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Dopamine-system genes and cultural acquisition: the norm sensitivity hypothesis☆

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Previous research in cultural psychology shows that cultures vary in the social orientations of independence and interdependence. To date, however, little is known about how people may acquire such global patterns of cultural behavior or cultural norms. Nor is it clear what genetic mechanisms may underlie the acquisition of cultural norms. Here, we draw on recent evidence for certain genetic variability in the susceptibility to environmental influences and propose the norm sensitivity hypothesis, which holds that people acquire culture, and rules of cultural behaviors, through reinforcement-mediated social learning processes. One corollary of the hypothesis is that the degree of cultural acquisition should be influenced by polymorphic variants of genes involved in dopaminergic neural pathways, which have been widely implicated in reinforcement learning. We review initial evidence for these predictions and discuss challenges and directions for future research.

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Introduction

The last two decades of research in cultural psychology shows that cultures vary in social orientations of the self as independent or interdependent [1–3]. Western cultures (e.g. European American cultures) value the independence of the self from others. In contrast, Eastern cultures (e.g. Asian cultures) value the interdependence of the self with others. The social orientation dimension of independence versus interdependence has systematic influences on cognition [4,2,5], emotion [6–8], and motivation [9••,10,11]. So far, however, it remains unclear what mechanisms might underlie the acquisition of the culturally sanctioned social orientations of independence and interdependence — in particular, the learning of explicit and implicit rules governing these orientations [12•], notwithstanding some initial evidence suggesting that culture-typical behavioral characteristics emerge after six or seven years of age and become more pronounced over the course of adolescence [13–15].

Here, we explore a novel perspective on the acquisition of explicit and implicit rules of social behavior, or cultural norms, by drawing on recent advancements in social genomics — a new field of research that investigates ways in which genetic and epigenetic processes are dynamically linked to socio-cultural processes to constitute various phenotypes including health and other psycho-social outcomes [3,16••,17,18]. Evidence suggests that individuals are genetically variable in terms of their sensitivity to environmental influences [16,17,19•]. Extending this work, we propose the norm sensitivity hypothesis [20••], which holds that people are genetically variable in their sensitivity to global patterns of cultural behaviors or social norms.

Mutual influences between culture and genes

Recent research in population genetics suggests that over the past 10 000 years of human history, numerous polymorphic genetic changes have been positively selected. Moreover, the rate of positive selection appears to have accelerated [21–23]. This exponential increase of genetic change seems likely to be related to the massive increase in human population and exposure to new environments (including domesticated animals and plants) and the resulting diversity in both infectious diseases and available nutrition. This is consistent with ideas in evolutionary biology and biological anthropology that genetic evolution and cultural evolution have proceeded in tandem as suggested by theories of dual inheritance [24] or gene–culture co-evolution [24–27]. Initial evidence for the gene–culture co-evolution came from effects of herding and milk production on emergence of genetic mutations that support the digestion of lactose — the milk

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sugar [28], leading to rapid incorporation of these mutations and supporting the growth of dairying culture.

One intriguing recent proposal is that some genetic variants may lend themselves to plasticity of behavior [17]; that is, carriers of certain alleles could be differentially susceptible to environmental influences [17,29,30]. Such individuals might be more susceptible to early childhood adversity or maltreatment. Indeed, early life traumas increase the risk of depression and posttraumatic stress disorder later in life, but particularly in carriers of specific alleles in the serotonin transporter gene (5-HTTLPR) [29], glucocorticocoid receptor chaperone gene (*FKBP5*) [31], and beta-2 adrenergic receptor gene (*ADRB2*) [32].

Extending this literature, Kim and colleagues argued that culture is but one element of one's eco-social environment that encourages certain behaviors and inhibits others. It would then seem to follow that genetic alleles that increase behavioral plasticity might also amplify cultural differences in behavior [16]. For example, it is normative to seek emotional or social support at times of distress in European American cultural contexts, but not in Korean cultural contexts; Kim and colleagues found cultural differences tended to be larger for carriers of the G allele of the oxytocin receptor gene (*OXTR*) polymorphism rs53576, previously linked to increased socioemotional sensitivity [33].

So far, work has focused on isolated behavioral traits such as social support [33] and emotion suppression [34], leaving open the question of whether genetic polymorphisms might modulate each individual's readiness to acquire global phenotypic traits such as norms and behavioral patterns of independence and interdependence. Although social learning has long been argued to be central in maintaining long-lasting cultural traditions [35,36,37•] (see also the Tomasello article in this Special Issue), rarely has this line of reasoning considered genetic factors that foster social learning.

The norm sensitivity hypothesis

Reinforcement-mediated social learning and dopaminergic system genes

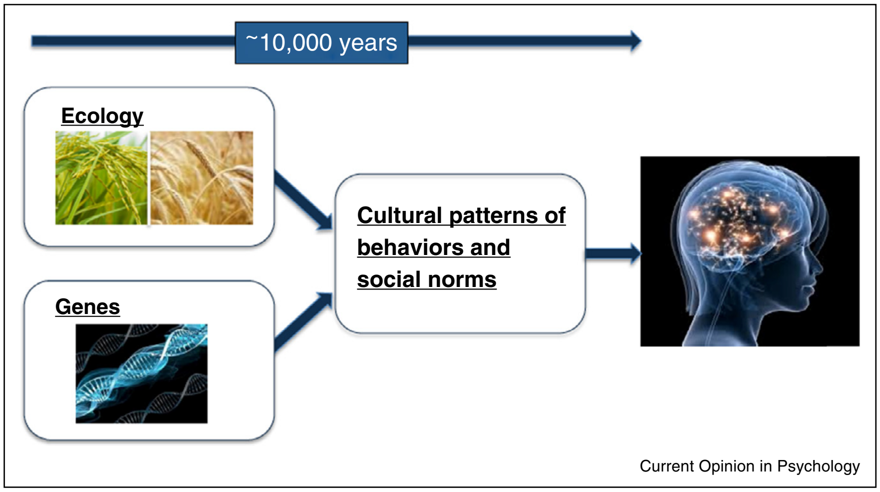
The norm sensitivity hypothesis suggests that acquisition of global behavioral patterns and norms of culture, such as independence and interdependence, is influenced by reinforcement-mediated social learning. This type of learning is based on a set of mechanisms that enable the organism to select behavioral options that maximize anticipated rewards [38]. These mechanisms include discerning of behavioral patterns, selection of one's behaviors, and tracking of the reinforcements given to these behaviors [39,40]. Major components of reinforcement-mediated social learning (e.g. social rule learning and reinforcement tracking) involve dopamine-mediated brain substrates (e.g. frontal cortex and striatal reward processing area) [41,42]. By highlighting the role of rewards in social learning, we hypothesize that cultural and social learning is not merely cognitive, but also inherently motivational. We may therefore anticipate that cultural acquisition would be facilitated by gene variants that increase the efficiency of central dopaminergic pathways.

To illustrate, children in any society must infer the rules governing their 'street' by trial and error. The emerging cognitive representation of others' response patterns constitutes the perceived norm for the community. Individuals respond to such norms by formulating their own responses, which may in turn be reinforced either positively (i.e. complimented and praised) or negatively (i.e. punished and ignored). This social mechanism is universal, although cultures vary in terms of how tight or loose in application of social norms [43]. The individuals must track reinforcement history to assess validity of inferred social norms. Resulting behaviors tend to be consistent with group norms, some aspects of which are culture-specific (e.g. independence versus interdependence) and others are more universal (e.g. within-group cooperation and altruistic behavior); although culture-unique socio-ecological conditions such as mobility and strength of within-group ties are likely to influence the extent of such behaviors [44].

Our theoretical framework, illustrated in Figure 1, explains contemporary cultural variations in terms of large-scale ecological considerations. Anatomically modern humans evolved in Africa approximately 200 000 years ago [45], spread out of Africa approximately 50 000 years ago, and started farming and herding approximately 10 000 years ago. One factor that initially differentiated Eastern versus Western regions of the Eurasian continent is the type of crops available and successfully domesticated (e.g. wheat versus rice) [46••]. This differentiation might have imposed a strong constraint on divergent paths of cultural evolution in the two broadly demarcated regions of the continent.

As a result of sedentary forms of living afforded by newly-emerged subsistence systems, human groups became increasingly large and started to incorporate non-kin members. We may assume social norms were utilized to breed much-needed within-group cooperation and coordination [47,48]. Dopaminergic system genes may therefore have played an instrumental role in facilitating the norm-based system of cooperation and coordination — the system we call culture. Given that human groups expanded in size over the last 10 000 years since the inception of sedentary living, the evolution of norm sensitivity must have been critical over this recent evolutionary past [49,50]. As argued by recent theorists [51], complex traits influencing social learning are likely to be

Figure 1



The norm sensitivity hypothesis is based on an observation that since the inception of sedentary forms of living, people have organized their groups by certain patterns and norms of social behavior that are afforded and constrained by the forms of subsistence (e.g. farming different crops such as rice and wheat and herding different animals). Acquisition of these cultural patterns and norms is hypothesized to have been facilitated by certain polymorphic variants of dopaminergic (DA) system genes, including those of the dopamine D4 receptor gene (*DRD4*), that increase the dopamine signaling efficiency.

highly polygenic, and to involve variations in multiple genes within the dopaminergic as well as other systems. However, it is plausible that individual mutations directly influencing dopaminergic functioning may have particularly pronounced effects on norm sensitivity.

Evidence for the norm sensitivity hypothesis

Dopamine D4 receptor gene (*DRD4*)

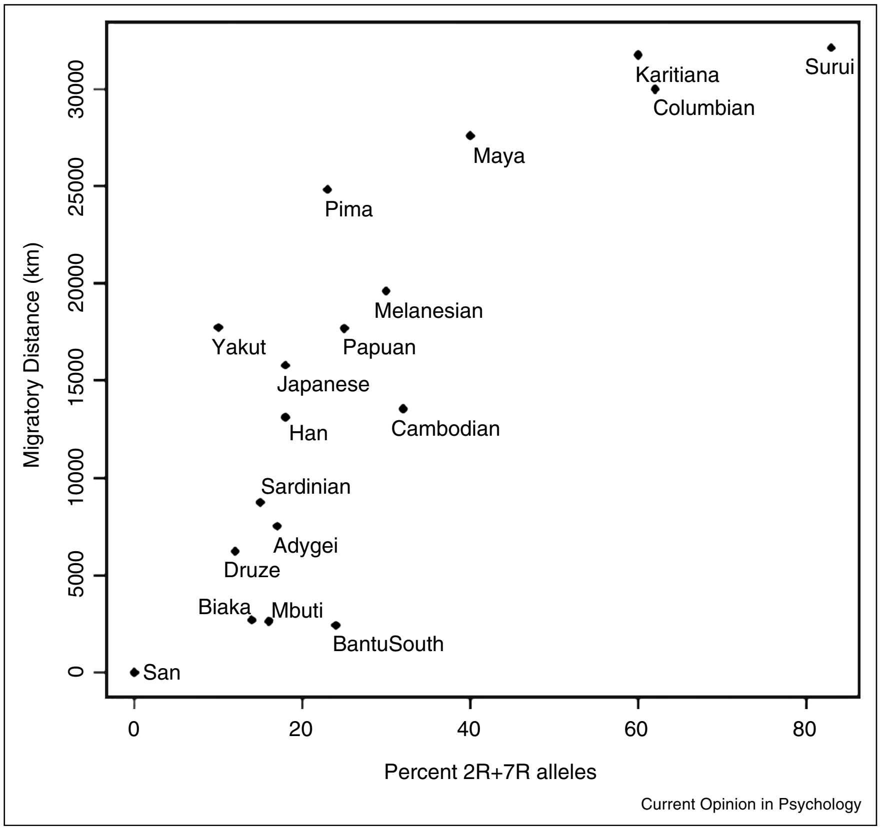
One candidate in the context of gene–culture co-evolution is the dopamine D4 receptor gene (*DRD4*). Exon 3 of *DRD4* has a variable number tandem repeat (VNTR) polymorphism (2–11 repeats), with 2, 4, and 7 repeat alleles (2R, 4R, and 7R) being the most frequent. Receptors coded by 7R alleles show less in vitro dopamine functioning and poorer response to agonists than 4R alleles [52,53], whereas the 2R allele is intermediate. Physiologically, diminished dopamine inhibitory feedback in 7R and 2R alleles carriers [23] is thought to lead to relatively higher physiological dopamine signaling capacity relative to 4R carriers [54].

Haplotype linkage disequilibrium (LD) patterns suggest the *DRD4* 7R allele was likely derived from the ancestral 4R allele 40 000–50 000 years ago, when humans started to expand their territory [23]. The 2R allele is more recent, purportedly appearing ∼10 000 years ago, when humans started herding and farming. Herding and farming, as well as the kind of crops farmed, all have systematic influences on cultural patterns of behavior [46,55,56]. Moreover, the 7R and 2R alleles may be under selection pressures associated with migration [57,58••]. The 7R allelic frequency increases as a function of migratory distance as humans spread over the globe (see Figure 2), suggesting that *DRD4* variants linked to altered dopamine signaling capacity could have co-evolved with cultural forms of human adaptation. Specifically, the population-level frequency of 7R and 2R alleles of *DRD4* might have increased over the last 10 000–50 000 years as different groups underwent a series of challenges to survive in 'frontier-like' social and ecological conditions fraught with a variety of life-threats [59]. A recent simulation suggests that such social and ecological conditions conduce to the emergence of strong social norms for cooperation and coordination within an ingroup [60••].

DRD4 and environmental sensitivity

Previous work reported associations between the 7R allele of *DRD4* and certain behavioral traits including novelty seeking [61], heavy drinking [61], and financial risk taking [62], although these associations are not always replicable [63]. Other evidence indicates that 7R allele carriers are sometimes relatively better socialized, with superior attention control [30] and greater prosocial orientations [19,64•]. The seemingly conflicting pattern could reflect environmental sensitivity of the *DRD4* 7R/2R alleles [17,19]. That is, under adverse environmental conditions (e.g. neighborhoods dominated by gangs), the 7R/2R alleles may be associated with more negative outcomes (e.g. impulsive, antisocial behaviors). The norm sensitivity hypothesis suggests that the behaviors that are considered less desirable or even explicitly anti-social may be rewarded and thus fostered in such adverse conditions. In contrast, under desirable environmental conditions, these alleles may be associated with more

Figure 2



Migratory distance out of Africa as a function of the prevalence of the 7R/2R allele of *DRD4*.
Taken from Matthews & Butler, 2011, *American Journal of Physical Anthropology, 145, 382–389*.

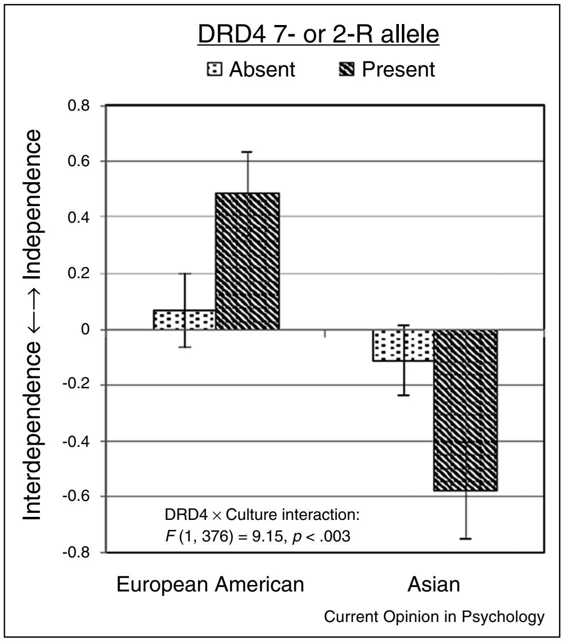
advantageous outcomes because such environments enforce norms encouraging desirable behaviors. In support of this analysis, developmental work shows that children with these alleles are influenced more by the quality of caregiving [65–68]. Consistent with the norm sensitivity hypothesis, children with 7R/2R alleles of *DRD4* might more readily infer informal behavioral norms from their caregivers.

DRD4 × culture interaction

Culture is an environment that is constituted by beliefs, values, and human behaviors derived from these beliefs and values [69]. On the basis of the norm sensitivity hypothesis, we may anticipate that higher dopamine signaling variants of *DRD4* (7R and 2R) will accentuate the cultural difference in the social orientations of independence and interdependence. In our recent work [20], 194 European Americans and 204 Asians completed several scales assessing independence (e.g. independent self-construal, self-efficacy) or interdependence (e.g. interdependent self-construal, holistic cognitive style). As summarized in Figure 3, the predicted *DRD4* × culture interaction was significant. Overall, Asians tended to be more interdependent or less independent than European Americans. Importantly, whereas this cultural difference was sizable for the 7R/2R allele carriers of *DRD4*, it was negligible for the 7R/2R allele non-carriers. Within each cultural group, the 7R/2R allele carriers showed to a greater extent the social orientations typical for their respective cultures. This finding resonates with an earlier study showing that when the prevalent norms are made salient through induction of accountability, individuals from individualistic and collectivistic societies behave in diametrically opposite ways in a social negotiation task. Whereas individualists become more competitive, collectivists become more cooperative [70].

If carriers of high dopamine signaling variants of *DRD4* acquire and internalize social norms, they may show more pronounced effects of priming of such norms. Consistent with this hypothesis, a recent study demonstrates that priming of religious ideas increases pro-social behaviors only among the carriers of these gene variants [19]. Consistent with the norm sensitivity hypothesis, this result might show that carriers of the high dopamine signaling variant of *DRD4* acquire religious ideas (which encourage altruism) more deeply. Also consistent is a recent review indicating that these gene variants are often

Figure 3



Composite measure of independent versus interdependent orientation (independent factor score − interdependent factor score) as a function of culture and DRD4 VNTR polymorphisms.
Taken from Kitayama *et al.*, 2014, *Psychological Science, 25, 1169–1177*.

associated with greater altruism — a behavior that is positively sanctioned in all societies [64].

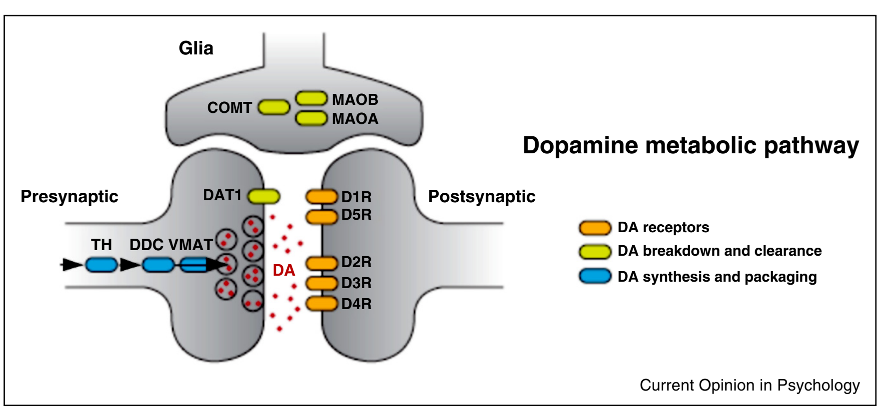
Challenges and future directions

There are important challenges and directions for future work. Future research should examine the function of genes within biological pathways and their interactions. In the context of dopamine, for example, this would include dopamine receptors (*DRD1* through *DRD5*), and those involved in dopamine synthesis (*TH*, *DDC*, *VMAT*), update (*DAT*), and clearance (*COMT*, *MAOA*, and *MAOB*) (Figure 4). These genes are assumed to work in highly interactive fashion [71•,72] to influence social cognition and behavior [73]. One important research agenda is to combine information from multiple genes for phenotypic traits including norm sensitivity [71•,74,75].

As compared to complex personality traits such as extraversion and neuroticism and disease categories such as anxiety disorder and schizophrenia, the dimension of norm sensitivity is relatively unitary. Thus, it may be seen as an endophenotype, or intermediate trait, that links the operation of genes to actual behaviors [76]. Nevertheless, as should be clear from our discussion, the norm sensitivity itself could be divided into various component processes (e.g. norm induction, reward sensitivity, and reward tracking), each of which could be influenced by different genes implicated in dopamine signaling. These processes may also be influenced by myriad background mutations that might produce certain perturbations and biases in genetic signaling [51,77]. Posing a major challenge to future work is the inherently polygenic nature of psychological parameters of social behavior, including norm sensitivity.

It is equally important to assess norm sensitivity directly. One promising approach may be to use economic games and test the degrees to which participants learn response patterns of other participants (rule induction) and change their own behaviors accordingly (reinforcement tracking) [71•]. Initial evidence shows that certain dopaminergic system genes are systematically related to relevant parameters (rule induction and reward tracking) estimated from such a behavioral experiment [71•]. Another promising approach may be to use a reinforcement learning paradigm and assess a rate with which individuals learn

Figure 4



Dopaminergic (DA) pathway genes.
Adapted from Set *et al.*, 2014, *Proceedings of National Academy of Sciences, 111, 9615–9620*.

from performance feedback (e.g., approval or disapproval of own actions by others) [78,79]. This rate, called the learning rate, may be tied to the norm sensitivity.

There may be other mechanisms of gene $\times$ culture interaction. As noted above, oxytocin (associated with enhanced sensitivity to certain socially relevant cues [80]) is likely to moderate certain cultural differences [33,34]. In another example, serotonin innervates cortico-limbic systems of emotion processing. Serotonergic genetic variants may then amplify culture-typical emotional response patterns [81,82•] as well as other processes that are linked to them [83,84]. Further, any effect of gene variants must be understood within a larger context in which genes are transcribed and expressed in response to a variety of environmental cues including significant social signals such as hierarchy and social inclusion or exclusion [18,85].

To conclude, although in its infancy, the social genomic analysis of cultural acquisition suggests some new avenues of research [3,16••,18]. We assert that some people may be genetically more sensitive to cultural norms than others. The norm sensitivity hypothesis sheds light on a genetic source of within-culture individual differences by examining biologically based reinforcement-mediated social learning mechanisms that are likely influenced by dopaminergic system genes.

Conflict of interest statement

Nothing declared.

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