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Investigating the Genetic Basis of Social Conformity: The Role of the Dopamine Receptor 3 *(DRD3)* Gene

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Key Words
Dopamine · *DRD3* · Social conformity · Reinforcement learning · Ser9Gly

Abstract
Background: People often change their opinions or behavior to match the responses of others, a phenomenon known as social conformity. Conforming behavior varies substantially across individuals. However, little is known about the genetic basis underlying individual differences in social conformity. A recent study demonstrated an association between enhanced dopaminergic function and increased conforming behavior. Given the effect of the dopamine receptor 3 gene *(DRD3)* Ser9Gly polymorphism (rs6280) on dopamine release in the striatum, this study investigated to what extent this polymorphism affects conforming behavior. ***Methods:*** We categorized Han Chinese individuals according to the polymorphism and tested them with a facial-attractiveness rating task. ***Results:*** We found that individuals with a greater number of the Gly alleles, which are related to an increased dopamine release in the striatum, were more susceptible to social influence and more likely to change their ratings to match those of other people. ***Conclusions:*** This finding demonstrates the importance of *DRD3* Ser9Gly as a genetic basis for social conformity and in predicting individual differences in social learning.

Introduction

Social conformity occurs when people change their opinions to act in accordance with others [1]. This phenomenon is highly pervasive, as conforming to the social group enables us to learn about the value of an object or event efficiently and accurately. In addition, social conformity ensures that we behave in a socially approved manner, particularly under circumstances of uncertainty [1].

Conforming behavior varies substantially across individuals [2, 3]. Recent twin studies suggest that individual differences in conforming behavior could be partly attributed to differences in gene expression, with the estimated heritability ranging from 28 to 47% [4, 5]. However, little

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is known about the genetic basis underlying individual differences in social conformity. The purpose of this study was to investigate to what extent the dopamine receptor 3 gene *(DRD3)* affects conforming behavior.

Previous studies have strongly implicated the dopaminergic system in reward-related incentive learning, such as reinforcement learning and social conformity [6]. On the one hand, studies have demonstrated that reinforcement learning is carried out by the phasic activity of midbrain dopaminergic neurons [6]; social conformity draws on mechanisms that comply with reinforcement learning principles [3, 7]. On the other hand, studies have also shown that the reward salience of a stimulus is heightened by dopamine release [8] and that conforming behaviors evoke activity in midbrain dopaminergic neurons similar to that of nonsocial rewards [7, 9]. These studies collectively suggest a role of dopaminergic neurotransmission in social conformity. Indeed, a recent work found that enhancement of dopamine responses via direct administration of a dopamine and noradrenalin agonist promotes conformity to group opinion [10]. Thus, it is possible that a receptor with the ability to regulate dopamine responses could modulate individuals' conforming behavior, which is related to social and reinforcement learning (see Discussion).

The dopamine D_3 receptor is 1 of the 5 (D_1 to D_5) dopamine receptors. Among these dopamine receptors, the D_3 receptor is primarily localized in limbic areas and highly expressed in the ventral striatum [11], a brain region involved in reward-related incentive learning [3, 7, 12]. Animal studies have demonstrated that blockade of the D_3 receptor impairs reward-related incentive learning, such as responding to cues for cocaine [13] and behavioral adjustment according to changing relationships between stimuli and rewards [14], while activation of the receptor enhances stimulus-reward learning [15]. In humans, the density of D_3 receptors is increased in cocaine abusers, suggesting an association between increased expression of the D_3 receptor and the reinforcing effects of cocaine [16]. Human studies have also reported an association between activation of the D_3 receptor and reward-related incentive learning [17, 18]. These findings demonstrate a prominent role of the D_3 receptor in reward-related incentive learning and suggest a possible involvement of the D_3 receptor in social conformity, a social form of reward-related incentive learning.

The dopamine D_3 receptor is encoded by the *DRD3* gene which is located on chromosome 3q13.3. Ser9Gly (rs6280) is one of the most investigated functional polymorphisms in the *DRD3* gene [19]. A thymine (T)-to-cytosine (C) substitution leads to a mutation of serine (Ser) to glycine (Gly) in the D_3 receptor, thereby causing an increase in the dopamine-mediated cyclic adenosine monophospate response in dopaminergic neurons and a 5-fold increase in the dopamine affinity of the D_3 receptor [20, 21]. A neuroimaging study reported that the Ser9Gly polymorphism affects dopamine responses to reward, with the Gly allele related to an increased dopamine release in the ventral and dorsal striata during receipt of an unpredictable reward [22]. As striatal dopamine signaling in response to a reward predicts individual differences in reinforcement learning [23, 24], it is possible that the Gly allele facilitates reinforcement learning. Previous studies have also shown that the Ser9Gly polymorphism is implicated in a variety of reward-seeking behaviors, particularly substance dependence, such that the Gly allele contributes to susceptibility to drug taking [25, 26] and reinstatement of drug-seeking behavior [27]. As drug taking and reinstatement are consequences of positive reinforcement derived from increased dopamine levels following drug administration [28], the association between the Gly allele and substance dependence could also suggest a contribution of the Gly allele to reinforcement learning.

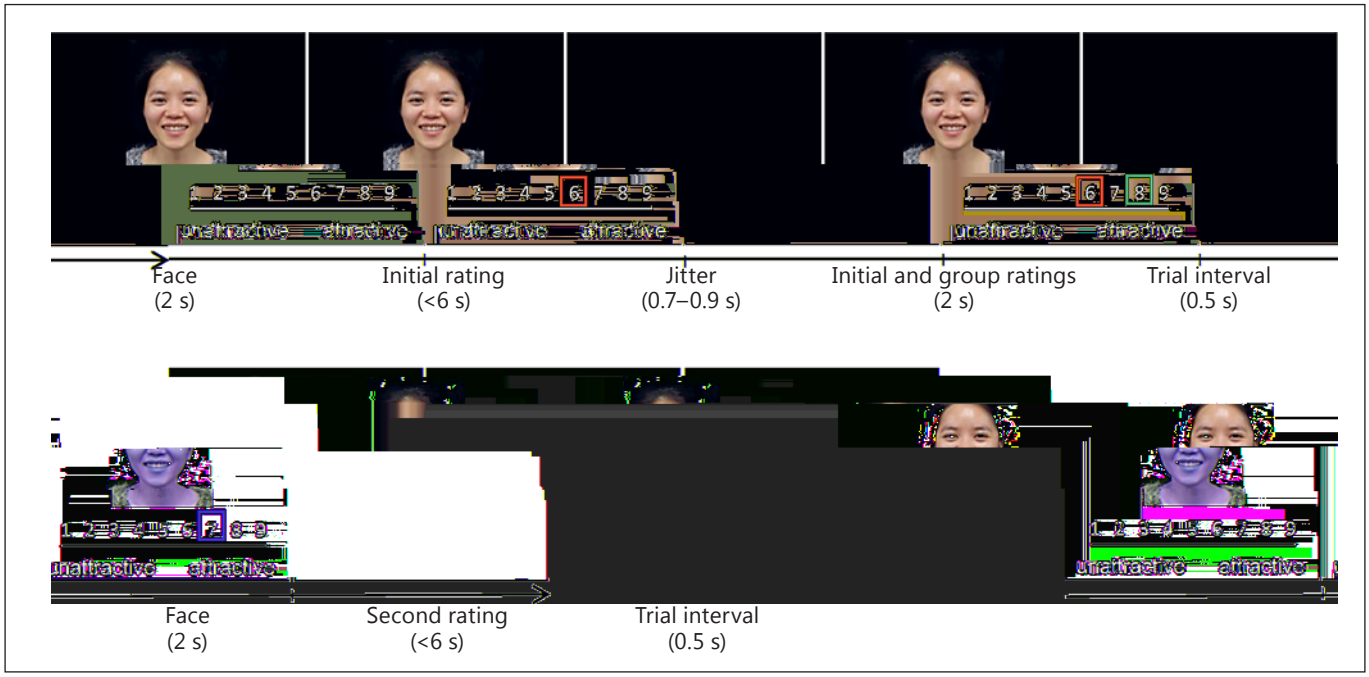

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Fig. 1. Procedure and timing of the conformity task. **a** Session 1 was composed of 120 trials. Each trial began by showing the participant a photograph of a smiling face and a 9-point Likert scale (1 = unattractive and 9 = attractive) (2 s). Faces were presented randomly. After that, a red box was presented in the middle of the scale and the participant was asked to rate the attractiveness of the face by pressing the corresponding arrow keys (<6 s). Following an interval of 0.7–0.9 s with a blank screen, the participant was shown the group rating of the face, which was highlighted by a green box (2 s). Colors refer to the online version only. The next trial began after an interval of 0.5 s with a blank screen. **b** Half an hour later, session 2 began. Session 2 was also composed of 120 trials. The procedure and timing of the first, second, and last screens of each trial in session 2 were, respectively, identical to those in session 1. Faces were presented randomly.

corrected-to-normal vision. They provided written informed consents prior to the experiments. This study was performed in accordance with the Declaration of Helsinki and approved by the Ethics Committee of the Department of Psychology of Peking University. One participant was excluded from the analysis because she did not respond to a large number of questions (>25%); 3 other participants were excluded because of their psychiatric history or severe psychiatric symptoms (>3 SD) as assessed by the Symptom Checklist-90 [30, 31]. It is important to note that including these participants did not change the pattern of the results.

Genotyping

Genomic DNA was extracted from 3–5 hair follicle cells of each participant via the Chelex-100 method [32]. The Ser9Gly in the *DRD3* gene was amplified by polymerase chain reaction (PCR), with the upstream primer 5′-AGGTGTAGTTCAGGTG-3′ and the downstream primer 5′-TCATTGCTCTATCTCC-3′. The PCR was carried out with an initial 4-min denaturation at 94°C, followed by 35 cycles of 94°C for 30 s, 55.5°C for 30 s, 72°C for 35 s, and a final extension period at 72°C for 5 min. The PCR product was digested by the restriction enzyme *Hae*III (Fermentas) at 37°C overnight. The digestion system contained 1.0 μl PCR products, 0.40 μl (10 U/μl) *Hae*III, 0.40 μl R buffer, and 3.2 μl H_2O. The incubated mixture was analyzed using 8% polyacrylamide gel electrophoresis at 220 V for 3.5 h, followed by silver staining. The genotypes were read using BioImaging Systems software. The DNA band of 231 bp represents the Ser allele, and the DNA bands of 19 and 212 bp represent the Gly allele. In the current sample of 148 individuals, the distribution of genotypes (Ser/Ser = 71, Ser/Gly = 59, and Gly/Gly = 18) showed no deviation from Hardy-Weinberg equilibrium (χ^2 = 1.08, p = 0.30). The genotype frequencies were similar to those found in East Asian samples [26, 33].

Conformity Task

A facial-attractiveness rating task was used as the conformity task, which is similar to that described by Klucharev et al. [3]. The participants were informed that the experiment was a research project on the human perception of facial attractiveness. During the task, the participants were instructed to rate the attractiveness of 120 faces on a 9-point Likert scale (1 = unattractive and 9 = attractive). They were also told that, after the rating in each trial, they would learn the average rating of the face given by a group of 200 students from universities in Beijing (fig. 1a). The participants then rested for about 30 min, during which time they were asked to complete a battery of questionnaires unrelated to the current study. After the break, the participants were unexpectedly asked to rate the faces again in the second session (fig. 1b). The long break between sessions ensured that the ratings in the second session in-

dicated the participants' own judgments rather than their explicit memory of their previous ratings or the group's ratings. All of the participants were debriefed after the experiment. No one reported any suspicion of the cover story or the task in the postexperiment interviews.

One hundred twenty digital color photographs of Chinese young adults (aged 18–35 years, 60 females) with a slight smile and moderate attractiveness (mean = 4.97, SD = 0.96) were used. These photos were drawn from a database [34] and additionally from the Internet. All the photos were taken in similar styles.

The group ratings were preprogrammed by an adaptive algorithm to ensure that the deviation (i.e. the difference between the participants' initial ratings and group ratings during the first session) ranged from –4 to 4, and the conflict level (i.e. the absolute

between '1 – initial rating' and 4 if the initial rating was lower than 5 and to a range between –4 and '9 – initial rating' if the initial rating was higher than 5. For example, in the case of an initial rating of 2, the range of the group ratings is constrained to 1–6 and the range of deviation is constrained to –1 to 4; whereas in the case of an initial rating of 7 the range of the group ratings is constrained to 3–9 and the range of deviation is constrained to –4 to 2. As a result, for each participant, the initial rating was negatively correlated with the value of the deviation (r ranged from –0.57 to –0.18) and with the subsequent rating change (r ranged from –0.77 to –0.09). Thus, the individual tendency to conform indexed by the raw conformity score (i.e. the correlation between the rating change and the deviation) could be overestimated because both the rating change and the deviation negatively covaried with the initial rating. To evaluate the net contribution of deviation to the subsequent rating change (i.e. the adjusted conformity score) for each participant, we followed the suggestions of Yu and colleagues [35, 38] and conducted hierarchical regression analyses with the subsequent rating change as the outcome variable as follows: step 1, enter the initial ratings, and step 2, enter both the initial ratings and the deviation. The adjusted conformity score (mean ± SD: 0.078 ± 0.093, range –0.156 to 0.297) was still significantly higher than zero [$t(147) = 10.124$, $p < 0.001$]. Regression analysis again revealed a significant association between the polymorphism and the adjusted conformity score [$F(1, 146) = 4.273$, $p = 0.040$, $\beta = 0.169$, $R^2 = 0.028$, and adjusted $R^2 = 0.022$; table 1].

Additionally, Schnuerch et al. [39] introduced a new approach that could isolate and quantify the conformity effect from a different perspective. They added a control group in which no group rating was ever shown and estimated the average effect of the initial ratings on the rating change (i.e. average slope γ_{10}). Then, for each item, the rating change induced by the initial rating of each participant in the experiment group could then be estimated by weighting the initial rating with the parameter γ_{10}, and the deviation-induced rating change could be estimated by subtracting the initial rating-induced rating change from the total rating change. This corrected rating change was used in the regression analyses to gain a true conformity score. Figure 3A of Yu and Chen [38] and figure 2B of Schnuerch et al. [39] show that the sizes of the effect of the initial ratings on rating change were very similar even though the two studies were conducted in different cultures (one on Chinese and the other on Germans). Given that we used essentially the same task as Yu and Chen [38] and Schnuerch et al. [39] for the assessment of conformity behavior, we used the parameter γ_{10} (–0.374) from the control group of Schnuerch et al. [39] to estimate the corrected rating change for each item for each participant in the current study and conducted regression analyses with the corrected rating change as the outcome variable. The corrected conformity score (mean ± SD: 0.103 ± 0.105, range –0.168 to 0.419) was still significantly higher than zero [$t(147) = 11.887$, $p < 0.001$]. Regression analysis again revealed a significant association between the polymorphism and the corrected conformity score [$F(1, 146) = 5.074$, $p = 0.026$, $\beta = 0.183$, $R^2 = 0.034$, and adjusted $R^2 = 0.027$; table 1]. Considering the potential group differences between our study and that of Schnuerch et al. [39], we also varied γ_{10} with ±1 SE and ±2 SE (i.e. –0.412, –0.393, –0.355, and –0.336). Regression analyses again confirmed a significant association between the polymorphism and the corrected conformity score (all p values <0.029).

Probability of Conforming Adjustments

We also examined the genotype effect on the probability of conforming adjustments. Trials with no conflict were treated as fillers. For the remaining trials, those in which the participant changed his/her ratings in the second session in the same direction as the deviation between his/her initial rating and the group rating were considered conforming; those trials in which the rating changes were in a direction opposite from the deviation and the trials with no rating change were considered nonconforming. Thus, an index of conforming probability for each participant can be calculated by dividing the number of conforming trials by the total number of conforming and nonconforming trials. Regression analysis revealed a significant association between the polymorphism and the probability of conforming adjustments [$F(1, 146) = 3.991$, $p = 0.048$, $\beta = 0.163$, $R^2 = 0.027$, and adjusted $R^2 = 0.020$; table 1].

Permutation Test

To confirm that the significant genotype effect on conforming behavior was not likely to have arisen by chance, we carried out permutation tests for the adjusted conformity score, the corrected conformity score, and the probability of conforming adjustments by shuffling the genotype across participants 20,000 times [40]. This procedure was to estimate the regression coefficient in each shuffled sample and the probability of the estimated regression coefficients being greater than the observed regression coefficient (i.e. permutation p). The permutation p values for the adjusted conformity score, the corrected conformity score, and the probability of conforming adjust-

ments were 0.039, 0.024, and 0.049, respectively, indicating that the observed genotype effect was significantly greater than that expected by chance alone.

Gender Differences

To avoid potential effects of mating motivation on facial attractiveness ratings, only female faces and female participants were selected in previous studies [3, 39]. However, in our study, both male and female participants were recruited to rate the attractiveness of both male and female faces. Given that cross-gender rating of attractiveness is related to mate selection [41], it may be the case that male and female participants changed their second ratings differently for the same-sex and opposite-sex faces. Therefore, we conducted regression analyses to estimate the adjusted conformity scores and the corrected conformity scores for male faces and female faces, separately. For the 2 indices, 2 (participants: male vs. female) × 2 (faces: male vs. female) ANOVAs revealed neither main effects nor interactions (all p values >0.130), suggesting that the extent to which male and female participants changed their second ratings in accordance with group ratings was similar for the same-sex and opposite-sex faces. Moreover, 3 (genotype: Ser/Ser vs. Ser/Gly vs. Gly/Gly) × 2 (participants: male vs. female) × 2 (faces: male vs. female) ANOVAs on the 2 indices again revealed only significant or marginally significant main effects of genotype (p = 0.039 and 0.068, respectively) but no significant interactions concerning genotype (all p values >0.131), suggesting that the genotype effect on conformity was similar across the gender of participants as well as the gender of faces.

Discussion

Previous research has demonstrated that enhancement of dopamine responses by direct administration of a dopamine and noradrenalin agonist (methylphenidate) facilitates the conformity effect [10]. The present study extended this finding by demonstrating that *DRD3*, an important player within the dopaminergic system, is associated with individual differences in conforming behavior. Individuals with a greater number of Gly alleles of the *DRD3* Ser9Gly polymorphism, which is related to increased dopamine affinity of the D_3 receptor, were more susceptible to social influence and more likely to adapt their own opinion to that of other people. On the surface, these findings are similar to those reported in a recent study demonstrating the genotype effect of a polymorphism (Val158Met) in the catechol-*O*-methyltransferase *(COMT)* gene on conforming behavior [42]. Homozygous Met allele carriers, which have the lowest COMT enzyme activity to degrade dopamine and norepinephrine, were more conformist than Val allele carriers. Given that methylphenidate and the COMT enzyme have broad effects on catecholamines, including but not limited to dopamine, the effect of methylphenidate and the *COMT* gene on conforming behavior may arise from their effects on both the dopaminergic and the noradrenergic systems. Our finding of the effect of the *DRD3* Ser9Gly polymorphism on conforming behavior, however, provides supportive evidence for implication of the dopaminergic system in social conformity.

As reviewed in the Introduction, one mechanism for the effect of the Ser9Gly polymorphism on conforming behavior has been suggested by prior research. The Gly allele has been shown to increase dopamine release in the ventral and dorsal striata during receipt of an unpredictable monetary reward. The increased reward-related dopamine activity is assumed to reflect the amplification of phasic dopamine responses to appetitive stimuli [22]. Methylphenidate, a drug that amplifies the dopamine response to appetitive stimuli [43], has been shown to increase conforming behavior after moderate social conflict [10]. The authors suggested that the enhanced dopamine response increases the magnitude of the incentive salience of agreeing with others [10]. This hypothesis is supported by evidence showing that the magnitude of an incentive is determined by the dopamine response [8] and that conformity is rewarding [7]. As such, a mechanism for the current results would be that the Gly allele amplifies the phasic dopamine activity during social conflict, which is accompanied by increases in the incentive salience of agreeing with others. That is, the Gly allele might predispose individuals to seek the approval of the group and thus exhibit more conformity.

It is important to note that prior studies have also proposed a reinforcement learning framework for conformity [3, 7]. Within that framework, the learning rate gauges the extent to which one updates the value of an object from the previous prediction error [36]. Likewise, the raw conformity score (i.e. the regression coefficient of rating changes on deviation) from the current study can be interpreted as a social learning rate (i.e. the extent to which one learns from group conflicts). The learning rate can be elevated via drugs enhancing dopaminergic function (e.g. L-DOPA) and it can be impaired via drugs reducing dopaminergic function (e.g. haloperidol) [44]. Given the enhanced dopamine activity by the Gly allele, it is possible that this allele amplifies the phasic dopamine

activity during social conflict, which increases the learning rate during social interaction. Individuals with the Gly allele are thus likely to weight the group opinion more when updating the value of an object or event. Whether the dopamine-enhanced conformity is due to an increased incentive salience of conformity or an enhanced learning ability is a question for future research.

A recent work by Kitayama et al. [45] reported that the dopamine receptor 4 gene *(DRD4)* interacted with culture to affect social orientation. Compared to noncarriers, carries of alleles linked to increased dopamine signaling showed higher levels of acquisition of cultural norms and values; that is, carriers in individualist cultures were more independent and less interdependent than carriers in collectivist cultures, but no cultural differences were apparent between noncarriers. One might wonder to what extent the current study extends our understanding of the relationship between dopaminergic genes and normative behaviors beyond the study of Kitayama et al. [45]. People in collectivist cultures showed higher levels of conformity than those in individualist cultures [46]. Both *DRD4,* examined by Kitayama et al. [45], and *DRD3,* investigated in the current study, may contribute to this conformity in collectivist cultures. However, Kitayama et al. [45] also showed that carriers of alleles linked to increased dopamine signaling would be more likely to behave in socially normative ways than noncarriers in individualist cultures (i.e. being more independent). As higher independence was found to be associated with less conformity [47], the pattern in individualist cultures [45] is different from the findings of positive associations between dopamine signaling and conforming behavior in pharmacological and genetic studies on individuals in individualist cultures (e.g. individuals in Denmark [10] or Germany [42]), suggesting that the acquisition of cultural norms is conceptually different from conformity to group opinions. The current study was conducted on participants in a collectivist culture. Given the universal existence of conformity phenomena and the positive associations between dopamine signaling and conformity in individualist cultures [10, 42] and a collectivist culture (the current study), we speculate that the impact of the *DRD3* gene on conforming behavior is similar across cultures. Obviously, further studies are needed to replicate the current findings in other collectivist cultures and, more importantly, in individualist cultures.

One might wonder whether the effect of *DRD3* on conformity observed in this study can be reduced to an effect of *DRD3* on memory. A participant with a good memory might actually recall his/her initial ratings and the group ratings, which could affect the conforming behavior. To minimize the possible contribution of memory performance to attractiveness rating changes between sessions, we used a large number of stimuli and a long break between the sessions [3]. Importantly, previous studies found no association of the *DRD3* Ser9Gly polymorphism with digital and spatial working memory spans [48], or with episodic and semantic memories [49], suggesting that the effect of the *DRD3* Ser9Gly polymorphism on conforming behavior is unlikely to have been due to the polymorphism's effect on memory performance.

In conclusion, by differentiating individuals according to the polymorphism Ser9Gly of *DRD3* and testing them with a facial-attractiveness rating task, we demonstrated a positive association between the Gly allele and conforming behavior. This finding highlights the role of *DRD3* Ser9Gly in predicting individual differences in social conformity and extends our knowledge regarding the impact of this polymorphism on reward-related incentive learning. Our findings, together with previous studies [10, 42], support the idea that factors involved in dopaminergic neurotransmission, which could change the stimulus' desirability or the individual's learning ability, should be treated as candidate contributors to social conformity.

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Authors' Contributions

C.Z., J.L., and P.G. designed the experiment and analyzed the data under the supervision of X.Z. C.Z., J.L., P.G., and J.H. performed the experiment. C.Z., J.L., P.G., and X.Z. wrote the paper.

Disclosure Statement

The authors declare that they have no conflict of interests with respect to their authorship or the publication of this article.

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