Religion priming differentially increases prosocial behavior among variants of the dopamine D4 receptor (DRD4) gene

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Building on gene–environment interaction (G × E) research, this study examines how the dopamine D4 receptor (DRD4) gene interacts with a situational prime of religion to influence prosocial behavior. Some DRD4 variants tend to be more susceptible to environmental influences, whereas other variants are less susceptible. Thus, certain life environments may be associated with acts of prosociality for some DRD4 variants but not others. Given that religion can act as an environmental influence that increases prosocial behavior, environmental input in the form of religion priming may have G × E effects. Results showed that participants with DRD4 susceptibility variants were more prosocial when implicitly primed with religion than not primed with religion, whereas participants without DRD4 susceptibility variants were not impacted by priming. This research has implications for understanding why different people may behave prosocially for different reasons and also integrates G × E research with experimental psychology.

INTRODUCTION
What compels some people to commit to prosocial causes and others to shy away? Accumulating evidence suggests that, in addition to societal influences, prosocial behavior may also be influenced by differences in genes (twin studies, e.g. Rushton et al., 1986; Stevenson, 1997; Rushton, 2004; Gregory et al., 2009; genotyping studies, e.g. Bachner-Melman et al., 2005; Reuter et al., 2010) and, crucially, by the interaction of genes with certain aspects of the environment. Genetic susceptibility to influences from the environment may compel some people to act more prosocially, but only under particular conditions (Bakermans-Kranenburg and van IJzendoorn, 2011; Knafo et al., 2011). This gene–environment interaction (G × E) perspective (e.g. Caspi et al., 2003; Taylor et al., 2006; Eisenberg et al., 2008) can be applied to social psychological phenomena to broaden the way that situational influences on behavior are understood. In the present study, we examine how the situational priming of religion may affect prosocial behavior differently depending on one’s genes.

DRD4 and prosocial behavior
A candidate polymorphism relevant to the topic of prosocial behavior is located in the dopamine D4 receptor (DRD4) gene, which is involved in mediating cortical dopamine neurotransmission (McClernon et al., 2007; Rivera et al., 2008; Zhong et al., 2010). The exon III region of DRD4 contains a 48-base pair variable number tandem repeat (VNTR) (Van Tol et al., 1992), and certain variants of the DRD4 VNTR polymorphism have been associated with risk-taking and antisocial traits and behaviors, including increased novelty or sensation seeking (Ebstein et al., 1996), gambling (Pérez de Castro et al., 1997) and financial risk-taking (Kuhnen and Chiao, 2009), attention deficit hyperactivity disorder (ADHD; for meta-analyses, see Faraone et al., 2001; Maher et al., 2002) and conduct disorders (Kirley et al., 2004), as well as decreased altruism (Bachner-Melman et al., 2005) and insensitivity to reciprocal fairness (Zhong et al., 2010). These findings support the general conclusion that people with certain DRD4 variants are more socially deviant than others, attracted to novelty and risk while shying away from social conventions and prosocial causes.

Some researchers have argued, however, that such a conclusion may be too broad and that DRD4 is better conceptualized as a susceptibility or plasticity gene (Bakermans-Kranenburg and van IJzendoorn, 2006, 2007, 2011; for further discussion of DRD4 and other plasticity genes, see Belsky et al., 2007, 2009; Obradović and Boyce, 2009; Way and Taylor, 2010). According to this perspective, ‘risky’ genetic variants are not strictly linked to prosocial versus antisocial behaviors, but rather, are more susceptible to certain environmental influences. For instance, a recent study showed that donating behavior was not related to...
attachment style for children with DRD4 non-susceptibility variants, but secure attachment predicted greater donating behavior for children with DRD4 susceptibility variants. Insecurely attached children with DRD4 susceptibility variants donated the least, and interestingly, securely attached children with the same susceptibility variants donated the most (Bakermans-Kranenburg and van IJzendoorn, 2011). Similarly, another study showed that children with DRD4 susceptibility variants were more likely to behave prosocially when parenting involved punishment, whereas parenting style was unrelated to prosocial behaviors for children with non-susceptibility variants (Knafo et al., 2011). Therefore, those with a genetic susceptibility to the environment may exhibit increased prosocial behavior when there is an external influence encouraging prosociality but decreased prosocial behavior when this pressure is absent. For those without the susceptibility variant, prosocial behavior may not be as easily swayed by environmental influences.

In the present research, we focused on a particular aspect of the social context—religious salience—among people with different DRD4 variants to test whether those with susceptibility variants would be more strongly influenced to behave prosocially in response to a religion prime. Environmental input in the form of experimental priming may have parallel G × E findings with life environment, and thus, an open question is whether genetic susceptibility to the environment moderates the extent to which people are influenced by priming.

Religion and prosocial behavior

Religion exists in some form across every human culture (Boyer, 2003; Atran and Norenzayan, 2004), and many of the world’s major religions explicitly teach prosociality as a virtue (Batson et al., 1993). The ‘golden rule’—that one should treat others as one would like to be treated—can be found in different forms across numerous religious philosophical texts, from the Bible of Judeo-Christian faiths (Leviticus 19:18) to the Tao Te Ching of Taoism (Lao-tzu, Ch. 49) and the Mahabharata of Hinduism (Anusasana Parva, Section 113, Verse 8). Thus, it may come as no surprise that studies using self-report measures of prosocial behavior show that religious people tend to perceive themselves as prosocial and report higher levels of altruism or charitable deeds compared to non-religious people (Batson et al., 1993). Behavioral studies or those using less subjective measures of prosociality, however, have mixed results. Some observational research has found that religious people demonstrate highly prosocial behaviors (e.g. Georgianna, 1984), while other behavioral studies have shown that religious people are no more likely than non-religious people to perform altruistic acts (Darley and Batson, 1973).

It may be that religion has an effect on prosocial behavior to the extent that it acts as an environmental pressure to behave prosocially. Shariff and Norenzayan (2007) found that inducing implicit thoughts of God increased prosocial behavior among the religious and atheists alike. The authors of this study argue that perhaps when people are reminded that ‘God is watching them’ (Shariff and Norenzayan, 2007), they are more likely to act prosocially toward others. A separate group of researchers found results consistent with this view: subliminally priming participants with positive religious words increased the number of charity pamphlets taken at the end of the study (Pichon et al., 2007). However, considering that past research on this topic has been mixed, the effect of religion on prosocial behavior may not be uniform across various groups and contexts. It is likely that some key moderators are at play. Twin studies have suggested that the relationship between religion and prosocial behavior is likely to be explained by both genetic and environmental effects (Koenig et al., 2007), but little, if any research has examined this topic from a G × E perspective.

The present research: DRD4 × religion prime interaction

Building on G × E research, this study examines whether people with DRD4 susceptibility variants are more impacted by religion priming compared to those with DRD4 non-susceptibility variants. We included people of both Caucasian and East Asian ancestry to test for this G × E effect across distinct ethnic groups. Past research in different populations has shown that DRD4 variants have alleles ranging from 2- to 11-repeats (Ding et al., 2002) and that the distribution of variants differs significantly across ethnic groups (Chang et al., 1996), perhaps due to different patterns of migration throughout history (Chen et al., 1999). Across populations, the 2-, 4- and 7-repeat alleles are the three most common variants, together comprising at least 90% of observed allelic diversity (Wang et al., 2004). The most common allele in Caucasian and East Asian populations is the 4-repeat allele, which is considered the non-susceptibility variant. In Caucasian populations, the 7-repeat allele is the second most common allele, followed by the 2-repeat allele. However, in East Asian populations, the 2-repeat allele is the second most common after the 4-repeat, and the 7-repeat is extremely rare (Chang et al., 1996). Studies with Caucasian samples have usually shown that risky/antisocial tendencies are highest among people with the 7-repeat allele (Erbstein et al., 1996) but sometimes show that these tendencies are highest among people with the 2-repeat allele (Keltikangas-Jarvinen et al., 2004). Studies on East Asian samples typically show that these tendencies are highest among people with the 2-repeat allele (Zhong et al., 2010) or the 2- and 7-repeat alleles combined (Reist et al., 2007).

Evidence suggests that the 2-repeat allele was derived from the 7-repeat allele (Wang et al., 2004), and that these alleles...
share some biochemical properties and functions (Reist et al., 2007). DRD4 variants coded by the 2- and 7-repeat alleles, compared to the 4-repeat allele, show a lower efficiency activating the downstream effector when dopamine binds to them (Asghari et al., 1995; Wang et al., 2004). Therefore, the 2- and 7-repeat alleles exhibit a ‘suboptimal’ response to dopamine and lower dopaminergic signaling (Wang et al., 2004), which is thought to underlie their connection to novelty seeking traits (Kluger et al., 2002), ADHD (Swanson et al., 2001) preference for immediate behavior reinforcement (Tripp and Wickens, 2008) and perhaps also their environmental sensitivity.

Thus, in the present research we grouped 2-repeat and 7-repeat alleles together as susceptibility variants and other alleles as non-susceptibility variants across European Americans and Asians/Asian Americans.3 We hypothesized a gene (DRD4 susceptibility variant) × religion (implicit religion prime) interaction on prosocial behavior such that people with susceptibility variants would show greater prosocial behavior (i.e. more willingness to volunteer for pro-environmental causes) when primed with religion than not, while people with non-susceptibility variants would not be affected by the religion prime.

METHOD
Participants
One hundred and eighty undergraduates participated in this study for course credit or $10. However, two participants were excluded from analyses because one had no DRD4 data available, and one was ethnically mixed. Thus, the final sample included 178 participants (68 males, 106 females and 4 declined to answer) of both European American (n = 109) and Asian/Asian American backgrounds (n = 69) with ages ranging from 17 to 53 (M = 19.32, s.d. = 2.96).4

Materials and procedure
Following informed consent, participants were randomly assigned to either the religion or the neutral implicit priming activity, which was introduced as a ‘verbal fluency task’ (Shariff and Norenzayan, 2007). All participants were given a set of 10 five-word strings and instructed to unscramble the words to make a four-word phrase or sentence by dropping the irrelevant word. For example, a participant given the string ‘felt she eradicate spirit the’ could create the sentence ‘she felt the spirit’. Of the 10 sentences given in the religion prime, half contained words relevant to religion: God, prophet, spirit, sacred or divine. The remaining half did not contain religion words, and neither was there a consistent theme in these alternate concepts. For the neutral prime, all 10 sentences contained non-religion words that did not form a cohesive theme (e.g. shoes, sky, holiday, worried).

To tap into prosocial behavior toward society in general rather than a specific person or group, we measured participants’ willingness to volunteer (i.e. donating time) for prosocial causes supporting the environment. After being introduced to an ostensibly separate study surveying students’ opinions about environmental issues on campus, they read brief descriptions of 36 actual organizations and clubs available at the college (e.g. the Green Campus Program, which promotes energy efficiency on campus) and indicated their behavioral intentions to get involved with each on a checklist (i.e. being added to the mailing list, participating in projects, requesting more information about the organization), with higher scores on the checklist indexing greater willingness to volunteer for pro-environmental causes. Last, participants completed a trait measure of religiosity (e.g. ‘My religious beliefs lie behind my whole approach to life’; Worthington et al., 2003) and demographics (e.g. age, sex, ethnicity) and provided saliva samples before debriefing.

DNA extraction and genotyping
Participants provided a saliva sample using the Oragene Saliva kit OG-500 (DNA Genotek, ON, Canada) for DNA analysis at the end of the study. Saliva collection and DNA extraction were conducted according to manufacturer (Oragene) recommendations. DRD4 genotypes were identified using the labeled forward primer VIC-5’-AGG ACC CTC ATG GCC TTG-3’ and the unlabelled reverse primer 5’-GCG ACT ACG TGG TCT ACT CG-3’ (Lichter et al., 1993). Polymerase chain reaction (PCR) was performed in a total volume of 10 µl containing 25 ng of DNA, 0.5 µl of each primer (10 µM stock), 0.1 µl Takara LA Taq, 5 µl 2 × GC Buffer II (Takara Bio Inc., USA) and 1.6 µl dNTP. PCR cycling conditions consisted of an initial 1 min denaturation at 95° C, followed by 30 cycles of 94° C for 30 s, 62° C for 30 s, 72° C for 2 min and finally 72° C for 5 min. PCR products were electrophoresed on an ABI 3730 DNA analyzer (Applied Biosystems) with a LIZ1200 size standard (Applied Biosystems). Data collection and analysis used Genemapper software (Applied Biosystems).

RESULTS

DRD4 distribution and variant grouping
Consistent with past research on similar ethnic groups (Chang et al., 1996; Chen et al., 1999), the 4/4 DRD4 variant was Asian/Asian Americans the most common among European Americans (53.2%) and Asians/Asian Americans (60.9%). For European Americans, variants with at least one 7-repeat allele were the next most common (23.9%), followed by variants with at least one 2-repeat allele (18.3%) and the main variants with 4- and 7-repeat alleles (4/4, 4/7, 7/7) were in Hardy–Weinberg equilibrium, \( \chi^2(2, n = 79) = 2.92, P = 0.23 \). For Asians/Asian Americans, variants with at least one 2-repeat allele were the next most common (37.6%) after the 4/4 variant, followed by those

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3Although culture can moderate the association between genes and behavior (Kim et al., 2010a,b, 2011; Sasaki et al., 2011), we did not expect a moderating impact of culture in this study because religious teaching emphasizes prosociality in the same manner in both cultures as mentioned above.
4Data were collected as part of a larger study (see Kim et al., 2011).
with at least one 7-repeat allele (1.4%), and the main variants with 4- and 2-repeat alleles (4/4, 2/4, 2/2) were in Hardy–Weinberg equilibrium, \( \chi^2(2, n = 67) = 0.39, P = 0.82 \).

Participants with at least one susceptibility variant (i.e., 2- or 7-repeat allele) were grouped together for analyses, and participants with only non-susceptibility variants (i.e., 3-, 4-, 5 or 6-repeat allele) were grouped together—a grouping that takes into account the functional and evolutionary similarity of DRD4 2- and 7-repeat alleles (Reist et al., 2007; see also Jovanovic et al., 1999). There were 71 participants with susceptibility variants (44 European Americans and 27 Asian/Asian Americans) and 108 with non-susceptibility variants (68 European Americans and 40 Asian/Asian Americans).

**Manipulation check and religiosity equivalence by genotype**

As a priming manipulation check and a test of religiosity equivalence by genotype, we conducted a two-way analysis of variance (ANOVA) on religiosity by Prime (religion vs neutral) and DRD4 (2-/7-repeat alleles vs no 2-/7-repeat alleles). Confirming the manipulation check, results showed that there was a significant main effect of Prime, \( F(1, 170) = 15.00, P < 0.001 \), such that people reported higher religiosity when primed with religion (mean = 3.39, standard deviation = 1.58) versus not (mean = 2.52, standard deviation = 1.32). Results also established religiosity equivalence by genotype given that there was no main effect of DRD4, \( F(1, 170) = 0.72, P = 0.40 \). That is, there was no difference in religiosity between people with 2-/7-repeat alleles (mean = 2.86, standard deviation = 1.42) and without 2-/7-repeat alleles (mean = 3.02, standard deviation = 1.58), and thus, any differential impact of the religion prime on prosocial behavior between DRD4 variants is not likely to be due to systematic differences in trait religiosity by genotype. Finally, there was no interaction between Prime and DRD4 on religiosity, \( F(1, 170) = 0.01, P = 0.97 \).

**Effects of ethnicity**

Generally, the ethnicity of participants did not significantly affect prosocial behavior. A three-way ANOVA of DRD4 (2- or 7-repeat alleles vs no 2-/7-repeat alleles), Prime (religion vs neutral) and Ethnicity (European American vs Asian/Asian American) showed no main effect of Ethnicity on willingness to volunteer (mean = 0.504) and Ethnicity did not significantly interact with any other variables: Ethnicity \( \times \) DRD4 (mean = 0.566), Ethnicity \( \times \) Prime (mean = 0.442), and Ethnicity \( \times \) DRD4 \( \times \) Prime (mean = 0.292). Removing the non-significant three-way interaction term revealed that the two-way interaction of interest—DRD4 \( \times \) Prime—was significant for both European Americans and Asians/Asian Americans (mean = 0.046 and 0.004, respectively); therefore, the results are reported collapsed across ethnicities.

**DRD4–religion prime interaction**

To test our hypothesis, we conducted a two-way ANOVA of DRD4 variant and religion prime on prosocial behavior. There was no main effect of DRD4, \( F(1, 174) = 0.23, P = 0.636 \), and a significant main effect of religion, \( F(1, 174) = 4.19, P = 0.042, \eta^2 = 0.02 \), such that people implicitly primed with religion (mean = 21.11, standard deviation = 15.56) were more willing to volunteer than people not primed with religion (mean = 18.16, standard deviation = 14.17). Importantly, this main effect was qualified by a significant interaction of DRD4 variant and religion prime, \( F(1, 174) = 11.87, P = 0.001, \eta^2 = 0.06 \). Planned pairwise comparisons showed differential effects of the religion prime on prosocial behavior for 2-/7-repeat allele and non-2-/7-repeat allele carrier groups. Whereas the religion prime did not significantly impact willingness to volunteer for people without 2-/7-repeat alleles, mean = 0.266, people with 2-/7-repeat alleles were significantly more willing to volunteer when primed with religion (mean = 26.08, standard deviation = 14.76) than not primed with religion (mean = 14.28, standard deviation = 12.00), \( P = 0.001, \) Cohen’s \( d = 0.88 \). Pairwise comparisons split by prime showed that people with 2-/7-repeat alleles were less willing to volunteer than people without 2-/7-repeat alleles in the neutral prime condition (mean = 20.64, standard deviation = 14.93), \( P = 0.040, \) Cohen’s \( d = 0.47 \). However, people with 2-/7-repeat alleles were more willing to volunteer than people without 2-/7-repeat alleles in the religion prime condition (mean = 17.52, standard deviation = 15.35), \( P = 0.006, \) Cohen’s \( d = 0.57 \). See Figure 1 for key findings.

**DISCUSSION**

**Summary of results**

Our findings demonstrate that DRD4 interacts with religion to impact prosocial behavior. We found an overall main effect of implicitly priming religion, consistent with previous research on the effect of religion primes on prosocial behavior (Pichon et al., 2007; Shariff and Norenzayan, 2007). However, the interaction of DRD4 and religion shows how implicit thoughts of religion may not encourage prosocial behavior in the same way for everyone.

These results build on past research on DRD4 and altruism (e.g. Bachner-Melman et al., 2005), showing that people with DRD4 susceptibility variants were less willing to volunteer compared to people with non-susceptibility variants in situations where there was no environmental pressure to behave prosocially, as in the neutral prime condition. Yet, when those with susceptibility variants were implicitly primed with religion, they were the most willing to volunteer—more than people with the same variants who were not primed with religion, and more than people with non-susceptibility variants who were primed with religion. The current findings are in line with research showing that people with susceptibility variants demonstrate greater prosocial behavior when they experience environmental pressure to do so (Bakermans-Kranenburg and van IJzendoorn,
Given the present findings, G × E research may make important contributions to a broad array of research on morality. Some research has already shown that DRD4 and other dopamine-related genes may predict altruistic behaviors (Bachner-Melman et al., 2005), preferences for fairness (Zhong et al., 2010), and disgust sensitivity (Kang et al., 2010). Yet a fuller picture of morality may come from investigating how genetic tendencies and situational variables interact to impact different aspects of moral judgment.

The present research focused on religion as an external influence to behave prosocially, but people extend good graces for reasons unrelated to religion, including secular institutions and laws (Shariff and Norenzayan, 2007) and social responsibilities (which tend to vary by culture; see Miller et al., 1990), among other motivations (see Batson et al., 2004), for review of research on prosocial behavior). Thus, future research should examine whether genetic sensitivity to these other forms of environmental influence also have consequence for prosocial behavior.

**Building on the susceptibility gene hypothesis in G × E research**

A large body of research is accumulating in support of the idea that certain genes are associated with susceptibility, plasticity or sensitivity in response to environmental inputs (Bachner-Melman et al., 2005; Belsky et al., 2007, 2009; Obradović and Boyce, 2009; Way and Taylor, 2010). This Susceptibility Gene Hypothesis is in contrast to the notion that genetic variants map onto ‘good versus bad’ traits and behaviors, and it seems best able to account for G × E studies, which show different outcomes for people with similar genetic tendencies depending on differences in their environments (Taylor et al., 2006). In conjunction with previous studies, the present research suggests that people with particular genetic tendencies are more likely to be impacted by different levels of environmental influence—from implicit experimental priming to the relational or interpersonal level (e.g. attachment-related: see Bakermans-Kranenburg and van IJzendoorn, 2011) and to the situational and societal level (e.g. cultural, see Kim et al., 2010a, 2010b, 2011).

Although some previous G × E research on European American and East Asian cultures has shown gene–culture interactions on behavioral outcomes (e.g. emotional support; Kim et al., 2010b), it is important to note that gene–culture interactions should only be expected when cultural norms differ with respect to the outcome of interest. Given that there are no known differences in the way religion emphasizes prosociality in mainstream American and East Asian cultures (see Batson et al., 1993), the current study did not show different outcomes for these groups according to genotype.

The current research is the first to demonstrate that an experimentally manipulated situational prime moderates the link between genes and an outcome, suggesting that environmental influences examined in G × E research should be extended to include features of the situational context that fluctuate from moment to moment. It is possible that, due to

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**Implications for theories on morality**

Philosophers and laypeople alike have long been preoccupied with issues of morality, discussing what makes an action moral or what motivates moral behavior. Some believe that the greatest moral actions derive from a sense of duty, as Kant argued, but why do people feel a sense of duty to behave prosocially in the first place? Given the role of dopamine in reward-related processes (Nemirovsky et al., 2009), an interesting, if controversial, possibility is that people with certain genetic variants are predisposed to behave prosocially for particular reasons. Some people may be motivated to act prosocially because the act itself makes them feel good, which is perhaps the case for people without 2- or 7-repeat alleles, since there is evidence that 4-repeat alleles tend to exhibit greater dopamine signaling compared to those with 2- or 7-repeat alleles (Wang et al., 2004). Others may engage in prosocial behavior because they feel pressured to do so, which may apply to those with 2-7-repeat alleles, who tend to experience lower dopamine signaling compared to those with 4-repeat alleles (Wang et al.). Interestingly, these same people with lower baseline dopamine signaling may exhibit the most prosocial behavior when they have an external reason to do so. The introduction of genes into the moral philosophy debate may change the way people understand motivations for moral behavior.

Psychologists have examined the topic of morality from the perspective of moral reasoning (Kohlberg, 1969) to the more recent perspective of moral intuitions (Haidt, 2008). Given the present findings, G × E research may make important contributions to a broad array of research on
different genetic susceptibilities to environmental influence for prosocial or antisocial behavior, people with certain DRD4 variants may have systematically different pro-/anti-social responses to certain experimental conditions. In addition, people with genetic variants of other genes, such as 5-HTTLPR, tend to be more susceptible to environmental influence for stress reactivity (Taylor et al., 2006) and may therefore show different stress-related responses to experimental conditions. Future research should examine how different susceptibility genes may be sensitive to different types of experimental manipulations.

CONCLUDING REMARKS

Debates surrounding morality—what is right versus wrong—may not be settled by scientific investigation. What research can provide, however, is an explanation (rather than a justification) of the conditions under which different people choose to act on what is right. Using the G x E perspective in concert with implicit experimental techniques, this research opens exciting possibilities for understanding how different people choose to behave prosocially and why.

Conflict of Interest

None declared.

REFERENCES


