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The biogeographic origins of novelty-seeking traits[☆]Erkan Gören^{*}

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ABSTRACT

This paper empirically investigates the evolutionary drivers of between-population variation of the human DRD4 exon III locus, a particular gene associated with the human personality trait of novelty-seeking behavior. Providing a novel compilation of worldwide DRD4 exon III allele frequencies in a large sample of indigenous populations around the world, this study employs population-specific biogeographic indicators to test the hypothesis of natural selection acting on the set of DRD4 exon III allele variants. The estimates suggest that migratory distance from East Africa and various population-specific biogeographic indicators, such as latitude, land suitability for agriculture, pasture land, and terrain ruggedness, contributed significantly to overall between-population DRD4 exon III polymorphism.

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1. Introduction

The human dopaminergic system has been the subject of increased research attention focusing on its pivotal role in the control of locomotion, endocrine function, reward, cognition, and emotion (Oak, Oldenhof, & Tol, 2000). The dopamine D4 receptor (hereafter called DRD4), located on chromosome 11 at position 11p15.5, contains four encoded regions called exons (Van Tol et al., 1992). The most extensive polymorphism is found in the third exon. This polymorphism occurs in a 48-base pair (bp) variable number of tandem repeats (VNTR), ranging from 2- to 11-repeats, with 2-, 4-, and 7-repeats being the most common alleles across populations (Lichter et al., 1993; Van Tol, Bunzow, et al., 1991; Van Tol, Wu, et al., 1992). Differences in the neurobiological functioning of the DRD4 exon III gene across allele variants make it particularly interesting for genetic association studies of personality as it regulates intracellular signaling in the brain. For example, Asghari et al. (1995) have shown that the DRD4 exon III 7-repeat allele variant exhibits a subsensitive reaction to dopamine levels compared to the 4-repeat and 2-repeat allele variants. It has been argued that these blunted responses require elevated dopamine levels that in turn result

in personality outcomes such as novelty-seeking or attention deficit hyperactivity disorder (ADHD) (Swanson et al., 2000; Wang et al., 2004). The view that human personality has a heritable component has been debated by Plomin, Owen, and McGuffin (1994). Most of the evidence pertaining to the influence of genetics on complex human behaviors results from twin studies on personality, vocational interests, scholastic achievement, and cognitive abilities (Bouchard, 1994). Pioneering work in the classification of personality was done by Cloninger (1987). The author categorized four different personality traits: novelty seeking, harm avoidance, reward dependence, and persistence. Especially the first personality trait of novelty seeking is a natural candidate to be biologically influenced by dopamine genes (Paterson, Sunohara, & Kennedy, 1999). Novelty-seeking individuals are characterized as impulsive, exploratory, fickle, excitable, quick-tempered, and extravagant, whereas those with low novelty-seeking scores tend to be reflective, rigid, loyal, stoic, slow-tempered, and frugal (Cloninger, Przybeck, & Svrakic, 1991). Two influential studies on the genetic association between a specific DRD4 exon III allele (namely, the 7-repeat) and novelty-seeking behavior by Benjamin et al. (1996) and Ebstein et al. (1996) led to a wide range of molecular genetic studies seeking a possible association between DRD4 polymorphism and novelty seeking, neuropsychiatric diseases, substance abuse, ADHD, and mood disorders, among other potential correlates.¹

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¹ See Oak et al. (2000) and Savitz and Ramesar (2004) for a general overview of DRD4 genetic association studies. Paterson et al. (1999) raise a number of statistical and methodological concerns about the putative genetic association between DRD4 and observed human behaviors.

Increased research attention has been devoted to the evolutionary drivers acting on the DRD4 exon III locus. In an influential study, Chang, Kidd, Livak, Pakstis, and Kidd (1996) have shown that there exist striking differences in DRD4 exon III allele frequencies across 36 populations around the world. It is important to point out that the 4-repeat was the most common allele variant and observed in almost all populations, qualifying it as the ancestral allele variant. The 7-repeat allele variant was the second most prevalent, common in European and American populations, but nearly absent in Asian populations. The 2-repeat allele variant was the third most common and observed mainly in Asian and Oceanic populations. The fact that DRD4 exon III allele frequencies vary considerably across populations and regions raises the important question of what evolutionary mechanisms might be consistent with this observed geographic pattern (Chang et al., 1996). Theoretical studies suggest that DRD4 exon III polymorphism might be the result of a recent mutational event of positive selection at some point after the exodus from East Africa (Ding et al., 2002; Wang et al., 2004). In a related context, Jensen et al. (1997) suggested that the recent phenomenon of childhood ADHD must be seen in relation to evolutionary theories of biology, emphasizing the adaptive nature of hyperactivity, inattention, and impulsivity in rapidly changing, hostile, and resource-depleted environments. The authors pointed out that such “response-ready” traits (including novelty-seeking or explorative behavior) might provide those individuals an evolutionary advantage who constantly moved through unfamiliar environments, corroborating the adaptive nature of such traits in the exodus of the human species out of East Africa. Consistent with this hypothesis, Chen, Burton, Greenberger, and Dmitrieva (1999) were among the first authors to provide empirical support for a positive association between the frequency of long allele variants of the DRD4 exon III gene (5- to 11-repeats) and historical migration routes in a sample of 39 populations across the world. This finding was further confirmed in a study by Matthews and Butler (2011) that covered 18 different populations and explicitly accounted for between-population phylogenetic relatedness.

However, the “Out of Africa” hypothesis remains silent on why the 7-repeat allele variant associated with novelty-seeking behavior existed in moderate frequencies among African populations before the prehistoric population movements (Harpending & Cochran, 2002). Presumably 7-repeat-bearing individuals possess an evolutionary advantage in certain environments. Specifically, Cochran and Harpending (2009) argued that the transition from hunter-gatherer practices to agricultural production naturally selected against the DRD4 exon III 7-repeat allele variant because of the rise of bureaucratic elites that favored more compliant farmers over more aggressive individuals. In fact, the proportion of the 7-repeat allele variant is nearly absent in Chinese populations that experienced the neolithic transition much earlier than populations in other parts of the world. In essence, this hypothesis nicely illustrates the process of human adaptation, suggesting that the kinds of human behaviors frequently attached to childhood ADHD are adaptive in hunter-gatherer environments. In contrast to farming, hunter-gatherer practices are technologically adapted to the natural environment to utilize marginal resources effectively in arid regions that are otherwise unsuitable for sedentary agriculture (Johnson, 1969).² This mode of production enables people to manage environmental risks through a wide range of mechanisms including food diversification and physical storage, regional mobility, and exchange (Koocheki & Gliessman, 2005), thus, favoring to some extent risky, explorative, and aggressive human personalities. Therefore, it seems unsurprising that such novelty-seeking traits appear less suitable in modern societies with a well functioning rule of law (Cochran & Harpending, 2009). Consistent with this hypothesis, Eisenberg, Campbell, Gray, and Sorenson (2008) showed that DRD4 exon III 7-repeat bearers had better

nutritional indices among nomadic Ariaal men than among a recently settled group of Ariaal men in northern Kenya.

Interestingly, the anecdotal hypothesis of natural selection operating on the DRD4 exon III gene is not supported by substantial empirical evidence from population geneticists. Although the adaptive nature of specific DRD4 exon III allele variants (e.g., the 7-repeat variant) in migratory societies appears important in areas unsuitable for sedentary practices, a thorough empirical investigation of this important issue is still lacking. There exists no study, to the best of the author's knowledge, that investigates the influence of biogeographic factors on the distribution of DRD4 exon III allele variants within the population in detail. The only existing studies on this topic, Chen et al. (1999) and Matthews and Butler (2011), examine the influence of migratory distance from East Africa but fail to control for important biogeographic factors (e.g., land suitability for agriculture, fraction of land allocated to pasture, and terrain ruggedness) as a possible source of human adaptiveness in resource-depleted, time-critical, and frequently changing environments. Furthermore, these studies are based on limited data sets that include only 39 and 18 populations, respectively. By compiling a novel data set that covers the distribution of worldwide allele frequencies of the DRD4 exon III gene from various molecular genetic studies, the current paper reaches a broader coverage of populations across the world. Furthermore, this unique data set permits an in-depth analysis of the most important biogeographic factors for between-population variation of DRD4 exon III polymorphism. These biogeographic indicators are constructed specifically for the location covered by each population using high-resolution geospatial data processed using geographic information system (GIS) techniques.

The baseline estimates reveal that migratory distance from East Africa is significantly correlated with between-population DRD4 exon III expected heterozygosity. In addition, the estimates uncover the most important evolutionary drivers (e.g., land suitability for agriculture, fraction of land allocated to pasture, and terrain ruggedness) that naturally selected for the set of DRD4 exon III allele variants, thus contributing significantly to between-population differences in DRD4 exon III polymorphism. Furthermore, the qualitative results are not sensitive to autocorrelation across populations, as I explicitly account for this possibility using the network disturbance regression model. In contrast to previous work, this study highlights the importance of DRD4 exon III polymorphism in diverse environments and among genetically distinct populations.

The remainder of the paper is organized as follows. Section 2 provides information about the population sample, the data sources and methods for the construction of population-specific biogeographic indicators, and the estimation methodology used to test the hypothesis of natural selection acting on the DRD4 exon III locus. Section 3 presents the main empirical findings and tests the sensitivity of the results to autocorrelation across populations. Finally, Section 4 concludes by summarizing the main results and identifying areas for future research.

2. Data and Methods

2.1. Population Sample

Genetic data on the worldwide distribution of DRD4 exon III allele frequencies among different populations have been compiled from a number of published molecular genetic studies, drawing mainly from studies reporting allele frequencies from healthy (non-psychiatric) individuals. The most reliable data source on DRD4 exon III allele frequencies consist of 1327 individuals from 36 different populations compiled by Chang et al. (1996). The populations analyzed in this study are historically native to their current geographical location and have not undergone recent genetic mixing with other populations. This fact is particularly important because genetic mixing of populations since the post-Columbian era has introduced a serious causality problem between DRD4 exon III allele frequencies on the one hand and historical

² The interested reader is referred to Salzman (2002) for some general observations on nomadic lifestyles based on research on nomadic populations residing in Iran.

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