)

With respect to neuropsychology, SSIRH proposes that the reported dissociations between musical and linguistic syntactic abilities in acquired amusia are due to damage to domain-specific representations of musical syntax (*e.g.*, long-term knowledge of

Box 1 Music perception in aphasia: predictions and a call for research

A critical test of the idea that language and music overlap in syntactic processing is provided by aphasia, a disorder of language that results from brain damage. Research on music perception in aphasia has been curiously absent from modern cognitive neuroscience, perhaps because of a lack of a theoretical motivation for such research. This review proposes that there is overlap in the neural areas and operations that provide the resources for syntactic integration in language and music (Shared Syntactic Integration Resource Hypothesis, SSIRH), a hypothesis that makes predictions about music perception in aphasia.

Several language researchers have argued that syntactic comprehension deficits in Broca's aphasia can be due to disruption of processes that activate and integrate information in posterior language areas, rather than damage to linguistic representations *per se*^{49,50,71,72}. For these aphasics, SSIRH predicts that syntactic comprehension deficits in language will be related to harmonic processing deficits in music. One way to test this prediction is by harmonic priming, a well-studied technique in music cognition⁷³. Harmonic priming refers to the influence of a harmonic context on the processing of a target chord. Numerous studies have shown that a target chord is processed more rapidly and accurately if it is harmonically close to its context^{74–78}, and that this advantage is not simply due to the psychoacoustic similarity of context and target but to their distance in a structured cognitive space^{79–81}.

One powerful approach to the study of music processing in aphasia would be to compare performance on harmonic and linguistic priming tasks in the same set of individuals. (The priming tasks in language would examine how the processing of a word is influenced by its syntactic or semantic relation to a prior linguistic context.) There is a literature on syntactic and semantic priming in Broca's aphasia^{50,82–85} that could serve to guide the design of comparable linguistic and musical tasks. If related processing deficits for language and music are found in aphasia, a question of outstanding interest will be whether such deficits can be accounted for in a common computational framework^{48,84}.

harmonic relations), rather than a problem with syntactic integration processes. Consistent with this idea, these cases have been associated with damage to superior temporal gyri^{12–16}, which are likely to be important in the long-term representation of harmonic knowledge. SSIRH also proposes that musico-linguistic syntactic dissociations in congenital amusia are due to a developmental failure to form cognitive representations of musical pitch⁴⁰. Consistent with this idea, Ayotte *et al.*¹⁶ suggest that congenital amusia is due to a problem with fine-grained pitch discrimination, which suggests that cognitive maps have not had the structured input they need in order to develop normally.

How can SSIRH account for reports of aphasia without amusia, such as a stroke which results in severe language impairment but spared musical abilities? A recent summary of such studies⁵³ highlights several problems with this evidence. First, these reports often focus on accounts of famous musicians¹¹. Such data, consisting of case studies of individuals with extraordinary musical abilities, may not be relevant to music processing in the larger population. Second, reports of aphasia without amusia are seriously out of date. Many of the 13 cases cited in ref. 53 are from the 1800s, and the most recent is from 1987. Needless to say, none contain any systematic

tests of musical syntactic processing (*e.g.*, harmonic processing of chords) in individuals with well-defined linguistic syntactic processing deficits. In fact, it is striking that there are no modern studies of harmonic processing in aphasia, despite suggestive older research⁵⁴. This is an area that merits careful study, and is a crucial testing ground for SSIRH (**Box 1**).

Predictions of SSIRH

A principal motivation for developing SSIRH is to generate predictions to guide future research into the relation of linguistic and musical syntactic processing. Box 1 provides predictions concerning musical processing in aphasia. In addition, SSIRH also makes predictions for behavioral research. In particular, since SSIRH proposes that linguistic and musical syntactic integration rely on common processing regions, and since syntactic processing resources are limited³⁶, it predicts that tasks which combine linguistic and musical syntactic integration will show interference between the two. In particular, SSIRH predicts that integrating distant harmonic elements will interfere with concurrent syntactic integration in language. This idea can be tested in paradigms in which a harmonic and linguistic sequence are presented together and the influence of harmonic structure on syntactic processing in language is studied. Studies pairing linguistic tasks with concurrent harmonic manipulations in music have recently attracted interest^{55,56} (also Curtis, M. & Bharucha, J.J., personal communication³⁰) but have yet to be directed toward syntactic issues. In pursuing this research, it will be particularly interesting to vary the relative timing of harmonic and linguistic stimuli to study the dynamics of their interaction.

Conclusion

A growing body of evidence suggests that language and music are more closely related than previously believed. Studying the precise nature of their overlap can reveal interesting things about the functional architecture of both domains and refine our understanding of the role of different brain areas in the processing of complex, hierarchically structured sound sequences. Comparative research is most likely to be fruitful when it is hypothesis-driven and based on empirically grounded cognitive theory in the two domains.

This review has addressed a contradiction between recent studies of syntax in language and music based on neuroimaging (which suggest overlap) and neuropsychology (which suggest dissociation). A possible resolution is suggested by a point of convergence between modern cognitive theories of syntactic processing in language and music. This leads to the hypothesis that linguistic and musical syntax share certain syntactic processes (instantiated in overlapping frontal brain areas) that apply over different domain-specific syntactic representations in posterior brain regions. This hypothesis yields testable predictions, including the prediction of musical syntactic processing deficits in Broca's aphasia.

Although this review has focused on syntax, it is important to note that research on language-music relations is growing rapidly in both breadth and depth. Topics that have not been mentioned here, but which have great promise for the future, include comparative studies of development^{57–59}, neural plasticity^{60,61}, pitch perception^{6,62–64}, the cortical representation of speech versus musical sounds^{5,65,66}, text and tune processing in songs^{67–69}, and the influence of experience or training in one domain on abilities in the other⁷⁰.

For too long, the neuroscience of language has been studied in isolation, depriving neurolinguistics of the power of the compara-

tive method in biology. Music is now stepping into this breach, and via comparative analysis with language, providing a more complete and coherent picture of the mind than can be achieved by studying either domain alone.

Note: Supplementary information is available on the Nature Neuroscience Website.

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