Moving beyond domain-specific vs. domain-general options in cognitive neuroscience

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Abstract

Comparative research on language, music, and action in cognitive neuroscience keeps finding evidence for both shared and non-shared components of cognitive systems. The discussions, then, tend to quickly fall into the sterile dichotomy between domain-specific vs. domain-general options. In this position paper, we take issue with this dichotomy and argue for an alternative account based on neural reuse theories to understand findings on the relationship between language, music, and action. We argue that the differences between those cognitive systems can be explained in terms of the specialization of the same brain mechanism(s) for each domain, which emerges in the course of development and/or evolution.

Keywords

Comparative research, neural reuse theories, language, music, action

1 Introduction

Cognitive science has been dominated by intense debates around key notions such as innateness or domain-specificity/modularity. Here we focus on the latter, and based on recent research reviving tensions, we suggest productive ways of going beyond sterile dichotomies. In particular, we capitalize on neural reuse theories and argue that cognitive systems can be understood as different uses of the same mechanisms. Although neural reuse theories have repeatedly gained attention in cognitive neuroscience and provided an explanatory account for the relationship between different cognitive systems (Anderson, 2010; Hernandez et al., 2019; Pulvermüller, 2018), they still often remain completely neglected by current comparative research when discussing issues like domain-specificity vs. domain-generality. So far, comparative research is dominated by classical ‘top-down’ approaches studying the relationship between language, music, and action based on ready-made theoretical concepts. In contrast, neural reuse theories offer a bottom-up comparative approach investigating different cognitive domains based on a set of basic operations performed by the brain. It is such a bottom-up approach that we argue resolves the dichotomy between domain-specific vs. domain-general options. We focus on the relationship between language, music, and action and more specifically their syntactic aspects to illustrate our position, but we think our message is not restricted to these.

2 Sharing and non-sharing: An unresolved issue

Three decades of comparative research on language and music in cognitive neuroscience have adduced evidence for both shared and non-shared components. In the beginning, the explanatory target of comparative research on language and music was the

discrepancy between findings from neuroimaging on shared neural resources (e.g., Koelsch et al., 2002; Patel, Gibson, Ratner, Besson, & Holcomb, 1998) and neuropsychology on domain-specificity (e.g., Ayotte, Peretz, & Hyde, 2002; Peretz et al., 1994). Patel's (2003, 2008) resource-sharing framework resolved this issue in a convincing way by distinguishing shared resources for syntactic integration in the frontal processing region from domain-specific representations in the posterior representation region. The same neural resources were suggested to be engaged in action (e.g., Fitch & Martins, 2014; Koelsch, 2012), building on early insights from Lashley (1951) and Miller et al. (1960). However, an increasing number of findings on language, music, and action as well as their interactions have revealed that the relationship between these domains is far more complex.

On the one hand, behavioral, neuroimaging, and neuropsychological studies continue to provide evidence for shared neural resources for syntax in language, music, and action. For example, behavioral and electroencephalography studies have shown that language syntactic processing interferes with music syntactic processing (e.g., Fedorenko, Patel, Casasanto, Winawer, & Gibson, 2009; Koelsch, Gunter, Wittfoth, & Sammler, 2005; Slevc, Rosenberg, & Patel, 2009) and action syntactic processing (Casado et al., 2018). Music syntactic knowledge influences action planning in trained pianists (Bianco et al., 2016; Sammler, Novembre, Koelsch, & Keller, 2013). Functional magnetic resonance imaging (fMRI) studies found that language syntactic processing overlaps with music syntactic processing in Broca's region (Chiang et al., 2018; Kunert, Willems, Casasanto, Patel, & Hagoort, 2015) and with tool-use in the basal ganglia (Thibault et al., 2021). Agrammatic aphasic patients show deficits in music syntactic processing (Patel, Iversen, Wassenaar, & Hagoort, 2008) and action planning (Fazio et al., 2009). Children with specific language impairment show the absence of an event-related potential (ERP) component for music syntactic processing (Jentschke, Koelsch, Sallat, & Friederici, 2008) and abnormal action syntactic processing (Roy et al., 2013).

These findings can be interpreted in light of the domain-general hierarchical processing mechanism underlying language, music, and action (Fitch & Martins, 2014).

On the other hand, an ever-increasing number of neuroimaging, meta-analytic, and neuropsychological studies provide evidence in support of functional separability between language, music, and action, both in terms of processing and representation. For example, fMRI studies have revealed a left-lateralized fronto-temporal core language network for ‘high-level’ linguistic processing including lexical and syntactic processing that is not sensitive to music processing (Chen et al., 2021; Fedorenko, Behr, & Kanwisher, 2011). Even within Broca’s region, there appears to be a portion specialized for language processing (Fedorenko, Duncan, & Kanwisher, 2012). Moreover, meta-analytic co-activation-based parcellation studies have shown that there are multiple subareas with different functionality even within the left BA44: the anterior portion of the left BA44 is associated with core aspects of language processing and shows connectivity with the left middle temporal gyrus, while action and music are rather located at the posterior portion, which exhibits a different connectivity profile (Clos, Amunts, Laird, Fox, & Eickhoff, 2013; Papitto, Friederici, & Zaccarella, 2020). Neuropsychological studies indicate preserved ability for music processing in aphasic patients (Chen et al., 2021; Chiappetta, Patel, & Thompson, 2022; Slevc, Faruqi-Shah, Saxena, & Okada, 2016). In sum, arguments have been put forth against the idea of a domain-general hierarchical processing mechanism common to language, music, and action (Fedorenko & Blank, 2020; Fedorenko & Shain, 2021; Fedorenko & Varley, 2016; Zaccarella, Papitto, & Friederici, 2021).

To some extent, these recently revived claims of neural specializations should not come as a surprise. After all, language, music, and action differ in several obvious ways (items they combine, categories for labeling units, and content they encode / are used to express (Asano & Boeckx, 2015)). It seems to us that the key question should not be whether music and action show all the features characteristic of language nor whether they activate the core language-

network. Those questions invariably lead to a contrastive, and ultimately, we think, sterile approach, as we have discussed in detail elsewhere (Asano & Boeckx, 2015). A more productive question, particularly for the growing number of researchers who have abandoned the classical stance of innately specified cognitive modules, should be how the differences, as well as the similarities, should be understood as emerging in the course of development and/or evolution.

3 Limitations of top-down comparative approaches

Comparative research has already advanced a couple of hypotheses regarding how to understand findings that favor shared and distinctive components of language, music, and action. However, they cannot fully account for the existing data. For example, it has been argued that commonalities between language and music arise as a result of a generic mental process responsible for processing deviant events and have little to do with ‘high-level’ linguistic processing (Fedorenko & Varley, 2016). This would be due to the fact that many studies which provided evidence for shared neural resources for language and music syntactic processing used a violation paradigm. However, this explanation does not have universal validity. Syntactically deviant chords in music, but not physically deviant tones (e.g., timbre deviants), influence the left anterior negativity (LAN), an ERP component associated with language syntactic processing (Koelsch et al., 2005). Moreover, there is at least one study providing evidence for shared neural resources for language and music syntactic processing without introducing any violation (Chiang et al., 2018). Thus, there should be something shared between language and music syntactic processing that cannot be explained in terms of a generic mental process for processing deviant events.

Another possible explanation for domain-commonality is that both domains at issue deal with pitch and rhythm processing and their shared components have little to do with ‘high-level’ linguistic processing (Chen et al., 2021). Indeed, prosodic structure parallels musical structure (Heffner & Slevc, 2015; Lerdahl & Jackendoff, 1983). However, again, this explanation alone cannot fully account for the existing data. Interference between language and music syntactic processing occurs even though the sentence was visually presented word-by-word without any prosodic cues (Carrus, Koelsch, & Bhattacharya, 2011; Koelsch et al., 2005; Steinbeis & Koelsch, 2008). Moreover, even though pitch and rhythm processing would partially account for the relationship between language and music, it leaves unexplained how prosody and music relate to syntactic processing in language. Thus, claiming or showing that language and music share general pitch and rhythm processing does not suffice as an explanation for shared components of language and music as seen in their syntactic processing.

Finally, one candidate explanation for the shared properties of language, music, and action is that they draw on domain-general executive function. Language, music, but also action processing, could share resources for working memory (Fitch & Martins, 2014; Kljajevic, 2010) or cognitive control (Jeon, 2014; Slevc & Okada, 2015), signaled by activity in Broca’s region, especially BA44. Indeed, the majority of studies providing evidence for shared neural resources for language, music, and action syntactic processing makes use of experimental paradigms that impose high control demands on participants (e.g., the need of selecting an alternative interpretation or processing temporally distant elements) (Slevc & Okada, 2015). Moreover, the executive-function-based explanation can account for hierarchical processing in language, music, and action because control processes to select, maintain, and inhibit goals are hierarchically organized (Asano, Boeckx, & Seifert, 2021; Fitch & Martins, 2014; Jeon, 2014; Slevc & Okada, 2015). Yet, several authors cast doubt on this explanation by pointing to dissociations between language syntactic processing and executive

function, highlighting the clear separation of the core language network and the domain-general cognitive control network revealed in several studies (Chen et al., 2021; Fedorenko & Blank, 2020; Fedorenko & Varley, 2016; Zaccarella et al., 2021). These authors conclude that the shared mechanism between language, music, and action has little to do with language syntactic processing.

So far, comparative research has been devoted to the investigation of whether shared components are ‘high-level’ linguistic components like syntax or whether they can be explained in terms of executive function. However, such top-down comparative approaches relying on the ready-made concepts of linguistics or psychology are clearly not able to provide a comprehensive explanation for the complex relationship between language, music, and action. Moreover, caution is needed when we map theoretical concepts from linguistics or psychology onto neuroscientific concepts (for discussions, see, e.g., Embick & Poeppel, 2015; Lenartowicz, Kalar, Congdon, & Poldrack, 2010; Poeppel & Embick, 2005; Price & Friston, 2005). Although the labeling of cognitive phenomena with top-down concepts is a reasonable first approximation, it could eventually obscure the need for detailed mechanistic investigations (Brick, Hood, Ekroll, & De-Wit, 2022). In what follows, based on the neural reuse theories (Anderson, 2010), we propose an alternative account to these top-down approaches in order to resolve the shared vs. distinct dichotomy in comparative research on language, music, and action.

4 A perspective from neural reuse theories: Going beyond the specific/general dichotomy

4.1 Neural reuse theories: Perspectives from bottom-up

Neural reuse theories come in many guises: massive redeployment hypothesis (Anderson, 2007), neuronal recycling hypothesis (Dehaene & Cohen, 2007), or neuronal

retuning hypothesis (Matchin, 2018). However, all of them revolve around the central idea that brain regions or circuits established for one function can be reused for various new functions during evolution (i.e., exaptation) or development, often without losing their initial functions (for reviews, see Anderson, 2010; Hernandez et al., 2019). For example, comprehending action verbs “kick”, “pick”, and “lick” activates motor regions associated with leg, arm, and face movements (Pulvermüller, 2005), indicating that those regions are reused in a newer context of language comprehension (Anderson, 2010). Moreover, as non-human primates display a certain degree of hierarchical combinatorial ability in the domain of action (Byrne & Russon, 1998; Hayashi, 2007; Matsuzawa, 1991), its reuse in syntax of language and music was suggested (Asano, 2021; Fujita, 2016; Greenfield, 1991; Hilton, Asano, & Boeckx, 2021; Pulvermüller, 2014). They all argue for continuity from action to language and music.

Moreover, all neural reuse theories agree on the distinction between the notion of “working”, i.e., a canonical information processing operation performed by a region or local anatomical circuits, and the notion of “use”, i.e., a cognitive function to which the working is applied in a unique way (Anderson, 2010). Thus, different cognitive functions such as language, music, and action could be explained in terms of different uses of the same working. Differences between those cognitive functions in terms of neural segregation can be explained in terms of the domain-specific configuration of the networks in which a region featuring a common operation is embedded. Importantly, neural reuse theories are in line with network approaches that suggest that computations performed by the language network (and its subregions) are unique and do not parallel that of music and action (Chen et al., 2021; Fedorenko & Blank, 2020; Fedorenko & Thompson-Schill, 2014). Neural reuse theories constitute a variant of the network approach, putting more emphasis on the common working of a region used in different domain-specific networks.

Neural reuse theories offer a bottom-up perspective to comparative research on language, music, and action by studying different cognitive domains based on a set of basic operations performed by the brain. They aim to identify the underlying mechanisms of cognitive systems independent of top-down linguistic or psychological concepts and to do so in a more neuro-biologically plausible way (Anderson, 2015; Pulvermüller, 2010, 2018; Stocco, 2019). Here, “mechanism” is understood as the way how different constituent parts performing unique operations work in tandem to bring about a given phenomenon (Bechtel & Shagrir, 2015). Moreover, neural reuse theories introduce developmental and evolutionary perspectives to comparative research on language, music, and action, complementing the studies on the fully developed brain in cognitive neuroscience (Anderson, 2010, 2016; Dekker & Karmiloff-Smith, 2010; Hernandez et al., 2019). Thus, neural reuse theories explain the relationship between language, music, and action in terms of common basic mechanisms that get organized into specialized networks in the course of development and/or evolution. Accordingly, there is no such dichotomy as domain-general hubs vs. domain-specific networks of the sort that can be found in the literature (e.g., in Figure 1 of Fedorenko & Shain, 2021).

Bottom-up perspectives of neural reuse theories have another advantage: they facilitate research on the relationship between syntax in language, music, and action beyond the cortex. For example, the significant role of the basal ganglia in language syntactic processing is repeatedly emphasized (Birba et al., 2017; Dominey & Inui, 2009; Kotz, Schwartze, & Schmidt-Kassow, 2009; Lieberman, 2002, 2016; Ullman, 2006), but did not get enough attention in comparative research on syntax in language, music, and action (but see Asano et al., 2021). The same can be said concerning the cerebellum, the hippocampus, the thalamus, and perhaps additional regions as well (Adamaszek & Kirkby, 2016; Boeckx & Theofanopoulou, 2018; Duff & Brown-Schmid, 2017). The traditional corticocentric view that ‘higher’ cognitive functions (e.g., ‘syntax’) are implemented by cortical structures and ‘lower

functions' by subcortical structures retains its dominant position despite the evidence pointing to cortical and subcortical structures working in tandem to bring about 'higher' cognitive functions (DeCasien, Barton, & Higham, 2022; Parvizi, 2009). Neural reuse theories overcome such a high- vs. low-level dichotomy by arguing that putatively low-level neural circuits are used and reused by high-level cognitive domains (Anderson, 2010). That is, there is no clear-cut distinction between neural circuits underlying high- and low-level processes. This is in line with the approach regarding motor and cognitive processes more as a gradient rather than as a categorical division (Marvel, Morgan, & Kronemer, 2019). Ultimately, it is also in agreement with the approach advocated by Cisek (2019) on "phylogenetic refinement" and several contributions to the thematic issue "Systems neuroscience through the lens of evolutionary theory" (see Cisek & Hayden, 2022 for an overview of the contributions).

4.2 Application to comparative research on language, music, and action

For comparative research on language, music, and action, one candidate working of the prefrontal cortex is the active maintenance of representations as evidenced by sustained neural activity (Fuster, 2008; E. K. Miller & Buschman, 2008; E. K. Miller & Cohen, 2001), which is also a possible working of BA44 and is crucial for language, music, and action to establish structural relationships between elements (Asano et al., 2021; Fitch & Martins, 2014). For example, the language-selective part of the left BA44 shows significant activation in challenging verbal working memory tasks (Fedorenko et al., 2012). Even the language-selective part of the left BA45 is devoted to the maintenance of the representations of language retrieved from long-term memory (Matchin, 2018). Thus, it is possible that there are multiple specialized storage and retrieval mechanisms within Broca's region (Fitch, 2018). According to neural reuse theories, specialized subparts of BA44 for language, music, and action with different connectivity profiles (Clos et al., 2013; Papitto et al., 2020) can be understood in such

a way that the common maintenance operation is embedded in different networks to solve different computational problems.

Moreover, the frontal cortex is organized along an abstraction gradient from the posterior portion buffering the goals associated with the concrete motor act (e.g., grabbing a pot) to the anterior portion maintaining abstract, temporally extended goals (e.g., coffee making) (Badre, 2008). Language processing is also organized alongside the abstraction gradient from phonology in the more posterior region to syntax to semantics in the more anterior region (Uddén & Bahlmann, 2012). In music, too, abstract structural processing is associated with a more anterior region than the one devoted to motor processing (Bianco et al., 2021). In processing sentences and musical sequences with center-embedding, the relationship between temporally distant elements should be established (Jeon, 2014). However, a review of neuroimaging studies on syntactic processing in the two domains showed that music syntactic processing relies on the coordination of abstract and motor processing circuits, while language syntactic processing more preferably engages abstract processing circuits (Asano et al., 2021). Thus, the difference between language, music, and action within the left BA44 as seen in some meta-analyses (Clos et al., 2013; Papitto et al., 2020) could also be explained in terms of this abstraction gradient with “language” clustering at the anterior portion and “music” and “action” clustering around the posterior portion.

It is not just the frontal maintenance operation that builds the common basis for language, music, and action, but also the inhibition and selection operation of the basal ganglia to control cortically maintained representations via the coordinated activity of the direct and indirect pathways (Lieberman, 2002; Marsden & Obeso, 1994). The basal ganglia are interconnected with the frontal cortex and form functionally segregated cortico-basal ganglia-thalamocortical (CBGT) circuits reflecting the gradient organization of the frontal cortex (G. E. Alexander, Delong, & Strick, 1986; Haber, 2003). The basal ganglia operations together

with the frontal maintenance operation constitute the hierarchical control mechanism underlying not only language, music, and action, but also cognitive control and working memory (Asano et al., 2021; Badre & Nee, 2018; Lustig, Matell, & Meck, 2005). Processing sentences, musical sequences, complex actions (e.g., coffee making), and cognitive control or working memory tasks (e.g., Wisconsin Card Sorting Task) all require a balanced choice between multiple representations. From the bottom-up perspective of neural reuse theories, these cognitive phenomena are not rigid categories, but rather, different uses of the same mechanism.

Importantly, such a mechanistic approach ideally goes hand in hand with a computational approach. For example, the Hierarchical Reinforcement Learning model is a computational neurocognitive model implementing the abstraction gradient as well as the maintenance, inhibition, and selection operations of the CBGT circuits and successfully simulates the behavior and neural dynamics of some cognitive control tasks (Badre & Frank, 2012; Frank & Badre, 2012). The Hierarchical reinforcement learning system adaptively learns to represent and maintain information at different levels of abstraction to optimally perform the task. The Hierarchical Error Representation model also implements the operations of the CBGT circuits and integrates them with a prediction mechanism (W. H. Alexander & Brown, 2018). The application of such models to comparative research on language, music, and action facilitates the exploration of how different domains emerge from common mechanisms. Simulation works with biologically plausible neurocomputational models can provide a proof-of-concept that the same neural circuits can realize the mechanistic basis of diverse cognitive domains (Pulvermüller, 2018).

Needless to say, what we discussed here is only a small subpart of the common mechanisms underlying language, music, and action. For example, a detailed analysis of the parietal and temporal cortex in light of neural reuse theories is likely to provide additional

insights. The posterior temporal cortex, especially the posterior middle temporal gyrus, is known as another important region involved in language syntactic processing to decode auditory sequences into hierarchical structures and link these with conceptual structures (Matchin & Hickok, 2020; Pylkkänen, 2019). The angular gyrus, the anterior superior temporal sulcus, and the temporal pole are sensitive to the constituent size of meaningful phrases (Pallier, Devauchelle, & Dehaene, 2011). For music, the generation of hierarchical structures according to a recursive rule activates the posterior superior temporal gyrus (Martins et al., 2020). The fronto-parietal and fronto-temporal networks are involved in pianists' motor planning and music syntactic processing, respectively (Bianco et al., 2021). For action, tool-use planning engages the parietal and temporal lobe in addition to the frontal lobe, which are interconnected to form fronto-parieto-temporal networks (for a review, see Maravita & Romano, 2018).

Although more research is necessary to identify the working of the parietal and temporal cortex, there are leading hypotheses such as the encoding of abstract structural relations (or rules) for the parietal lobe (Orpella et al., 2020; Summerfield, Luyckx, & Sheahan, 2020) as well as hierarchical combinatorial object formation for the temporal lobe (Rauschecker & Scott, 2009). The notion of an abstraction gradient is also applicable to the parietal and the temporal cortex (Braunsdorf et al., 2021; Choi, Drayna, & Badre, 2018; Fuster, 2008). Clarification of the operations performed by the parietal and temporal cortex could further inform the relationship between language, music, and action in light of neural reuse theories.

4.3 Towards evolutionary-developmental approaches

From the perspective of neural reuse theories, we should expect specialization to emerge in the course of development. For instance, the left inferior frontal gyrus as well as the left posterior superior temporal gyrus of the core language network is expected to become functionally specialized as their structural connection via the arcuate fasciculus matures in the

course of the development (Skeide & Friederici, 2016). Strikingly, a study conducted with an individual born without the left temporal lobe showed that the language-selective frontal areas do not emerge without the ipsilateral temporal lobe (Tuckute et al., 2022). The same study also showed that the non-language-dominant right hemispheric fronto-temporal network is sufficient for language function, indicating that the right frontal and temporal regions implement the same operations as their left counterparts and can become specialized for performing linguistic computation. The right inferior frontal gyrus is generally more associated with music, action execution and inhibition, social cognition, emotion, and executive function (Hartwigsen, Neef, Camilleri, Margulies, & Eickhoff, 2019). Thus, the specialized language-network is an emergent property of the developing brain.

Once one takes the specialized core language network as an emerging property of the cortical as well as subcortical (re-)organization, and language, music, and action syntactic processing as different uses of the same mechanism(s), the boundaries between domain-specific and domain-general processes blur and a novel, more productive comparative perspective emerges. From the perspective of the neural reuse theories, research on the developing brain becomes more central to comparative research on language, music, and action (see also Goswami, 2012; Maffongelli, D'Ausilio, Fadiga, & Daum, 2019). In particular, the neuroconstructivist approach to brain development (Dekker & Karmiloff-Smith, 2011; Karmiloff-Smith, 2013) provides some useful predictions. According to this approach, the brain's initial state is coarsely coded so that each neurobiological bias (e.g., cell types, firing thresholds) is more suitable for certain types of information processing over others. Through neural competition, the coarsely coded system becomes increasingly more domain-specific over time in the development and gives rise to the developed brain of the adults with computational specializations. The neuroconstructivist approach predicts that the infant's

developing brain should show more broad activations than the specialized adult's brain to perform specific computations (Karmiloff-Smith, 2013).

We think that this point is important because so far, studies that highlight the existence of a specialized core language network mainly focus on the first-language processing of adults, with a fully developed brain in which language processing is automatized. However, language processing in the subjects with a low level of proficiency such as children and adult second language learners is known to engage far more extended brain regions than for adult first language speakers (Jeon & Friederici, 2015). Thus, it is possible that language processing in the (developing) brain without automatized processing relies on the resources of broader brain regions than the developed brain with automatized processing does. For example, studies conducted with German 2-year-olds showed that the early left anterior negativity (ELAN) associated with automatic language syntactic processing emerges later in the development, while the P600 associated with controlled syntactic processing is present earlier (Oberecker & Friederici, 2006; Oberecker, Friedrich, & Friederici, 2005). This points to a developmental change toward more automatic syntactic processing (Friederici, 2017). P600 is affected by the lesions to the frontal, temporal, and/or parietal sites (Kaan, 2007) as well as the deficient basal ganglia (Friederici & Kotz, 2003) and might be indicative of more widespread brain activations.

The neuroconstructivist approach to brain development together with the mechanistic approach accompanied by computational neurocognitive modeling could advance future research on neural specialization. For example, the Hierarchical Reinforcement Learning model can be regarded as a model of the neural specialization where control processes get specialized via the learning mechanism implemented in cortico-basal ganglia-thalamocortical circuits. The interplay between the frontal cortex and the basal ganglia plays a central role in the acquisition of abstract rules through statistical learning (E. K. Miller & Buschman, 2008; Orpella, Mas-Herrero, Ripollés, Marco-Pallarés, & de Diego-Balaguer, 2021; Ullman, Earle,

Walenski, & Janacsek, 2020). Especially, the basal ganglia are considered to implement an implicit, associative learning mechanism and tune the cortico-cortical top-down control pathways (E. K. Miller & Buschman, 2008; Ullman et al., 2020). This is in line with the findings that the early learning mode as seen in infants (or children) is associative, implicit, and independent of top-down control, while the adult learning mode relies more on top-down control and explicit knowledge (Friederici, Mueller, Sehm, & Ragert, 2013; Smalle, Daikoku, Szmalec, Duyck, & Möttönen, 2022; Ullman et al., 2020). Thus, in light of neural reuse theories, research on development and learning can inform computational research focusing on neurocognitive mechanisms and vice versa.

Last but not least, neural reuse theories have important implications for evolutionary research, as they point to a more continuous view of the evolution of cognitive functions in a similar vein to Darwin's idea of descent with modification (see also Boeckx & Fujita, 2014). For example, Anderson's massive redeployment hypothesis investigates the evolution of the brain in light of an exaptive account of cognitive functions by suggesting that a new cognitive function can emerge based on the recombination of the old, existing components (Anderson, 2007). Another related idea is "duplication and divergence" by which new systems are created based on modified copies of older systems (Chakraborty & Jarvis, 2015; Marcus, 2006; Marcus, Rabaglia, & Rabagliati, 2006), as argued for the evolution of vocal learning through the duplication of the brain mechanisms from an ancient motor learning (Feenders et al., 2008). Importantly, neural reuse theories imply the emergence of different cognitive systems through the modification of shared components. Thus, again, it is unsurprising that language, music, and action show specializations of brain networks. However, as we argue here, the existence of these specialized networks does not reject the existence of shared mechanisms that serve as common bases for the emerging specializations of cognitive systems. Neural reuse theories make it clear that cognitive systems such as language, music, and action cannot be explained

in terms of the domain-specific vs. domain-general dichotomy. Rather, they are better understood as different uses of the same mechanisms.

5 Concluding remarks

To summarize, neural reuse theories suggest that syntactic aspects of language, music, and action are emergent properties of the brain, arising through the specialization of the common brain mechanisms in the course of development and/or evolution. As the brain becomes specialized for each domain over time, likely through automatization and the accumulation of sub-routines, the less language, music, and action syntactic processing should rely on the shared neural resources, except when there is an unusually large task demand. In the developed, adult brain, solving specific computational problems should result in more segregated, domain-specific networks than in the developing brain. This, we insist, should not come as a surprise. Importantly, the operations of the regions should remain unchanged even though it is used to solve different computational problems in specialized networks. Thus, even though differences between language, music, and action can be detected in neuroimaging studies, comparative research should take neural reuse theories into account and avoid the sterile dichotomy between the domain-specific vs. domain-general options. Especially now that the idea of innate modules has lost its appeal, the question driving research across cognitive domains should not be “whether there are domain-specific and -general brain regions / networks”, but rather “how and why the brain becomes specialized as it does, when it does”.

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