biolinguistics

Subcortical Contributions
to the Uniqueness of Human Cognition:
A Commentary on Laland & Seed (2021)

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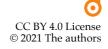
1.   Introduction

Laland and Seed (2021) address the issue of the evolution of human unique cognition. Having reviewed comparative evidence on five candidate traits—mental time travel, tool use, problem solving, social cognition, and communication—the authors conclude that no single trait could explain human superior cognition, and humans are probably cross-domain/modality/modular thinkers leading to a high-level intelligence which underlies human cognitive uniqueness. Such a comprehensively theoretical review attracts multidisciplinary readers, and the attempt to answer the question of whether human cognition is unique or not is highly significant in cognitive science. However, although the target paper provides numerous comparative data, we think that the continuous view of human cognition is not novel.

The solution the authors offer seems to be devoid of explanatory power. We agree that in general there is a continuum between nonhuman animal and human cognition, and it is not surprising that human cognition is superior because information from different modules interact. However, the authors fail to explain how different cognitive abilities interact and why there is still a gap between human language and animal communication systems. Take mental time travel as an example, various animals have been shown to have limited ability to recall the past

and predict the future (Clayton & Dickinson 2010). However, the creative use of language enables humans to escape from current situations and produce meaningful utterances that refer to things and situations outside of the here and now. This is referred to as displacement (Hockett 1960, Bickerton 2009). It is worth noting that such displacement that we focus on in this paper is distinct from that repeatedly mentioned in the literature of generative grammar, where displacement is a property of linearized syntactic structure where phrases are interpreted in one place but pronounced in another.

We suggest that in order to achieve displacement, information from different cognitive domains needed to be encoded into lexical items. The combination of lexical items via syntax allows the generation of an in principle infinite number of different syntactic structures. Syntactic operations are assumed to be domain general, in the sense that they not only produce lexical items and sentences (Boeckx 2014) in the language domain but also extend to other domains like music (Shi & Zhang 2020) and movements (Pulvermüller 2014). In this commentary, we would like to focus on displacement, and suggest that domain general syntax serves as the underlying mechanism which enhances the combination of information from different cognitive domains. The importance of language in human unique cognition has been highlighted in the existing literature (e.g., Darwin 1871, Spelke 2009, Berwick & Chomsky 2016).

From a neurocognitive perspective, we would like to further argue that syntax beyond the language domain supported by the hippocampus and basal ganglia could play a key role. Moreover, we suggest that the interaction between these two subcortical structures in humans gives rise to the creative use of language that makes displacement possible which in turn lays the foundation for the uniqueness of human cognition. We are fully aware that neuroimaging and lesion studies point to the conclusion that syntactic operations are mainly supported by cortical areas and cortico-cortical connections (e.g., Friederici 2011). Nevertheless, subcortical regions have also been shown to be involved in syntactic operations (see Shi & Zhang 2020 for a review).

From an evolutionary perspective, subcortex is conserved across species, while neocortex is specific to mammals. Although it has been shown that neocortex is important for the evolution of high-level cognition, studies on birds who lack neocortices show that they exhibit high intelligence, like crows' tool use (Hunt 1996) and parrots' vocal imitation (Chakraborty et al. 2015), suggesting an important role of subcortex in cognition. On the other hand, if domain-general functions of the subcortical regions lay the foundation for domain-general syntax, it could be the case that in evolution cortical areas coordinate with subcortical ones to achieve a better efficiency of information transformation (Shi & Zhang 2021).

2. Displacement, Other Cognitive Abilities, and a Domain-General Syntactic Operation

Displacement is fulfilled through linguistic tools. For example, in the sentence *I played football yesterday*, it is clear that both the lexical item *yesterday* and the syntactic past tense *-ed* refer to an event that happened in the past. Both lexical items

and syntax are evolutionary novelties (Bickerton 2009). Syntax not only produces words but also puts words together into infinite combinations of phrases, clauses, and sentences which in turn are used to express our thought. As the carrier of displacement that makes mental time travel possible, syntax not only serves as the engine hub for lexical items and hierarchically structured sentences in the domain of language but can also be extended to other domains and cognitive abilities listed in Laland and Seed (2021). For example, syntactic operations have been suggested to be analogous to tool making and use (e.g., Stout & Chaminade 2012). Neuroimaging studies also suggest that syntactic operations and tool-making could share the same set of neural circuits (Hecht et al. 2014; Putt et al. 2017).

Besides, language has been assumed to play an essential role in problem solving (Baldo et al. 2005). Problem solving requires multi-facet abilities. For instance, inferential reasoning, as Völter and Cho (2017) noted, usually needs the transformations of mental representations to make predictions and the combination of spatiotemporally separate events. Hence, inferential reasoning is also closely linked to displacement, which enables humans to predict future events at the dimensions of both space and time.

In addition, as Laland and Seed state, language and language-related activities such as teaching play a crucial role in complex social cognition of humans. Social cooperation is closely related to displacement. For example, in the case of megafauna scavenging of ancient humans, when detecting a dead deinotherium, in order to persuade other members in the group to cooperate, the members must exchange information of where and when they found it, since only by themselves they cannot exploit it. This kind of high-end scavenging could have distinguished human ancestors from bone-crunching garhi and habilis.

Furthermore, Laland and Seed treat communication flexibility as the most obvious divide between humans and other animals. They highlight the syntactic properties "unbounded merge" (Chomsky 1995) and "recursion" (Hauser, Chomsky, & Fitch 2002) that underlie the creation of an infinite number of structures and the creativity use of language which in turn allows us to cope with different situations when we need to communicate with others. Hence, the syntactic operation serves as the prerequisite of human flexible communication.

Collectively, it seems that all five candidate traits reviewed by Laland and Seed are related to syntactic operations. This implicates that the domain-general thinking the authors assume could be realized with the advent of domain-general syntactic operation. We will focus on how the domain-general syntactic operation is supported by the subcortical regions in the following section.

3.   Evidence from a Neurocognitive Perspective

At the brain level, high-level cognition could be derived from improved neural connectivity, diversification of cell types and general cortical enlargement in evolution (Striedter 2005). However, we would like to focus on how two subcortical regions, the basal ganglia and hippocampus, and their connectivity could have contributed to human unique cognition in the present commentary. Both areas exhibit domain-general cognitive functions. The basal ganglia have been assumed to be involved in motor planning and control (Wise et al. 1996), context-dependent

rule-based selection (Peigneux et al. 2000), and sequence learning (Chan 2007). The hippocampus serves as the hub for the interaction between semantic memory and episodic memory (Takashima et al. 2014). Moreover, the hippocampus is not only related to the storage of information from different cognitive domains (Tsao et al. 2018), but is also involved in the process of relational binding which is defined as

> rapidly, continuously, and obligatorily form associations among disparate elements across space and time, and further to enable the comparison of internal representations with current perceptual input.
>
> (Olsen et al. 2012)

Both areas are also implicated in language processing. It has been established that the cortical centered view of language network is insufficient to cover the updated data (Kensinger et al. 2001, Teichmann et al. 2015, Copland & Angwin 2019). For example, patients with impaired basal ganglia will have symptoms similar to non-fluent aphasia (Lieberman 2006). Further, if basal ganglia are affected along with cortical impairment, aphasic patients' probability to recover is lower (Crosson et al. 2005, Shi & Zhang 2020). Hence, the contributions of subcortical structures to language processing have received attention in cognitive and neurological research (see Shi & Zhang 2021 for a review). For example, the basal ganglia have been established to be related to syntactic processing of language (Kotz et al. 2003, Friederici & Kotz 2003, Progovac et al. 2018). Further, Boeckx, Martinez-Alvarez, and Leivada (2014) proposed that the basal ganglia are involved in the syntactic process of 'Linearization', the operation transferring hierarchical syntactic structures into temporal sequences. Shi and Zhang (2020) also provide more evidence for the functions of the basal ganglia in syntactic processing from a clinical perspective.

The hippocampus is involved in the process of lexicalization (Takashima et al. 2014) and lexical retrieval (Hamamé et al. 2014). Studies of developmental amnesia have shown that patients with atrophy of the hippocampus show difficulties of acquiring new semantic memory (Duff et al. 2020). Recent studies have also revealed that the hippocampus is involved in online syntactic processing (Piai et al. 2016). Further evidence suggests that the hippocampus seems to be the interface between language and memory (Shi & Zhang 2021). These functions imply that being the possible basis for displacement as well as lexical and syntactic operations, the hippocampus could play a crucial role when different cognitive abilities interact.

Since both the hippocampus and basal ganglia are highly conserved brain regions, some of their functions linked to displacement have also been found in nonhuman animals, but very limited when compared with humans (Shi & Zhang 2021). Shi and Zhang (2021) suggest that the reason why humans have superior displacement abilities can be partly due to the better coordination between the hippocampus and basal ganglia.

Furthermore, the functions of the hippocampus and basal ganglia are both domain-general, and the coordination between these two subcortical structures has been observed in learning and memory systems. For example, the hippocampus and the striatum (a subregion of the basal ganglia) were reported to be jointly

involved in episodic memory encoding (Sadeh et al. 2011). Increased functional connectivity between the hippocampus and striatum was also found in learning temporal associations (van de Ven et al. 2020). Their interactions also contribute to arbitrary associative learning (Mattfeld & Stark 2015). Moreover, the hippocampal-striatal interaction is evident in spatial navigation (Goodroe, Starnes, & Brown 2018). It has also been reported that the hippocampus and striatum both play crucial roles in decision-making (Johnson, van der Meer, & Redish 2007). The interactions between the nucleus accumbens (a subregion of the striatum) and hippocampus in rats were shown to be involved in decision-making about time trade-off (Abela, Duan & Chudasama 2015). In the domain of language, Ullman's (2004) declarative/procedural model posits that declarative and procedural memory, supported by the hippocampus and basal ganglia respectively, interact with each other in first and second language learning.

Genetic studies also provide supporting evidence. Foxp2 was discovered as a gene affecting the coordination of speech production, together with problems in language production and comprehension in a family with fifteen relatives presenting verbal dyspraxia (the KE family; Lai et al. 2001). Two amino acid changes were detected in exon 7 of human FOXP2 when compared with the chimpanzee protein (Enard et al. 2002), suggesting that these two substitutions could have played a crucial role in human evolution. Such a humanized FOXP2 inserted in mice enhances the information transformation between procedural and declarative memory (Schreiweis et al. 2014), suggesting that the basal ganglia-hippocampal coordination could lead to better interaction among information from different cognitive domains, since both brain structures are involved in multiple cognitive domains. However, subsequent studies on FOXP2 revealed that the two mutations found in humans is shared with Neanderthals, thus the uniqueness of the human version FOXP2 become controversial (Fisher 2019). Nonetheless, it is less controversial that humans are the only species acquiring language and FOXP2 is in some way contributed to the evolution of human language.

By and large, since both subcortical regions are involved in syntactic processing, it is reasonable to propose that it is the domain-general syntactic operation that forms the basis for domain-general interaction.

4.   Conclusion

All in all, we agree with Laland and Seed (2021) that human cognitive uniqueness arises from some combination of abilities, but we suggest that from the neurocognitive perspective, the domain-general functions of the hippocampus and basal ganglia play a key role. To be specific, we suggest that the enhanced coordination between the hippocampus and basal ganglia possibly support domain-general syntax which makes humans' cross-modular thinking possible. In the end, we would like to cite the following image:

> Another metaphor for the cognitive effect of human language would be the Swiss Army knife. Until language emerged, the minds of our ancestors were full of various tools, each tailored to specific needs. With language, all these tools were combined into a flexible all-in-one

tool that makes available a variety of solutions (tools) whose effects can be combined spontaneously.   (Boeckx 2010: 131)

Indeed, Laland and Seed (2021) also suggest that at the higher cognitive level, language could have enhanced the interaction between different cognitive domains, but when language is decomposed into subcomponents at the lower level, nothing seems to be unique to humans. This is consistent with the perspective of comparative biology that language *per se* is a very coarse term. In conclusion, we would like to propose that it is a domain-general syntax that could serve as the Swiss Army knife in human evolution and give rise to the uniqueness of human cognition.

Author Contributions

Both authors jointly conceptualized and wrote the paper.

Declaration of Interest Statement

The authors declare no competing interests.

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