Thin-slicing study of the oxytocin receptor (OXTR) gene and the evaluation and expression of the prosocial disposition

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Individuals who are homozygous for the G allele of the rs53576 SNP of the oxytocin receptor (OXTR) gene tend to be more prosocial than carriers of the A allele. However, little is known about how these differences manifest behaviorally and whether they are readily detectable by outside observers, both critical questions in theoretical accounts of prosociality. In the present study, we used thin-slicing methodology to test the hypotheses that (*i*) individual differences in rs53576 genotype predict how prosocial observers judge target individuals to be on the basis of brief observations of behavior, and (*ii*) that variation in targets' nonverbal displays of affiliative cues would account for these judgment differences. In line with predictions, we found that individuals homozygous for the G allele were judged to be more prosocial than carriers of the A allele. These differences were completely accounted for by variations in the expression of affiliative cues. Thus, individual differences in rs53576 are associated with behavioral manifestations of prosociality, which ultimately guide the judgments others make about the individual.

compassion | nonverbal behavior | thin slices

Oxytocin is a neuropeptide that is synthesized in the hypothalamus (1) and broadly involved in emotional and social processes (2). Animal models have shown that oxytocin is related to parental and pair bonding across mammalian species (2, 3). Within humans, experimental inductions that increase oxytocin increase many facets of prosociality, including trust (4), generosity (5, 6), empathy (6), and sacrifice (7), all tendencies that enable affiliative behavior in the face of stress (8, 9). One of the central determinants of oxytocin functionality is the specific receptor through which oxytocin operates throughout the body and the brain (10). Indeed, animal research suggests that differences in distribution and expression of the oxytocin receptor (OXTR) underlie variation in sociability across species (11–13). Given the central role of this receptor in the functionality of oxytocin, an emergent line of inquiry has focused on the correlates of polymorphisms of the OXTR gene, located on chromosome 3p25 (14).

One particular SNP of OXTR (rs53576) has been implicated in social behavior. Individuals homozygous for the G allele (GG genotype) compared with carriers of the A allele (AA, AG genotypes) are at lower risk for autism (15) and self-report higher levels of empathy (16), positive emotions (17), sociality (18), and parental sensitivity (19). Neurologically, people homozygous for the G allele tend to have larger hypothalamic volumes and increased amygdala activation when viewing emotionally salient social cues, compared with carriers of the A allele (18). Collectively, these findings suggest that individuals who are homozygous for the G allele of rs53576 tend to respond to the needs of others with greater prosociality than carriers of the A allele.

To date, however, no research has examined whether variation in rs53576 is related to nonverbal behavioral displays of prosociality. Numerous lines of inquiry suggest that prosocial intent is signaled nonverbally. For example, one study demonstrated that socioeconomic status—a key predictor of altruism (20)—is quickly communicated through engagement and disengagement cues (21). Similarly, research on the nonverbal expression of positive emotions—such as compassion, gratitude, and love—has shown that these prosocial states are signaled in brief patterns of facial muscle movements, postural behavior, tactile contact, and vocalization (22–25). Based upon this work, we reasoned that if individual differences in rs53576 are indeed related to people's proclivity toward prosocial behavior, then it is likely that individuals homozygous for the G allele will display their prosociality in specific nonverbal displays.

These nonverbal displays of prosocial behavior, we further reasoned, should reliably signal the prosociality of individuals homozygous for the G allele to naive observers. Dozens of empirical studies have established that naive observers can make rapid and accurate judgments about the traits and intentions of target individuals based on the briefest of observations, or "thin slices," of behavior (26). For example, naive observers can make reliable judgments about a target's personality traits (26–28), socioeconomic status (21), and the truthfulness of his or her confessions (29) based upon seeing 1 min or less of the target's behavior, often with no sound. Some evidence also suggests that behavioral patterns associated with different testosterone levels are also detectable from thin slices (30). Therefore, we hypothesized that the nonverbal behavioral cues associated with differences in rs53576 would be readily detectable to naive observers on the basis of seeing target individuals for only a brief period (20 s).

Guided by this reasoning, in the present research we tested three hypotheses. First, we predicted that naive observers would rate target individuals homozygous for the G allele (compared with people carrying the A allele) as more prosocial based on seeing only a few seconds of that individual interacting with a person in need, even in the absence of auditory information and knowledge about the social context. Second, we predicted that individuals homozygous for the G allele would signal their prosociality through increased nonverbal displays of affiliative cues when interacting with a person in need than would individuals carrying the A allele. Finally, we predicted that these differences in the display of affiliative cues would account for the differences in prosocial judgments naïve observers make about the target individuals homozygous for the G allele versus target individuals carrying the A allele.

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Results

To test these three hypotheses, a sample of naive observers watched 20-s, silenced video clips of 23 target individuals with varying rs53576 genotypes. In the video clips, targets were listening to their romantic partner disclose an experience of personal suffering; thus, the target was the listener in the conversation. This conversation was selected because displays of vulnerability are compelling elicitors of prosocial behavior (31, 32) and should provide targets with a clear opportunity to respond to another person in need.

We first tested whether target differences in rs53576 predicted the prosocial judgments observers made about them. In these analyses, the focus was on the observers and their inferences about the prosociality of the targets. Because of the nested design of the study (i.e., each observer watched 23 videos), hierarchical linear modeling was used to analyze the data (33); specifically, ratings of targets (level 1) were nested within individual observers (level 2). As predicted, and portrayed in Fig. 1, observers judged targets homozygous for the G allele (M = 4.21, SD = 1.40) as more prosocial than targets carrying an A allele (M = 3.80, SD = 1.41), $b = 0.41$, $t(2,628) = 8.22$ $P < 0.001$. In fact, of the 10 most trusted targets, 6 were homozygous for the G allele; of the 10 least trusted targets, 9 were carriers of the A allele. These results demonstrate that differences in rs53576 systematically predict outside observers' judgments of the prosociality of carriers based on observations of 20 s of silent behavior.

Our next set of analyses focused on several ancillary questions. First, we tested whether the effect of target genotype was invariant across observers. That is, did observers make similar inferences about the prosociality of the target, or was there significant variation in these inferences? To test this, we modeled the effect of target genotype as random at level 2 within the hierarchical linear model. In this analysis, we did not observe significant individual differences in the association between target genotype and the observers' prosociality ratings of the targets, $\chi^2 = 110.10$, $df = 115$, $P > 0.500$. Therefore, the rated differences in prosociality between targets homozygous for the G allele and those carrying the A allele were consistent across the observers.

Next, we tested whether the sex of the targets moderated the effect of genotype on the prosociality judgments of observers. Observers tended to see a bigger difference in prosociality between the male targets who were homozygous for the G allele compared with carriers of the A allele than for the female targets, $b = 0.14$, $t(2,626) = 1.85$, $P = 0.063$. It should be noted, however, that the difference in prosociality judgments of the female targets homozygous for the G allele and the A allele was still highly significant, $b = 0.32$, $t(2,626) = 5.39$ $P < 0.001$. It is also important to note that male targets were on average judged to be less prosocial than the female targets, $b = -0.27$, $t(2,628) = -5.38$ $P < 0.001$. Therefore, these findings suggest that observers judge both male and female targets homozygous for the G allele to be more prosocial than those with the A allele, although this difference may be more pronounced for males, a topic worthy of future investigation.

Our second hypothesis held that targets homozygous for the G allele would display more affiliative nonverbal cues than carriers of the A allele. For these analyses, the central unit of analysis was the target because they made the behavioral displays. Thus, we used an ordinary least-squares regression approach. In line with our prediction, we found that targets homozygous for the G allele (M = 0.33, SD = 0.56) displayed more affiliative nonverbal cues than targets carrying an A allele (M = −0.25, SD = 0.56), $b = 0.58$, $t(22) = 2.48$, $P = 0.022$. Of the 10 targets displaying the most affiliative cues, 6 were homozygous for the G allele; of the 10 targets displaying the fewest affiliative cues, 8 were carriers of the A allele. Thus, differences in display of affiliative cues as a function of target genotype closely mirrored the observers' prosociality ratings.

Finally, we conducted mediation analyses to ascertain whether differences in affiliative cues accounted for the link between target rs53576 genotype and observer judgments of prosociality. We used a multilevel mediation approach as outlined by Zhang, Zyphur, and Preacher (34). To calculate the 95% confidence interval (CI) for the indirect effect, we used the Monte Carlo Method for Assessing Mediation using 20,000 repetitions (35). Only the relationship between affiliative cues and prosociality ratings ($\chi^2 = 171.23$, $P = 0.001$) varied across observers; therefore, the genotype effect was modeled as fixed at level 2 and the affiliative cues effect was modeled as random at level 2. Supporting our hypothesis and as shown in Fig. 2, the difference in prosociality judgments of targets homozygous for the G allele versus carrying an A allele became nonsignificant [$b = 0.05$, $t(2,627) = 1.00$ $P = 0.318$] when mediated by affiliative cues, CI 95% (0.08, 0.67). In contrast, target display of nonverbal affiliative cues remained a highly significant predictor of the prosociality judgments observers made about the targets, $b = 0.62$, $t(115) = 12.88$, $P < 0.001$. Thus, consistent with our hypothesis, individuals who are homozygous for the G allele were judged to be more prosocial as a function of displaying more affiliative cues within the period of observation.

Discussion

Cooperation among nonkin is enabled when individuals can reliably identify the prosocial intentions of other individuals based on brief observations. In line with this reasoning, studies have documented that the prosocial intent of others is highly detectable on the basis of brief observations of nonverbal behavior (21, 26–29). The present study extends this research by showing that based on witnessing only 20 s of silent behavior of the targets, naive observers attributed greater prosociality to targets homozygous for the G allele on an SNP of OXTR (rs53576), which has been found in other studies to predict prosociality (15–19), than

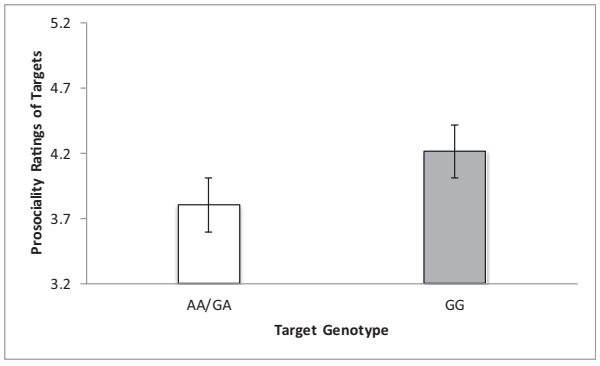

Fig. 1. Differences in prosociality ratings of targets by genotype. Targets homozygous for the G allele ($M = 4.21$, SD = 1.40) were judged to be more prosocial than targets carrying an A allele (M = 3.80, SD = 1.41) ($b = 0.42$, $P < 0.001$). Error bars reflect standard deviations.

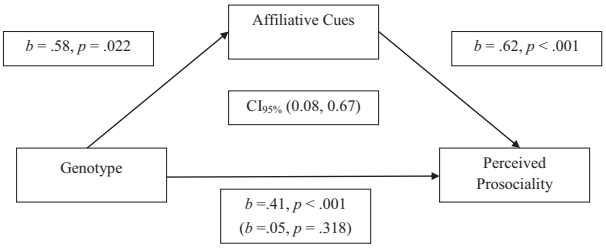

Fig. 2. Mediating role of affiliative cues. Genotype represents a dichotomous variable that modeled whether each target was homozygous for the G allele. Sobel test (*z*-value) was used to determine whether the mediation was significant.

to carriers of the A allele. Furthermore, the targets homozygous for the G allele displayed greater nonverbal affiliative cues associated with prosociality (e.g., head nods, smiles) than targets carrying the A allele, which in turn ultimately accounted for how prosocial the observers judged the targets to be.

Taken together, these findings demonstrate that an SNP (rs53576) known to predict prosocial tendencies is signaled through display behavior that leads to reliable observer inferences of the target's prosociality. Our findings shed light on how people's friendship networks can align along genetic lines; recent evidence finds that people tend to have friends that share similarity among certain genes and differences among other genes (36). The communicability of genetic information on the basis of a few brief moments of behavior provides a potential mechanism for how friendship networks develop as a function of such genetic similarities and differences. The more general implication is that even SNPs can yield systematic influences upon the social inferences and relationships important to social life.

It is important, however, to take caution in interpreting the present results. Social traits like prosociality are no doubt influenced by a multiplicity of genetic and epigenetic factors, and thus single-gene paradigms are ultimately limited in their ability to explain large portions of variability in social behavior (37). We therefore suggest that variation in rs53576 is a contributing factor to people's proclivity toward prosociality, although it is certainly not the only one. Efforts should be taken to better understand its role within the context of other factors underlying a prosocial disposition, especially given that oxytocin functions through a single receptor, unlike most neuromodulators. It is important to note that the exact functional consequences of rs53576 are presently unknown; it is located in an intron that has been implicated in transcriptional repression (38). More research is required to understand how differences in this specific location of OXTR contribute to physiological processes that underlie social functioning. Nonetheless, our results are consistent with a growing number of studies linking variation in rs53567 to social functioning across numerous social domains (15–19). It is also important to note that the present study featured a limited number of targets; thus, more work is necessary to replicate and extend the present results to a larger, more diverse sample. Finally, several studies have documented that the relationship between rs53576 and social functioning is culturally dependent, and that the distribution of genotypes varies heavily by ethnicity (39–41). In the present study, all of the targets were Caucasian. This approach allowed us to avoid potential cultural and ethnic biasing of our results, but it also limits the generalizability of the present findings. Future research should investigate whether a different pattern of results emerges for targets of other ethnicities.

Collectively, our results speak to the communicability of even slight genetic variations and the power of human intuition and inference to recognize the nonverbal signatures associated with specific genotypes. What remains, however, is the challenge of understanding the specific pathways through which genes bias behavior, especially within the context of other vital endogenous and exogenous factors shaping behavioral tendencies.

Methods

Procedure. In the present study, we showed 116 observers 23 video clips of target individuals; every observer watched every video clip. After watching each video clip, observers indicated on seven-point scales how much they felt the target was trustworthy, compassionate, and kind. The three ratings of each target made by each observer were combined into a single prosociality index (video level: $\alpha = 0.93$; observer level: $\alpha = 0.97$). In total, we gathered 2,630 ratings of the targets. Informed consent was gathered from all participants at the beginning of the study.

Observers. We recruited 116 undergraduates (52% female) from the University of Toronto Mississauga to serve as the observers. The observers were ethnically diverse: 36.2% Caucasian, 38.9% Asian, and 24.9% other ethnicities. Their age ranged from 17 to 23 y (M = 18.69 y, SD =1.16). Observers completed the study online.

Targets. We selected 23 targets from a broader pool of 45 participants who partook in a previous study of dating couples (42). To balance sex and rs53756 genotypes in the pool of targets to be judged by observers, we selected the following set of targets: 10 targets with the GG genotype (five male, five female), 10 targets with the GA genotype (five male, five female), and three targets with the AA genotype (two male, one female). We selected these 23 targets before viewing any of the videos, and the selection was completely random with the exception of balancing for sex and ethnicity from targets' self-reports. We collected saliva samples from the couples study participants using Oragene kits (DNA Genotek).

All targets were ethnically Caucasian, ranging in age from 18 to 33 y (M = 23.78 y, SD = 3.49). Given the small number of targets with the AA genotype and past work on rs53576 (10, 13, 14), all analyses focused on comparing targets homozygous for the G allele versus carriers of the A allele. No Asian targets were included in the study because previous research has demonstrated that variation in rs53576 may relate to different functionalities across ethnic groups (29). Furthermore, within the parent study from which targets were selected, very few of the Asian participants had the GG genotype, which would have made it difficult to test the hypotheses from the present study with Asian targets.

Target Genotyping. All DNA samples were labeled with an anonymous code and were extracted and purified by an external laboratory (the DNA Bank at the University of California, San Francisco, CA). The extracted DNA was then sent to the Genomics Core Facility (University of California, San Francisco, CA) to conduct the genotyping assay. All PCR reactions and allelic discrimination reactions were performed on an ABI 7900HT Real-Time PCR System (Applied Biosystems) and analyzed using SDS 2.3 software (Applied Biosystems). The SNP marker for rs53576 was genotyped using TaqMan SNP Genotyping Assays (Applied Biosystems).

Videos. All videos were selected from a conversation between the target and his or her romantic partner in which the target's partner talked about a time of personal suffering. A research assistant blind to the genotypes of the targets and the study hypotheses first identified the specific time of the most intense emotional moment in each conversation. Video clips presented to observers captured the 10 s before this most intense instant of the disclosure of suffering and the 10 s after, thus presenting 20 s of behavior. Only the target was fully visible in each video clip; however, part of the arm and back of each target's romantic partner was also visible, indicating to the observers that each target was engaged in a conversation. To avoid biasing observers with any information about the situation, no information was provided about the context or the content of the conversation.

Coding of Affiliative Cues. To document which signal behaviors observers relied upon to make inferences about targets' prosociality, two trained coders coded each video clip for four behavioral cues involved in the prosocial response: number of head nods ($\alpha = 0.97$), gaze duration ($\alpha = 0.72$) on a 5-point scale (0: no eye contact, to 4: eye contact for the entire video); openness of arm posture ($\alpha = 0.88$), also on a 5-point scale (0: completely closed, to 4: completely open), and whether the target smiled during the duration of the video ($\kappa = 0.90$). We chose to focus on these four displays based on empirical studies (21) of affiliative nonverbal display (see more detailed description in *SI Text*) and given the constraints of the context in which targets were observed—listening to a romantic partner describe an experience of suffering—which rendered certain affiliative displays unlikely. The two coders were unaware of the rs53576 genotype identity of the targets. Because the codes were on different scales, we standardized all of the codes by *z*-scoring each of the variables. After standardizing, we combined the four codes into an affiliative cues composite.

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Correction and Retraction

CORRECTION

PSYCHOLOGICAL AND COGNITIVE SCIENCES, GENETICS

Correction for "Thin-slicing study of the oxytocin receptor (OXTR) gene and the evaluation and expression of the prosocial disposition," by Aleksandr Kogan, Laura R. Saslow, Emily A. Impett, Christopher Oveis, Dacher Keltner, and Sarina Rodrigues Saturn, which appeared in issue 48, November 29, 2011, of *Proc Natl Acad Sci USA* (108:19189–19192; first published November 14, 2011; 10.1073/pnas.1112658108).

The authors note that Fig. 1 appeared incorrectly. The corrected figure and its legend appear below. This error does not affect the conclusions of the article.

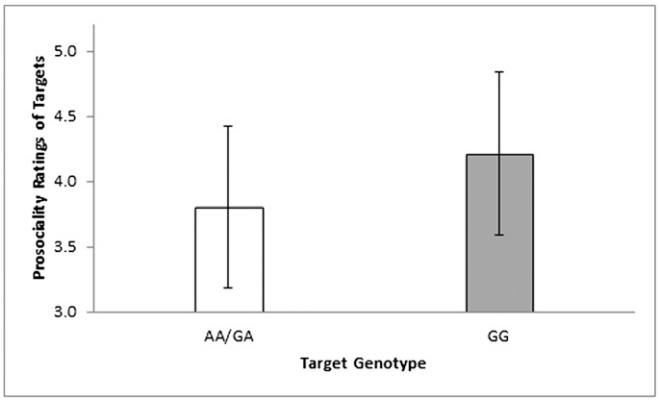

Fig. 1. Differences in prosociality ratings of targets by genotype. Targets homozygous for the G allele (M = 4.21, SD = 0.63) were judged to be more prosocial than targets carrying an A allele (M = 3.80, SD = 0.55), (b = .42, P < .001). Error bars reflect standard deviations.

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RETRACTION

PHARMACOLOGY

Retraction for "Structural basis for nucleotide exchange on Gαi subunits and receptor coupling specificity," by Christopher A. Johnston and David P. Siderovski, which appeared in issue 6, February 6, 2007, of *Proc Natl Acad Sci USA* (104:2001–2006; first published January 30, 2007; 10.1073/pnas.0608599104).

The authors wish to note the following: "In our paper, a co-crystal structure at 2.2 Å resolution was described of the heterotrimeric G-protein alpha subunit Gαi1 bound to two peptides: one from an artificial sequence that promotes nucleotide exchange (KB-752) and a second peptide (D2N) from the third intracellular loop of the D2 dopamine receptor (PDB ID code 2HLB). Further examination of the unbiased electron density map has revealed that, while electron density exists for the KB-752 peptide, there is a lack of clear and continuous electron density for the D2N receptor peptide in the complex. Because the structural model represents a major conclusion of the paper but is unsupported by the experimental electron density map, we wish to retract the paper. Both authors deeply regret this mistake and sincerely apologize."

Christopher A. Johnston
David P. Siderovski

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