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
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 D3 receptor is 1 of the 5 (D1 to D5) dopamine receptors. Among these dopamine receptors, the D3 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 D3 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 D3 receptors is increased in cocaine abusers, suggesting an association between increased expression of the D3 receptor and the reinforcing effects of cocaine [16]. Human studies have also reported an association between activation of the D3 receptor and reward-related incentive learning [17, 18]. These findings demonstrate a prominent role of the D3 receptor in reward-related incentive learning and suggest a possible involvement of the D3 receptor in social conformity, a social form of reward-related incentive learning.

The dopamine D3 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 D3 receptor, thereby causing an increase in the dopamine-mediated cyclic adenosine monophosphate response in dopaminergic neurons and a 5-fold increase in the dopamine affinity of the D3 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 various 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.

Given the role of Ser9Gly in reward-related dopamine responses [22] and the role of dopamine responses in social conformity [3, 7, 10], it is possible that the Ser9Gly polymorphism is related to social conformity, with the Gly allele being associated with increased conforming behavior. In the present study, 152 participants were genotyped for the Ser9Gly polymorphism and tested with a facial-attractiveness rating task [3]. Participants in this task are asked to rate the attractiveness of faces twice; in between these two ratings, the others’ ratings are conveyed to the participants. It has been shown that participants’ second ratings are highly susceptible to the group’s ratings, with their ratings getting closer to the group’s ratings [3, 10]. This task can precisely quantify the degree of social conformity, providing a much more sensitive measurement of conformity than other coarse measurements (e.g. questionnaires) employed in certain previous studies [4, 5, 29]. One drawback of using this measurement is that the task takes each participant about 60 min to finish, which is much longer than coarse measurements.

**Methods**

**Participants**

One hundred fifty-two unrelated, unselected Han Chinese students (61 females, age range 18–27 years) from Tongji University participated in this study. All of the participants had normal or...
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 HaeIII (Fermentas) at 37°C overnight. The digestion system contained 1.0 μl PCR products, 0.40 μl (10 U/μl) HaeIII, 0.40 μl R buffer, and 3.2 μl H2O. 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 (χ2 = 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) (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.

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Results

Raw Conformity Score

Behavioral data were analyzed according to the procedures described by Klucharev et al. [3]. For each participant, we performed a regression analysis, with the deviation as a single predictor and the rating change (i.e. the difference between the participants’ initial ratings and group ratings during the first session) as the outcome variable, to generate individual standardized coefficients (β), which were used as a raw conformity score (i.e. an index of the individual tendency to conform) [35]. The mean raw conformity score (mean ± SD: 0.263 ± 0.095, range 0.016–0.511) was significantly higher than zero [t(147) = 33.726, p < 0.001], indicating that overall the participants changed their ratings of attractiveness in accordance with the group’s ratings [3, 35].

We also used a simple reinforcement learning algorithm (Rescorla-Wagner) to model the rating change between the initial and second ratings. The Rescorla-Wagner rule probes learning through a prediction error signal [36, 37]. Unlike typical reinforcement learning models in which each stimulus is repeated several times, the learning model in our study was based on only 2 observations per face stimulus. Thus, the prediction error signal was defined as the difference between the participants’ initial ratings and group ratings during the first session (i.e. deviation). The prediction error signal could be used to subsequently update the second ratings weighted by a fixed learning rate (i.e. α: rating2 = rating1 + α ∙ deviation). We fitted the Rescorla-Wagner model to the participants’ second ratings using a linear regression model to derive the best-fitting model parameter (α). Because there were only 2 observations for each face stimulus, the parameter α was mathematically equivalent to the raw conformity score. Consequently, we focused on the raw conformity score in the following analysis.

To examine the relationship between the DRD3 Ser9Gly polymorphism and an individual’s conformity score, we performed a regression analysis with the genotype (0 = Ser/Ser, 1 = Ser/Gly, and 2 = Gly/Gly) as a single predictor of the raw conformity score. The result indicated that the polymorphism accounted for a significant proportion of the variance in the conformity score [F(1, 146) = 5.292, p = 0.023, β = 0.187, R² = 0.035, and adjusted R² = 0.028]. Individuals with a greater number of Gly alleles, which are associated with a higher dopamine affinity of the D₃ receptor, were more likely to change their ratings in accordance with the group’s ratings (table 1). ANOVA with the genotype as a between-participant factor also showed a significant main effect of genotype [F(2, 145) = 3.272, p = 0.041]. A post hoc t test revealed that the Gly/Gly carriers conformed significantly more than the Ser/Gly carriers (uncorrected p = 0.034) and the Ser/Ser carriers (uncorrected p = 0.015), although the difference between the Gly/Gly carriers and the Ser/Gly carriers became nonsignificant with Bonferroni’s correction (p = 0.135). It is important to note that ANOVAs with genotype as a between-participant factor revealed no main effect of genotype on the initial ratings [F(2, 145) < 1] or on the second ratings [F(2, 145) < 1], suggesting that the significant genotype effect observed above resulted from differential impacts of conformity in different groups.

Adjusted Conformity Score

It is important to note that the adaptive algorithm was constrained such that the deviation was limited to a range

Table 1. Effect of the DRD3 Ser9Gly polymorphism on conforming behavior

<table>
<thead>
<tr>
<th>DRD3 genotype</th>
<th>Raw conformity score</th>
<th>Adjusted conformity score</th>
<th>Corrected conformity score</th>
<th>Probability of conforming adjustments, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ser/Ser</td>
<td>0.251 ± 0.099</td>
<td>0.067 ± 0.099</td>
<td>0.090 ± 0.109</td>
<td>43.7 ± 7.8</td>
</tr>
<tr>
<td>Ser/Gly</td>
<td>0.263 ± 0.088</td>
<td>0.076 ± 0.088</td>
<td>0.101 ± 0.101</td>
<td>44.0 ± 6.7</td>
</tr>
<tr>
<td>Gly/Gly</td>
<td>0.314 ± 0.086</td>
<td>0.125 ± 0.076</td>
<td>0.160 ± 0.084</td>
<td>48.5 ± 6.9</td>
</tr>
</tbody>
</table>

Values are presented as means ± SD.

DRD3 and Social Conformity

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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) = 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 \( \gamma_{10} \) 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 non-conforming. 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-
mements 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 D3 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 response to appetitive stimuli.
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, carriers 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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