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Displacement and Evolution: A Neurocognitive and Comparative Perspective

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Abstract

By re-evaluating Crow (2000)'s claim that "Schizophrenia [is] the price that Homo sapiens pays for language", we suggest that displacement, the ability to refer to things and situations outside from here and now, partly realized through syntactic operation, could be related to the symptoms of schizophrenia. Mainly supported by episodic memory, displacement has been found in nonhuman animals, but more limited than that in humans. As a conserved subcortical region, the hippocampus plays a key role in episodic memory across species. Evidence in humans suggests that the parietal lobe and basal ganglia are also involved in episodic Memory. We propose that what makes human displacement more developed could rely on the better coordination between the hippocampus and the parietal lobe and basal ganglia. Given that all these areas taking part in language processing, displacement could have served as an interface between episodic memory and language.

Keywords: displacement; schizophrenia; episodic memory; hippocampus; comparative cognition

Introduction: the central paradox

Despite the substantial disadvantage in survival, the genetic predisposition of schizophrenia has not been eliminated from population within a few generations. This is the central paradox concerning schizophrenia raised in Huxley et al. (1964). In order to resolve this paradox, Crow (2000) approached this issue from the evolutionary perspective and claimed that "schizophrenia [is] the price that Homo sapiens pays for language". To be more specific, he proposed that language, the most characteristically human capacity, was the balancing advantage for the Homo sapiens-specific predisposition to schizophrenia (not always pathologically expressed). However, with the advancement in cognitive neuroscience and accumulating evidence from comparative biology, it gets clear that some of the claims in Crow (2000) seem to be hardly maintained and need to be updated.

In the present work, through the lens of episodic memory deficits of schizophrenia and evidence from comparative biology, we focus on the capacity of displacement and how it relates to the evolution of language. Displacement enables humans to refer to things and situations outside from here and now (Bickerton, 2009), and it is traditionally assumed to be one of the design features that distinguishes human language from nonhuman animal communicative signals (Hockett, 1960). However, it is not necessarily a feature of language. In the following sections, we will first explain how displacement could be realized by, but beyond the

mechanism of episodic memory. Data from behavioral studies in comparative biology have revealed that animals also have episodic-like memory but very limited in terms of displacement.

Secondly, at the brain level, as a major long-term memory hub, the hippocampus is assumed to be the basis for episodic memory. Further, since the hippocampus is a highly conserved brain structure, its functions could shed light on comparative studies from evolutionary perspective. Going into the details of neural basis of displacement, existing evidence has shown that displacement is not human- or language-specific but a domain-general property closely linked to episodic memory in both temporal and spatial dimensions. We propose that what makes humans superior to animals in terms of displacement is the better coordination between the hippocampus and basal ganglia as well as the parietal lobe, with the evidence in humans that the basal ganglia and parietal lobe both contribute to episodic memory in different ways. Furthermore, findings of all three brain areas involved in language processing suggest displacement could be an interface between episodic memory and language.

Finally, we come back to schizophrenia and relate its core symptoms to the functions of the hippocampus, basal ganglia and parietal lobe. Schizophrenia patients exhibit not only cognitive problems related to episodic memory, but also language problems, both of which could be related to displacement.

"Schizophrenia as the price that Homo sapiens pays for language"?

To evaluate Crow's claim that "schizophrenia [is] the price that Homo sapiens pays for language", we need to have a better understanding of how language evolved, and which parts of language that have distinguished humans from other nonhuman animals could have contributed to the emergence of schizophrenia. To this end, two basic questions from a bottom-up perspective will be revealing. First, which property of language is the most characteristically human capacity? Second, is/are the component(s) human unique or shared with nonhuman animals? Beyond behavioral level, we aim to emphasize that the neural basis of such component(s) could provide more straightforward insights to the questions above.

Crow (2000) claimed that "arbitrariness", the absence of any relationship between a word's form and its meaning, is the distinctive characteristics of human language. However,

from evolutionary perspective, Bickerton (2009) argued that "arbitrariness" is also a feature of some animal communication system, for instance, the vervets' alarm calls for eagles, leopards and snakes. These calls function differently from words in human language system. Take the eagle call as an example. it does not translate as "eagle" nor evokes the image of eagle or anything that eagle could do. It just draws attentions to the predators from air. It seems more efficient and functional to translate the call as "Look out, an eagle is coming!" or "Danger from the air!" or "Quick, find the nearest bush and hide in it!" (Bickerton，2009:44)

At the brain level, lateralization has been proposed as the critical change giving rise to the emergence of language Crow, 2008; Corballis, 2003). Literature suggested that lateral asymmetry is unique in our species (Harrington, 1989). Crichton-Browne (1879) first related mental disorder with brain asymmetry from the perspective of evolution. Other studies provided further evidence on asymmetries and some suggested anatomical asymmetries at the cortical level contribute to speciation event (Geschwind & Levitsky 1991). Further, it is assumed that asymmetry at the brain level has genetic endowment and gives rise to the phenomena of handedness which is specific to Homo sapiens (Harris, 1991).

However, with the accumulating evidence from comparative studies (see Fitch and Braccini, 2013 for a review), the central position of lateralization in distinguishing Homo sapiens as a species has been challenged, so that it is inconclusive to explain the emergence of language. One of the basic features of the vertebrate brain is neural asymmetry (Vallortigara & Rogers, 2005), and species-typical patterns of left-hemispheric dominance provided neural basis for conspecific communication in chimpanzees (Taglialatela et al., 2008) and rhesus monkeys (Hauser & Andersson, 1994). Going beyond the primates, left-hemispheric dominance effect concerning language evolution has been found in birds. For instance, vocal learning in zebra finches (Moorman et al., 2012), song discrimination in Bengalese finches (Okanoya et al., 2001) and hypoglossal functions in canaries (Nottebohm, 1971).

Hence, the claims in Crow (2000) seem not to be maintained. In the next section, we will focus on the property of language that is different from animal calls, namely displacement. The key difference is that language makes human beings escape from the limitation of here and now while animal calls are confined to current situations.

Displacement and episodic memory

Displacement, the ability to talk about things and event outside from here and now (Bickerton, 2009), heavily relies on episodic memory, which enables one to revisit the past event and imagine possible future scenarios (Tulving, 2001). It is worth noting that displacement involves both temporal and spatial information, which are important for episodic memory formation and retrieval in both time and space scales. Tulving (2002) claimed that episodic memory

is human-unique, indicating that displacement may also be human-unique. Hockett (1960) also posited that displacement is one of the design features of human language which is distinct from animal communication signals. It thus seems that displacement could be both language- and human-specific from the theoretical perspective. However, as we have access to more data of nonhuman animal behavior, episodic-like memory has been argued to be detected in nonhuman animals, but inferior to that found in humans in terms of time interval and space distance.

Clayton & Dickinson (2010) have argued that in nonverbal animals, it is impossible to take advantage of their verbal output, so ethological criteria for episodic memory in nonhuman animals need to be established. Observations in the wild and lab have demonstrated that nonhuman animals possess episodic-like memory with reference to the criteria of "what-where-when". Examples include food caching birds (Clayton & Dickinson, 1998), rodents (Crystal & Smith, 2014), and nonhuman primates (Martin-Ordas et al., 2010), but it is limited by the length of time interval of the two measured incidents (Cook et al., 1985). Furthermore, displacement as a whole has been reported to be detected in invertebrates: waggle dance of honeybees (Root-Bernstein, 2010), and food navigation (Schwarz et al., 2017) and recruitment systems in ants (Holldobler & Wilson, 1978), but still within the limit of distance (Yule, 2010). These data suggest that although short-distance (time and space) displacement has been found in nonhuman animals, long-distance displacement could be specific to humans. We suggest that such human-specific long-distance displacement can be explained from both neurological and theoretical perspectives.

Hippocampal contribution to episodic memory in humans and nonhuman animals

The hippocampus is assumed to be involved in explicit long-term memory and episodic memory (Graf & Schacter, 1985; Voss et al. 2017). To be more specific, it is well established that the hippocampus is involved in spatial information (Eichenbaum, 2017; Schiller et al., 2015) and encoding of time (Eichenbaum, 2015). The hippocampus is also assumed to store information of when, where and what (Tsao et al., 2018).

In addition to the function of information storage from multisensory input, the hippocampus was also proposed to be engaged in dynamic process like conjunctions of complex elements including items, context, and temporal information (Cowell et al., 2019: 5; Shimamura, 2010). When experience unfolds overtime, interrelated stimuli are processed and bound together to form coherent memory (Eichenbaum & Cohen 2004). This actually anchors the mechanism of relational binding of the hippocampus which referred to as the function of "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). Such functions of the hippocampus seem to form the essential basis for displacement.

Comparative data also suggest the role of the hippocampus in episodic memory. In avian species, as we have stated in the previous section, food-caching behavior to some extent reflects episodic-like memory. Investigation from the brain level reveals that the hippocampus plays a crucial role in food-storing. Black-capped chickadees and dark-eyed juncos with hippocampal lesions show memory impairment for location (Hampton & Shettleworth, 1996; Sherry & Duff, 1996), suggesting that the functions of avian hippocampus could be homologous to mammalian hippocampus (Colombo & Broadbent, 2000; Sherry & Vaccarino, 1989). Hippocampal lesions also impacted the performance of spatial learning in Japanese quails (Lormant et al., 2020). The size of the hippocampus relative to telencephalon in food-storing passerines is considerably larger than that in non-food-storing ones (Sherry & Duff, 1996). This enlargement of the hippocampus relative to other brain areas indicated that memory for food caches could drive the increase of the hippocampal neurons for survival (Clayton, 1998). Indeed, it has been found that the seasonal change in caching is correlated with the seasonal change in hippocampal size in food-storing birds (Sherry & Hoshooley, 2010).

Studies on rodents have shown that different subregions of the hippocampus are involved in episodic memory which can be decomposed into components, recognition, temporal order and spatial memories (Aggleton & Pearce 2001). The novel object recognition (NOR) task for the purpose of investigating nonspatial memory in rodents has shown that the hippocampus is not only taking part in object recognition, but also sensitive to the time delay between the sample and test sessions (Cohen & Stackman, 2015), suggesting that the recognition role of the hippocampus may depend on temporal information. Temporal order has been explored using odors in rodents (Fortin et al., 2002; Kesner et al., 2002). The data suggested that the hippocampus is involved in remembering events in sequence. Besides, the result of the visual object presentations in rats with lesion in the dorsal CA1 and CA3 of the hippocampus further suggested that only CA1 is critical for temporal information processing (Hoge & Kesner, 2007), whereas the temporal order of the spatial information was reported to be processed by ventral hippocampus (Howland et al., 2008). With respect to spatial memory, early studies have demonstrated that hippocampal lesions in rats exhibit impaired spatial learning (Jarrard, 1993). The discovery of "place cell" (O'Keefe & Nadel, 1978) also suggested the important role of the hippocampus in spatial cognition.

In nonhuman primates, sub-components of episodic memory were also examined separately as well as in combination. The what-where association was investigated in macaques by recording single hippocampal formation neurons, and the results showed that both separation and combination of representations of objects and where they locate involved the hippocampus, which is a required property in an episodic memory system (Rolls et al., 2005). Recording 644 neurons from the hippocampus, and entorhinal and perirhinal cortex in the medial temporal lobe in two macaques, Naya & Suzuki (2011) found that the most prominent "time cells" signals were observed in the hippocampus, suggesting that the hippocampus is sensitive to time scale. Lesion studies also suggested the role of the hippocampus in episodic memory in nonhuman primates. For instance, conducting delayed nonmatching to sample task on cynomolgus monkeys, Zola et al. (2000) found that object recognition memory was impaired in hippocampal lesion group. Taken together, comparative evidence indicated that the hippocampus is involved in episodic(-like) memory in nonhuman animals, homologous to the functions of human hippocampus.

What makes human displacement highly developed?

In humans, apart from the fact that the hippocampus is responsible for episodic memory, the parietal cortex is equally important to be mentioned. The parietal lobe is evidenced to play a role in integrating multisensory inputs, which is essential for the formation of episodic memory. Neuroimaging studies indeed address the role of the parietal lobe in episodic memory. Both time and space travel tasks elicit activation of the inferior parietal lobe (Gauthier & van Wassenhove, 2014). The angular gyrus, a region lying at the ventral posterior parietal cortex, was shown to be involved in both encoding and retrieval episodic memory (Tibon et al., 2019). The left lateral parietal cortex was also reported to be activated in time travel of past, present and future (Nyberg et al., 2010). On the other hand, although it is generally assumed that the basal ganglia are the neural basis for procedural memory while the hippocampus supports long-term memory, evidence has shown that these functions are actually distributed in the brain (Schreiweis et al., 2014). Neuroimaging and neuropsychological evidence suggests that the basal ganglia are also involved in encoding and retrieval of long-term memory (Han et al., 2010; Shohamy & Adcock, 2010). Scimeca & Badre (2012) also proposed that the function of cognitive control of the basal ganglia enhances the likelihood of the success of retrieval.

On the coordination between the hippocampus and the parietal lobe and basal ganglia, evidence has shown that the hippocampus is involved in the network including medial temporal lobe and posterior parietal cortex (Szczepanski & Saalmann, 2013). Further, anterior hippocampus is connected with dorsal parietal cortex which related to items consistent with retrieval goals, and posterior hippocampus is functionally connected with ventral parietal cortex which processes unexpected items (Ciaramelli et al., 2020). Resting state Functional Magnetic Resonance Imaging (fMRI) scanning on normal subjects showed robust connection between the hippocampal formation and various subregions of the parietal cortex including precuneus, posterior cingulate, retrosplenial cortex, and bilateral inferior parietal lobule (Vincent et al., 2006). In the case of

the basal ganglia, evidence has shown that humanized FOXP2 inserted in mice enhances the information transformation between the basal ganglia and hippocampus (Schreiweis et al., 2014), suggesting a human specific basal ganglia-hippocampal coordination. These data suggest that the hippocampus works with the parietal lobe and basal ganglia to serve the functions of encoding and retrieval of episodic memory, and thus displacement in humans could be obtained by better coordination between the hippocampus and the parietal lobe and basal ganglia respectively.

Displacement as an interface between episodic memory and language

In addition to the aforementioned contributions to episodic memory, the hippocampus, basal ganglia, and parietal lobe have also been shown to be involved in different aspects of language processing. In this sense, displacement could serve as an interface between episodic memory and language.

The hippocampus has been implicated in new grammar learning (Opitz & Friederici, 2003; Kepinska et al., 2018), syntactic integration in language comprehension (Meyer et al., 2005), and naming ability (Davies et al., 1998; Matthews, 2015). The results of Glikmann-Johnston et al. (2015) suggested that the hippocampus is involved in brain network which selectively supports verbal semantic fluency. Further, Liégeois et al. (2004) showed that lesions at the left language area did not associate with the activation in the analogous regions in the right hemisphere, while in patients with hippocampal lesion, right-lateralized, or bilateral language related regions, activation were detected. This indicates that the hippocampus may be implicated in language lateralization. Using blank filling tasks, Piai et al. (2016) have found that the theta-oscillatory activity supported by the hippocampus is stronger in the condition of semantically associated sentences than semantically neutral sentences. Such direct evidence of involvement of the hippocampus in language online processing encouraged Covington & Duff (2016) to propose a domain general prediction role of the hippocampus in language-memory interface.

Parietal lobe has been implicated in contributing to language evolution and development. In the dual-stream hypothesis for language processing, the dorsal pathway II connecting the superior temporal gyrus (STG) to inferior frontal gyrus (IFG, BA 44) via the arcuate fasciculus (AF) going through the parietal cortex has been proposed to be involved in complex sentence processing (Friederici, 2012). The enlargement of the parietal lobe has been detected in evolution in humans (Boeckx & Benítez-Burraco, 2014), which could have provided humans with enough space (Deacon, 1989) for the maturation and emergence of the dorsal pathway II in development and evolution. Furthermore, Boeckx (2016) has hypothesized that the two-dimensional recursive structure of syntactic computation could have been formed by paring two existing one-dimensional sequences supported by frontal-parietal and fronto-temporal connection which already present in nonhuman primates, emphasizing the important role of the parietal cortex of humans. Moreover, comparing human AF with that of chimpanzees and macaques, Rilling et al. (2008) found that human AF is more strongly enhanced and widely connected.

Evidence has shown that the basal ganglia are also involved in language processing. In Event-Related Potential (ERP) studies, syntactic inconsistency elicits P600 wave. In a series of event-related fMRI studies, patients with basal ganglia lesion and Parkinson's disease were asked to process the syntactic incorrect sentences and the modulations of P600 wave were detected (Kotz et al. 2003). Further, results show that the basal ganglia are involved in syntactic processing (Friederici & Kotz, 2003). In an fMRI study, the authors found increased activation in both right and left basal ganglia when the participants process sentences with complicated syntactic structures (Progovac et al., 2018). From clinical perspective, Shi & Zhang (2020) propose that the basal ganglia are involved in the process where hierarchical syntactic structures are transferred into linearized structures.

Having established that displacement could serve as an interface between memory system and language. Let's take a closer look at how this interface is captured in both clinical and linguistic terms and how linguistic theories could map onto brain functions. Besides, the question of why human beings has superior displacement will also be discussed.

Cognitive deficits and corresponding biomarkers of Schizophrenia

Dating back to 1950s, Bleuler (1950) has maintained that the cognitive deficits associated with schizophrenia is partly due to inability to organize or associate ideas in memory. Impairment of episodic memory has also been well documented in schizophrenia (Leavitt & Goldberg, 2009), leading to the distortion of the subjective experience of space (Jaspers, 1963), time (Fuchs, 2013) and person (Crow, 2000). The absence of subjectivity in schizophrenia involves experiences of fragmentation, meaninglessness, and ineffable strangeness (Sass & Pienkos, 2013). This symptom is related to the malfunction of displacement and manifested as the anomalous use of deixis in patient's speech. Deixis is the use of words or phrases referring to specific time, place or person. There are various attempts to capture this symptom in linguistic terms and no consensus has been achieved as for whether there are lexical or syntactic deficits. For example, it has been proposed that the semantic memory of schizophrenic patients is impaired (see McKenna and Oh 2005 for a review), accordingly lexical accessing including deixis is malfunctioned. On the other hand, Hinzen & Sheehan (2013) proposed that this symptom is related to grammatical deficits which is manifested as building the deictic frame of reference. Since lexical items consists of deixis, the deficits of using deixis could be

related to the process of lexical accessing (Pomarol-Clotet et al. 2008 among others). Moreover, Boeckx (2015) has proposed that the formation of lexical items involved syntactic operation. Furthermore, syntax is an essential aspect of human language (Chomsky et al. 2019), without which we cannot express full-fledged meaning. Hence, as a subcomponent of language, syntax might be related to displacement and the symptoms of schizophrenia. The neurological deficits of schizophrenia suggest that this might be the case.

Although there are very few studies addressing the correlation between these symptoms related to language and brain function or structural changes, a lot of which focused on memory and other cognitive deficits of schizophrenia patients. Both the structure and function of the hippocampus have been found to be deviant in schizophrenia patients (Harrison, 2004). Structural Magnetic Resonance Imaging (MRI) studies have shown reduced volume and altered shape of the hippocampus in prodromal and first episode patients (Velakoulis et al., 1999). The neuropsychological deficits attributed by the hippocampus were reported to be correlated to the hippocampal volume and activation (Jessen et al., 2003). For example, related to our proposal, deactivation of the hippocampus in episodic memory task—conscious recollection of the words—was detected in schizophrenia patients compared to controls (Heckers et al., 1998). Positron emission tomography (PET) studies provided evidence of positive correlation between the symptoms and hippocampal metabolic activity (Medoff et al., 2001).

Schizophrenia patients with lesions at the inferior parietal lobule, exhibit diverse cognitive deficits. Using spatial cueing paradigm, Maruff et al. (1998) found that patients with schizophrenia had difficulties in directing visual spatial attention, and processed linguistic cues more slowly relative to spatial cues (Posner et al., 1988). The patients also showed deficits in both gestural perception (recognition) and production (performance) (Walther et al., 2015). Gray matter reduction was observed in the inferior parietal lobe predominantly in patients with schizophrenia (Dutschke et al., 2018). Compared to controls, patients with schizophrenia performed worse in auditory 2-back task which tests phonological working memory, and neuroimaging data show a hypo-activation in dorsolateral prefrontal cortex, supramarginal gyrus, inferior parietal lobule, and superior parietal areas (Menon, Anagnoson, Mathalon, et al., 2001; Schneider et al., 2007).

Gunduz et al. (2002) conducted a structural MRI study comparing the volume of the basal ganglia structures and the limbic forebrain in first episode schizophrenia to healthy subjects, and the results showed no difference between two groups. However, increased volume and shape change of the basal ganglia were reported by Mamah et al. (2007). The enlarged volumes of the total basal ganglia and subregions, especially the caudates, are associated with worse performance of finger tapping and Hebb's Recurring Digits (Hokama et al., 1995), suggesting the abnormal volume is reflected in dysfunction of the basal ganglia in schizophrenia patients. In addition, using a motor sequencing task, Menon et al. (2001) investigated the activation difference of the basal ganglia regions and the thalamus between schizophrenia patients and healthy controls. Significant bilateral deficits in the posterior putamen, globus pallidus, and thalamus were found in schizophrenia subjects.

Both functional and structural anomalies were detected in the hippocampus, basal ganglia and parietal lobe in individuals with schizophrenia. And these regions underlie language processing, especially syntax. Since syntactic operation is domain-general and cross-modular, and displacement possibly serves as the interface between episodic memory and language, we propose that schizophrenia is the price that Homo sapiens pays for syntax.

Conclusion

In this paper, by re-evaluating Crow's (2000) statement that "schizophrenia [is] the price that Homo sapiens pay for language", we propose that displacement, which is supported by syntactic operation, is the key factor that distinguishes humans from nonhuman animals, the disruption of which could be a possible candidate giving rise to symptoms of schizophrenia. Through illustrating the relation between episodic memory and displacement, we provide evidence of episodic-like memory present in nonhuman animals, yet more limited than in humans. At the brain level, we highlight that the functions of the hippocampus in episodic memory play a crucial role in displacement. With the evidence that the parietal lobe and basal ganglia are both involved in episodic memory, we further propose that what makes human displacement more developed than nonhuman animals could be the better coordination between the hippocampus, basal ganglia and parietal lobe. The involvement of these three areas in language processing indicates that displacement might be an interface between episodic memory and language.

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