

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

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Building on gene–environment interaction ($G \times E$) 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 $G \times E$ 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 $G \times E$ 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 ($G \times E$) 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.¹ For instance, a recent study showed that donating behavior was not related to

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¹Though most genetic susceptibility studies are correlational, experimental or quasi-experimental studies also show that people with genetic susceptibilities are more affected by interventions (Blair, 2002; Klein Velderman *et al.*, 2006; Bakermans-Kranenburg *et al.*, 2008).

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 $G \times E$ 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 $G \times E$ perspective.

The present research: DRD4–religion prime interaction

Building on $G \times E$ 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 $G \times E$ 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 (Ebstein *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).²

Evidence suggests that the 2-repeat allele was derived from the 7-repeat allele (Wang *et al.*, 2004), and that these alleles

²A few researchers have examined the association between 5-repeat alleles and novelty seeking, but this analysis is not always possible given the particularly low frequency of 5-repeat alleles (it is a rare variant, along with 3-, 6- and 8-repeat alleles; Ding *et al.*, 2002). See Tsuchimine *et al.* (2005) for finding that 5/5 DRD4 genotypes (1.8% of sample) were highest on novelty seeking trait in Japanese sample and Keltikangas-Jarvinen *et al.* (2004) for finding that 5-repeat alleles (3.2% of sample) were similar to 2-repeat alleles in novelty seeking among Finnish.

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 (Klugar *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) \times 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 pro-social 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 μ l containing 25 ng of DNA, 0.5 μ l of each primer (10 μ M stock), 0.1 μ l Takara LA Taq, 5 μ l 2 \times GC Buffer II (Takara Bio Inc., USA) and 1.6 μ l 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

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 ($M = 3.39, s.d. = 1.58$) versus not ($M = 2.52, s.d. = 1.32$). 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 ($M = 2.86, s.d. = 1.42$) and without 2-/7-repeat alleles ($M = 3.02, s.d. = 1.58$), 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-/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 ($P = 0.504$), and Ethnicity did not significantly interact with any other variables: Ethnicity \times DRD4 ($P = 0.566$), Ethnicity \times Prime ($P = 0.442$), and Ethnicity \times DRD4 \times Prime ($P = 0.292$). 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 ($P = 0.046$ and 0.004 , respectively);⁵ 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 ($M = 21.11, s.d. = 15.56$) were more willing to volunteer than people not primed with religion ($M = 18.16, s.d. = 14.17$). 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, $P = 0.266$, people with 2-/7-repeat alleles were significantly more willing to volunteer when primed with religion ($M = 26.08, s.d. = 14.76$) than not primed with religion ($M = 14.28, s.d. = 12.00$), $P = 0.001$, 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 ($M = 20.64, s.d. = 14.93$), $P = 0.040$, 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 ($M = 17.52, s.d. = 15.35$), $P = 0.006$, 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,

⁵Results are consistent for European Americans when comparing 7-repeat alleles to 4-repeat alleles, as in Bachner-Melman *et al.* (2005), though the interaction is marginal ($P = 0.088$) due to reduced sample size. Results are consistent for Asians/Asian Americans when comparing 2-repeat to 4-repeat alleles, as in Zhong *et al.* (2010). The interaction remains significant ($P = 0.001$).

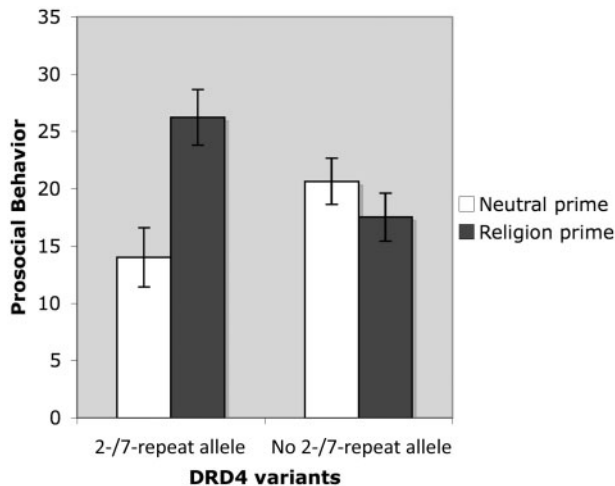


Fig. 1 Religion prime increases prosocial behavior for those with DRD4 2-/7-repeat alleles but not for those without 2-/7-repeat alleles. Error bars represent standard error of the mean.

2011; Knafo *et al.*, 2011), but this research is the first to show that a situational prime has differential effects for people with different genetic predispositions.

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, $G \times E$ 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 and Powell, 2003, 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 $G \times E$ 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 $G \times E$ 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 $G \times E$ 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 $G \times E$ research should be extended to include features of the situational context that fluctuate from moment to moment. It is possible that, due to

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 $G \times E$ 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

- Asghari, V., Sanyal, S., Buchwaldt, S., Paterson, A., Jovanovic, V., Van Tol, H.H. (1995). Modulation of intracellular cyclic AMP levels by different human dopamine D4 receptor variants. *Journal of Neurochemistry*, 65, 1157–1165.
- Atran, S., Norenzayan, A. (2004). Religion's evolutionary landscape: counterintuition, commitment, compassion, communion. *Behavioral and Brain Sciences*, 27, 713–770.
- Bachner-Melman, R., Girsenko, I., Nemanov, L., Zohar, A.H., Dina, C., Ebstein, R.P. (2005). Dopaminergic polymorphisms associated with self-report measures of human altruism: a fresh phenotype for the dopamine D4 receptor. *Molecular Psychiatry*, 10, 333–335.
- Bakermans-Kranenburg, M.J., van IJzendoorn, M.H. (2006). Gene-environment interaction of the dopamine D4 receptor (DRD4) and observed maternal insensitivity predicting externalizing behavior in preschoolers. *Developmental Psychobiology*, 48, 406–409.
- Bakermans-Kranenburg, M.J., van IJzendoorn, M.H. (2007). Research review: genetic vulnerability or differential susceptibility in child development: the case of attachment. *Journal of Child Psychology and Psychiatry*, 48, 1160–1173.
- Bakermans-Kranenburg, M.J., van IJzendoorn, M.H. (2011). Differential susceptibility to rearing environment depending on dopamine-related genes: new evidence and a meta-analysis. *Development and Psychopathology*, 23, 39–52.
- Bakermans-Kranenburg, M.J., van IJzendoorn, M.H., Pijlman, F.T.A., Mesman, J., Juffer, F. (2008). Experimental evidence for differential susceptibility: dopamine D4 receptor polymorphism (DRD4 VNTR) moderates intervention effects on toddlers' externalizing behavior in a randomized control trial. *Developmental Psychology*, 44, 293–300.
- Batson, C.D., Powell, A.A. (2003). Altruism and prosocial behavior. In: Millon, T., Lerner, M.J., editors. *Handbook of Psychology: Personality and Social Psychology*, Vol. 5, Hoboken, NJ, US: John Wiley and Sons Inc, pp. 463–84.
- Batson, C.D., Schoenrade, P., Ventis, W.L. (1993). *Religion and the Individual: A Social-Psychological Perspective*. New York: Oxford University Press.
- Belsky, J., Bakermans-Kranenburg, M.J., van IJzendoorn, M.H. (2007). For better and for worse: differential susceptibility to environmental influences. *Current Directions in Psychological Science*, 16, 300–304.
- Belsky, J., Jonassaint, C., Pluess, M., Stanton, M., Brummett, B., Williams, R. (2009). Vulnerability genes or plasticity genes? *Molecular Psychiatry*, 14, 746–54.
- Blair, C. (2002). Early intervention for low birth weight preterm infants: the role of negative emotionality in the specification of effects. *Development and Psychopathology*, 14, 311–32.
- Boyer, P. (2003). Religious thought and behaviour as by-products of brain function. *Trends in Cognitive Sciences*, 7, 119–24.
- Caspi, A., Sugden, K., Moffitt, T.E., et al. (2003). Influence of life stress on depression: moderation by a polymorphism in the 5-HTT gene. *Science*, 301, 386–9.
- Chang, F.-M., Kidd, J.R., Livak, K.J., Pakstis, A.J., Kidd, K.K. (1996). The world-wide distribution of allele frequencies at the human dopamine D4 receptor locus. *Human Genetics*, 98, 91–101.
- Chen, C., Burton, M., Greenberger, E., Dmitrieva, J. (1999). Population migration and the variation of Dopamine D4 Receptor (DRD4) allele frequencies around the globe. *Evolution and Human Behavior*, 20, 309–24.
- Darley, J.M., Batson, C.D. (1973). "From Jerusalem to Jericho": a study of situational and dispositional variables in helping behavior. *Journal of Personality and Social Psychology*, 27, 100–8.
- Ebstein, R.P., Novick, O., Umansky, R., et al. (1996). Dopamine D4 receptor (DRD4) exon III polymorphism associated with the human personality trait of Novelty Seeking. *Nature Genetics*, 12, 78–80.
- Eisenberg, D.T.A., Campbell, B., Gray, P.B., Sorenson, M.D. (2008). Dopamine receptor genetic polymorphisms and body composition in undernourished pastoralists: an exploration of nutrition indices among nomadic and recently settled Ariaal men of northern Kenya. *BMC Evolutionary Biology*, 8, 173.
- Faraone, S.V., Doyle, A.E., Mick, E., Biederman, J. (2001). Meta-analysis of the association between the dopamine D4 7-repeat allele and attention deficit hyperactivity disorder. *American Journal of Psychiatry*, 158, 1052–7.
- Georgianna, S.L. (1984). Is a religious neighbor a good neighbor? *Humboldt Journal of Social Relations*, 11, 1–16.
- Gregory, A.M., Light-Häusermann, J.H., Rijdsdijk, F., Eley, T.C. (2009). Behavioral genetic analyses of prosocial behavior in adolescents. *Developmental Science*, 12, 165–74.
- Haidt, J. (2008). Morality. *Perspectives on Psychological Science. Special Issue: From Philosophical Thinking to Psychological Empiricism*, 3, 65–72.
- Jovanovic, V., Guan, H.C., Van Tol, H.H. (1999). Comparative pharmacological and functional analysis of the human dopamine D4.2 and D4.10 receptor variants. *Pharmacogenetics*, 9, 561–8.
- Kang, J.I., Kim, S.J., Namkoong, K., An, S.K. (2010). Association of DRD4 and COMT polymorphisms with disgust sensitivity in healthy volunteers. *Neuropsychobiology*, 61, 105–12.
- Keltikangas-Jarvinen, L., Raikkonen, K., Ekelund, J., Peltonen, L. (2004). Nature and nurture in novelty seeking. *Molecular Psychiatry*, 9, 308–11.
- Kim, H.S., Sherman, D.K., Mojaverian, T., et al. (2011). Gene-culture interaction: oxytocin receptor polymorphism (OXTR) and emotion regulation. *Social Psychological and Personality Science*, 2, 665–72.
- Kim, H.S., Sherman, D.K., Sasaki, J.Y., et al. (2010b). Culture, distress and oxytocin receptor polymorphism (OXTR) interact to influence emotional support seeking. *Proceedings of the National Academy of Sciences*, 107, 15717–21.
- Kim, H.S., Sherman, D.K., Taylor, S.E., et al. (2010a). Culture, the serotonin receptor polymorphism (5-HT1A), and locus of attention. *Social Cognitive and Affective Neuroscience*, 5, 212–8.
- Kirley, A., Lowe, N., Mullins, C., et al. (2004). Phenotype studies of the DRD4 gene polymorphisms in ADHD: association with oppositional defiant disorder and positive family history. *American Journal of Medical Genetics Part B: Neuropsychiatric Genetics*, 131B, 38–42.
- Klein Velderman, M., Bakermans-Kranenburg, M.J., Juffer, F., van IJzendoorn, M.H. (2006). Effects of attachment-based interventions on

- maternal sensitivity and infant attachment: differential susceptibility of highly reactive infants. *Journal of Family Psychology*, 20, 266–74.
- Klugar, A.N., Siegfried, Z., Ebstein, R.P. (2002). A meta-analysis of the association between DRD4 polymorphism and novelty seeking. *Molecular Psychiatry*, 7, 712–7.
- Knafo, A., Israel, S., Ebstein, R.P. (2011). Heritability of children's prosocial behavior and differential susceptibility to parenting by variation in the dopamine receptor D4 gene. *Development and Psychopathology*, 23, 53–67.
- Koenig, L.B., McGue, M., Krueger, R.F., Bouchard, T.J. Jr (2007). Religiousness, antisocial behavior, and altruism: genetic and environmental mediation. *Journal of Personality*, 75, 265–90.
- Kohlberg, L. (1969). Stage and sequence: the cognitive-developmental approach to socialization. In: Goslin, D.A., editor. *Handbook of Socialization Theory and Research*. Chicago: Rand McNally.
- Kuhnen, C.M., Chiao, J.Y. (2009). Genetic determinants of financial risk taking. *PLoS ONE*, 4, e4362.
- Lichter, J.B., Barr, C.L., Kennedy, J.L., Van Tol, H.H.M., Kidd, K.K., Livak, K.J. (1993). A hypervariable segment in the human dopamine receptor D4 (DRD4) gene. *Human Molecular Genetics*, 2, 767–73.
- Maher, B.S., Marazita, M.I., Ferrell, R.E., Vanykov, M.M. (2002). Dopamine system genes and attention deficit hyperactivity disorder, a meta-analysis. *Psychiatric Genetics*, 2, 207–15.
- McClernon, F.J., Hutchison, K.E., Rose, J.E., Kozink, R.V. (2007). DRD4 VNTR polymorphism is associated with transient fMRI-BOLD responses to smoking cues. *Psychopharmacology*, 194, 433–41.
- Miller, J.G., Bersoff, D.M., Harwood, R.L. (1990). Perceptions of social responsibilities in India and in the United States: moral imperatives or personal decisions? *Journal of Personality and Social Psychology*, 58, 33–47.
- Nemirovsky, S.I., Avale, M.E., Brunner, D., Rubinstein, M. (2009). Reward-seeking and discrimination deficits displayed by hypodopaminergic mice are prevented in mice lacking dopamine D4 receptors. *Synapse*, 63, 991–7.
- Obradović, J., Boyce, W.T. (2009). Individual differences in behavioral, physiological, and genetic sensitivities to contexts: implications for development and adaptation. *Developmental Neuroscience*, 31, 300–8.
- Pérez de Castro, I., Ibáñez, A., Torres, P., Sáiz-Ruiz, J., Fernández-Piqueras, J. (1997). Genetic association study between pathological gambling and a functional DNA polymorphism at the D4 receptor gene. *Pharmacogenetics*, 7, 345–8.
- Pichon, I., Boccato, G., Saroglou, V. (2007). Nonconscious influences of religion on prosociality: a priming study. *European Journal of Social Psychology*, 37, 1032–45.
- Reist, C., Ozdemir, V., Wang, E., Hashemzadeh, M., Mee, S., Moyzis, R. (2007). Novelty seeking and the dopamine D4 receptor gene (DRD4) revisited in Asians: haplotype characterization and relevance of the 2-repeat allele. *American Journal of Medical Genetics Part B: Neuropsychiatric Genetics*, 144B, 453–7.
- Reuter, M., Frenzel, C., Walter, N.T., Markett, S., Montag, C. (2010). Investigating the genetic basis of altruism: the role of the COMT Val158Met polymorphism. *Social Cognitive Affective Neuroscience*. [Epub ahead of print].
- Rivera, A., Peñafiel, A., Megías, M., et al. (2008). Cellular localization and distribution of dopamine D4 receptors in the rat cerebral cortex and their relationship with the cortical dopaminergic and noradrenergic nerve terminal networks. *Neuroscience*, 155, 997–1010.
- Rushton, J.P. (2004). Genetic and environmental contributions to pro-social attitudes: a twin study of social responsibility. *Proceedings of the Royal Society London*, 271, 2583–5.
- Rushton, J.P., Fulker, D.W., Neale, M.C., Nias, D.K.B., Eysenck, H.J. (1986). Altruism and aggression: the heritability of individual differences. *Journal of Personality and Social Psychology*, 50, 1192–8.
- Sasaki, J., Kim, H.S., Xu, J. (2011). Religion and well-being: an analysis of an oxytocin receptor polymorphism (OXTR) and culture. *Journal of Cross-Cultural Psychology*, 42, 1394–405.
- Shariff, A.F., Norenzayan, A. (2007). God is watching you: priming god concepts increases prosocial behavior in an anonymous economic game. *Psychological Science*, 18, 803–9.
- Stevenson, J. (1997). The genetic basis of personality. In: Cooper, C., Varma, V., editors. *Processes in Individual Differences*. London: Routledge, pp. 39–58.
- Swanson, J., Deutsch, C., Cantwell, D., et al. (2001). Genes and attention-deficit hyperactivity disorder. *Clinical Neuroscience Research*, 1, 207–16.
- Taylor, S.E., Way, B.M., Welch, W.T., Hilmert, C.J., Lehman, B.J., Eisenberger, N.I. (2006). Early family environment, current adversity, the serotonin transporter polymorphism, and depressive symptomatology. *Biological Psychiatry*, 60, 671–6.
- Tripp, G., Wickens, J.R. (2008). Research review: dopamine transfer deficit: a neurobiological theory of altered reinforcement mechanisms in ADHD. *Journal of Child Psychology and Psychiatry*, 49, 691–704.
- Tsuchimine, S., Yasui-Furukori, N., Kaneda, A., Saito, M., Sugawara, N., Kaneko, S. (2009). Minor genetic variants of the dopamine D4 receptor (DRD4) polymorphism are associated with novelty seeking in healthy Japanese subjects. *Progress in Neuropsychopharmacology Biological Psychiatry*, 33, 1232–5.
- Van Tol, H.H.M., Wu, C.M., Guan, H.C., et al. (1992). Multiple dopamine D4 receptor variants in the human population. *Nature*, 358, 149–52.
- Wang, E., Ding, Y.C., Flodman, P., et al. (2004). The genetic architecture of selection at the human dopamine receptor D4 (DRD4) gene locus. *American Journal of Human Genetics*, 74, 931–44.
- Way, B.M., Taylor, S.E. (2010). Social influences on health: is serotonin a critical mediator? *Psychosomatic Medicine*, 72, 107–12.
- Worthington, E.L., Wade, N.G., Hight, T.L., et al. (2003). The Religious Commitment Inventory-10: development, refinement, and validation of a brief scale for research and counseling. *Journal of Counseling Psychology*, 50, 84–96.
- Zhong, S., Israel, S., Shalev, I., Xue, H., Ebstein, R.P., Chew, S.H. (2010). Dopamine D4 receptor gene associated with fairness preference in ultimatum game. *PLoS One*, 5, e13765.