

Ignorance is no excuse: Moral judgments are influenced by a genetic variation on the oxytocin receptor gene

Nora T. Walter^{a,b,*}, Christian Montag^{a,b}, Sebastian Markett^{a,b}, Andrea Felten^{a,b,c}, Gesine Voigt^{a,b}, Martin Reuter^{a,b,c}

^a Department of Psychology, University of Bonn, Kaiser-Karl-Ring 9, 53111 Bonn, Germany

^b Laboratory of Neurogenetics, University of Bonn, Kaiser-Karl-Ring 9, 53111 Bonn, Germany

^c Center for Economics and Neuroscience (CENs), University of Bonn, Nachtigallenweg 86, 53127 Bonn, Germany

ARTICLE INFO

Article history:

Accepted 8 January 2012

Available online 31 January 2012

Keywords:

Moral judgment

Perspective-taking

Oxytocin

OXTR gene

ABSTRACT

Perspective-taking has become a main focus of studies on moral judgments. Recent fMRI studies have demonstrated that individual differences in brain activation predict moral decision making. In particular, pharmacological studies highlighted the crucial role for the neuropeptide oxytocin in social behavior and emotional perception. In the present study $N = 154$ participants were genotyped for a functional polymorphism (rs2268498) in the promoter region of the OXTR gene. We found a significant difference between carriers and non-carriers of the C-allele in exculpating agents for accidental harms ($F_{(1,152)} = 11.49$, $p = .001$, $\eta^2 = .07$) indicating that carriers of the C-allele rated accidentally committed harm as significantly more blameworthy than non-carriers. This is the first study providing evidence for a genetic contribution to moral judgments.

© 2012 Elsevier Inc. All rights reserved.

1. Introduction

1.1. Moral judgments, emotions, and theory of mind

What is more blameworthy – an intended but failed harm or an accidentally committed harm? Usually we tend to blame attempted but failed harm and exculpate agents for accidentally and unknowingly caused harm to others. This observation is primarily based on the basic requirement that we are able to consider the agent's mental state in the process of our moral judgment. The degree to which the agent's mental state is taken into account in moral decision making has been neglected in traditional studies on moral dilemmas so far as mounting evidence suggests, that human morality is primarily based on emotions, particular on emotions that make individuals care about others, like altruism, cooperation and norm-following (reviewed by [Greene & Haidt, 2002](#)). Classical dilemmas ask participants to judge if it is permissible to harm one person in order to save many. Those dilemmas usually require a trade-off between an emotional aversive committed (and intended) harm and a utilitarian maximization of aggregated welfare ([Young & Saxe, 2009](#)). The confrontation with and the requirement to solve those trade-offs have been shown to activate those brain areas typically involved in emotion processing and

abstract cognitive reasoning ([Greene, Nystrom, Engell, Darley, & Cohen, 2004](#); [Greene & Haidt, 2002](#)). The two-process theory of moral judgment that was based on these findings distinguishes between an emotional implicit and autonomic rejection of causing harm to an innocent person on the one hand and a cognitively controlled abstract reasoning process on the other ([Greene et al., 2004](#); [Haidt, 2001](#); [Young & Saxe, 2009](#)). Due to the extension of the two-process theory by the consideration of the agent's mental state, the question arises if and to which extent moral judgments are influenced by individual differences. People differ in the degree in which mental states of agents are taken into account and therefore also in the extent to which agents are exculpated for accidentally committed harms ([Cohen & Rozin, 2001](#); [Wu & Keysar, 2007](#); [Young & Saxe, 2009](#)).

From a developmental perspective, the ability to consider mental states of others is acquired with the development of a theory of mind (e.g. [Wimmer & Perner, 1983](#)). Interestingly, the development of the fundamental ability to differentiate between private knowledge and the knowledge of others seems to be universal and independent of culture or the development of executive functions (e.g. [Sabbagh, Xu, Carlson, Moses, & Lee, 2006](#); [Avis & Harris, 1991](#)). However, the ability to distinguish between one's own mental state and that of others and additionally, to consider the perspective of our counterparts play a pivotal role for empathic, cooperative, or competitive behavior and thus for social interactions ([Decety & Sommerville, 2003](#); [Saxe & Kanwisher, 2003](#); [Wu & Keysar, 2007](#)). The consideration of an agent's belief or mental

* Corresponding author at: Department of Psychology, University of Bonn, Kaiser-Karl-Ring 9, 53111 Bonn, Germany. Fax: +49 228 73 439.

E-mail address: nora.walter@uni-bonn-diff.de (N.T. Walter).

state can serve as a contribution to solve judgments that require a decision how much blame the agent deserves for his or her behavior (Knobe, 2005). Therefore, the moral judgment whether to blame someone for his behavior is based on the comprehension of the agent's mind in so far that the intentionality of the respective behavior should be considered. Judgments that require the consideration of someone acting intentionally or accidentally are typical theory-of-mind judgments (Knobe, 2005). This is also the case in common law tradition. A conviction is based on a committed harm and intent to harm (Young, Cushman, Hauser, & Saxe, 2007). Difficulties in judgments occur if only one of both factors is present: either a committed harm but no intention to do so or an attempt to harm but no execution. Young children base their judgments on the outcome or consequences of a certain behavior rather than on the underlying intention whereas older children are able to consider the intention to behave in a certain way (Yuill & Perner, 1988; Zelazo, Helwig, & Lau, 1996). Young et al. (2007) suggest that the consideration of an agent's mental state to judge his behavior is not only based on the development of theory of mind but also on the ability to integrate information about mental states and behavioral consequences in moral judgments.

1.2. A possible role of the OXTR gene

Neuroscientific research has focused on investigating specific brain areas involved in moral reasoning so far (reviewed by Greene & Haidt, 2002). Evidence, which neurotransmitters and hormones are involved in moral decision making is still lacking. The neuropeptide oxytocin has been shown to influence a whole range of behavior relevant for moral decision making within the domains of social cognition and emotion (e.g. reviewed by Neumann (2008)), such as emotion recognition (e.g. Fisher-Shofty, Shamay-Tsoory, Harari, & Levkovitz, 2009), altruism (De Dreu et al., 2010), pair bond formation (e.g. reviewed by Young & Wang (2004)), and trust (Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005).

The heritability of social behavior has been demonstrated with heritability estimates ranging from 10% to 60% (Cesarini et al., 2008; Knafo, Israel, & Ebstein, 2011; Knafo, Zahn-Waxler, Van Hulle, Robinson, & Rhee, 2008). Based on the fact that oxytocin influences social cognitive and emotional processes and behavior relevant for moral reasoning and that the heritability of such behavior is demonstrated, it is quite reasonable to hypothesize that genetic variations on oxytocin relevant genes contribute to individual differences in moral judgments.

The oxytocin receptor gene (OXTR) on chromosome 3p25 is a candidate gene for individual differences in a wide range of social behavior. In fact, this assumption has been corroborated by a variety of studies on knock-out mice (e.g. Higashida et al., 2010; Lee, Caldwell, Macbeth, & Young, 2008). Molecular genetic studies in humans demonstrated that variations in the OXTR gene account for individual differences in altruism (Israel et al., 2009), the etiology of autism (e.g. Lerer et al., 2008), for negative emotionality in interaction with the serotonin transporter polymorphism (5-HTTLPR) (Montag, Fiebach, Kirsch, & Reuter, 2011) and trust (unpublished data from our own workgroup, see Montag et al., 2011). The latter two studies emphasized the influence of the OXTR rs2268498 polymorphism (genotypes: CC/CT/TT) in the promoter region. This polymorphism has been associated with higher mRNA expression in C allele carriers and thus might influence the number of oxytocin receptors (unpublished data from our own workgroup). Carriers of the T allele showed significantly more trust behavior in the economic trust-game. In this game, two subjects interact anonymously to enhance their own financial outcome which depends on whether subjects trust or defect each other. Thus, subjects make decisions with a financial consequence under uncertainty of the

partner's decision. Furthermore, Montag et al. (2011) linked the C allele together with the short (s) allele of the 5-HTTLPR polymorphism to higher negative emotionality. The underlying mechanism might be based on the number of oxytocin receptors and the resulting oxytocin signaling. Given the fact that C-allele carriers show an enhanced mRNA expression for the oxytocin receptor it can be suggested that these individuals have more oxytocin receptors in general. According to Montag et al. (2011) TT-genotype carriers exhibit a decreased number of oxytocin receptors which can be more easily occupied resulting in a more efficient oxytocin signaling pathway (Shankaran, Wiley, & Resat, 2007).

1.3. Summary, aims and hypotheses

In sum, the two process theory of moral judgment involves an implicit and aversive emotional evaluation of the committed harm to an innocent person and a cognitively controlled process including the evaluation and processing of the agent's mental state (Greene et al., 2004; Haidt, 2001; Young & Saxe, 2009). With the present study we want to bridge the gap between studies investigating the role of perspective-taking in moral judgments, brain imaging studies investigating moral reasoning, molecular genetic studies on the OXTR gene and relevant social cognitive and emotional processes. For this reason we genotyped our participants for the OXTR rs2268498 polymorphism. To assess moral judgments in our participants, we adapted the design and the moral dilemmas of Young and Saxe (2009) which require a judgment of blameworthiness regarding different kinds of harm: intentional harm, attempted harm and accidental harm. The authors reported that the activation of the right temporo-parietal junction (RTPJ) predicts individual differences in exculpating agents for accidental harms. With respect to oxytocin and its strong impact on social behavior relevant for perspective taking such as emotion recognition (e.g. Fisher-Shofty et al., 2009), autism (Guastella et al., 2009) and mental-state attribution (Domes, Heinrichs, Michel, Berger, & Herpertz, 2007) we suggest that the functional variant rs2268498 of the OXTR gene contributes to explain individual differences in moral judgments that require the consideration of an agent's mental state.

We hypothesize that carriers of the C-allele make a more emotionally driven moral decision which should become apparent by higher blameworthiness ratings. This assumption is based on the suggestion that C-allele carriers are more affected by negative consequences and emotions arising from a committed harm to an innocent person.

2. Methods

2.1. Participants

N = 154 Caucasian participants ($n = 28$ males, $n = 122$ females, $n = 4$ not reported) provided buccal swaps for genotyping the OXTR rs2268498 polymorphism. All participants (age $M = 21.85$, $SD = 4.5$) were psychology students at the University of Bonn. Written informed consent to participate was obtained prior to the study. Additionally, subjects were screened for possible present or former neurological and psychiatric disorders which led to an exclusion of the study. The study was approved by the local ethics committee of the University of Bonn.

2.2. Genotyping

DNA was extracted from buccal cells. Automated purification of genomic DNA was conducted by means of the MagNA Pure[®]LC system using a commercial extraction kit (MagNA Pure LC DNA

isolation kit; Roche Diagnostics, Mannheim, Germany). Genotyping of OXTR rs2268498 was performed via real time PCR using fluorescence melting curve detection analysis by means of the Light Cycler System 1.5 (Roche Diagnostics, Mannheim, Germany). The primers and hybridization/simple probes (TIB MOLBIOL, Berlin, Germany) were as follows:

Forward primer: 5'-ACCGGTCAGGGGCTCATA-3';
 Reverse primer: 5'-TGTGCAATCTGAGGGTTCAA-3';
 Anchor hybridization probe: 5'-LCRed640-CTGGATGAAGGCA-GATTTTCCCTATGA-phosphate-3';
 Sensor hybridization probe [C]: 5'-AAAACACC_GCCTACCCCACG-fluorescein-3'.

2.3. Moral judgments

For a detailed description of the task see Young and Saxe (2009). Participants were presented the same moral dilemmas (24 short stories) in a German version. Each story consisted of four different parts: The four parts were (a) Background information (b) Foreshadow (c) Protagonist's belief (d) Story outcome. The background information introduced the setting and topic of the dilemma. The foreshadowing information anticipated the outcome. Participants were explicitly told that the foreshadowing information was only provided to them and was not available for the story's protagonist. The protagonist's belief pointed to the protagonist's behavior, anticipation and intention regarding the circumstances independent of the actual event and outcome. The story's outcome illustrated the consequences of the protagonist's belief and resulting behavior. Stories varied in the kind of outcome (negative vs. neutral) and in the protagonist's belief (negative: protagonists believed that they were causing harm vs. neutral: protagonists believed that they were causing no harm). Each story was foreshadowed (negative vs. neutral) anticipating the story's outcome. Negative outcomes were always foreshadowed by a negative anticipation, neutral outcomes by neutral anticipations. Outcomes were independent of the protagonist's belief. Negative as well as neutral outcomes were preceded by negative as well as neutral beliefs. Thus, four different kinds of stories result (see Table 1; see also Fig. 1):

Each of the 24 stories, differing with regards to their contents, was available in the four different versions. Participants read all 24 stories but each single story was only presented once in one of the four different versions. Which story was presented in which version was completely randomized so that each of the four story types was presented six times ($6 \times 4 = 24$ short stories). In the study of Young and Saxe (2009) participants read the stories during an fMRI scan so that we adapted the presentation of stories. Each story was presented in total on one slide on a 19 in. computer screen. Participants were told that they had to press the spacebar after reading a story. Then, the judgment-question was presented on the next slide, requiring participants to judge how much blame the protagonists deserve for their behavior. For the exemplary story in Fig. 1, the question was "How much blame does John deserve for keeping his mouth shut?" Additionally, a five-point Likert-scale was presented running from 1 (none) to 5 (a lot). Subjects answered the question by pressing the corresponding keys on

the keyboard. Then, the next story was presented. Stories were presented in a randomized order. Participant's ratings were recorded as blameworthiness ratings separately for the four different kinds of stories.

2.4. Statistical analyses

First, we focused on differences in ratings of the blameworthiness of the protagonist's behavior in the different kind of stories. Additional t-tests were conducted to test for possible gender differences in ratings. Because in story type (4) neither any harm is attempted nor committed, this story type is not further considered in order to analyze the blameworthiness ratings in detail separately for the different kinds of harm. To test for possible rating differences in the three remaining harm-conditions (intended and committed harm; accidentally committed harm; attempted but failed harm) a repeated measure ANOVA and additional t-tests were conducted. Effects of the rs2268498 allelic groups (C+ vs. C-) on the three different blameworthy ratings were analyzed by three separate ANOVAs (one ANOVA for each harm condition). Furthermore, a multivariate ANOVA was conducted to test the effect of the rs2268498 on moral judgments in general. No gender differences in the ratings of intentional, attempted failed and accidental harm occurred (all $p > .25$). Age was not correlated to any of the ratings (all $p > .14$). Therefore both gender and age do not need to be controlled for in the following analyses. Bonferroni-corrections were conducted in order to adjust for multiple testing.

3. Results

3.1. Genetics

The observed genotype frequencies in our sample were as follows: TT: $n = 37$; CT: $n = 84$; CC: $n = 33$. Genotype frequencies were in Hardy-Weinberg-Equilibrium ($\chi^2 = 1.29$, $df = 1$, $p > .05$). Because higher mRNA expression for the oxytocin receptor was found in C-allele carriers (unpublished data of our own workgroup) and following Montag et al. (2011) subjects were grouped into C-allele carriers (C+ group) and non-carriers (C- group) resulting in $n = 117$ C+ carriers and $n = 37$ C- carriers (homozygous for the T-allele). Gender was equally distributed across the different genotypes ($\chi^2 = 2.68$, $df = 2$, $p = .262$).

3.2. Moral judgments

The repeated measure analysis of variance with the ratings of the three different harm conditions yielded a significant effect of the within-subject factor ($F_{(2,312)} = 414.03$, $p < .001$, $\eta^2 = .726$). Subjects rated intentionally committed harm as most blameworthy ($M = 4.5$, $SD = 0.42$) followed by attempted but failed harm ($M = 4.15$, $SD = 0.63$). The lowest scores were observed for accidental harm ($M = 2.78$, $SD = 0.74$). T-tests revealed that all three ratings differed significantly (intentional vs. attempted failed harms: $t = 7.45$, $df = 153$, $p < .001$; attempted failed vs. accidental harms: $t = 18.65$, $df = 153$, $p < .001$; accidental harms vs. intentional harms: $t = -25.20$, $df = 153$, $p < .001$).

Table 1
Design of the four different kinds of dilemmas.

Story type	Back-ground information (BI)	Protagonist's belief	Foreshadow	Story outcome	Harm
(1)	BI	Negative	Negative	Negative	Intended and committed harm
(2)	BI	Neutral	Negative	Negative	Accidentally committed harm
(3)	BI	Negative	Neutral	Neutral	Attempted but failed harm
(4)	BI	Neutral	Neutral	Neutral	No harm at all

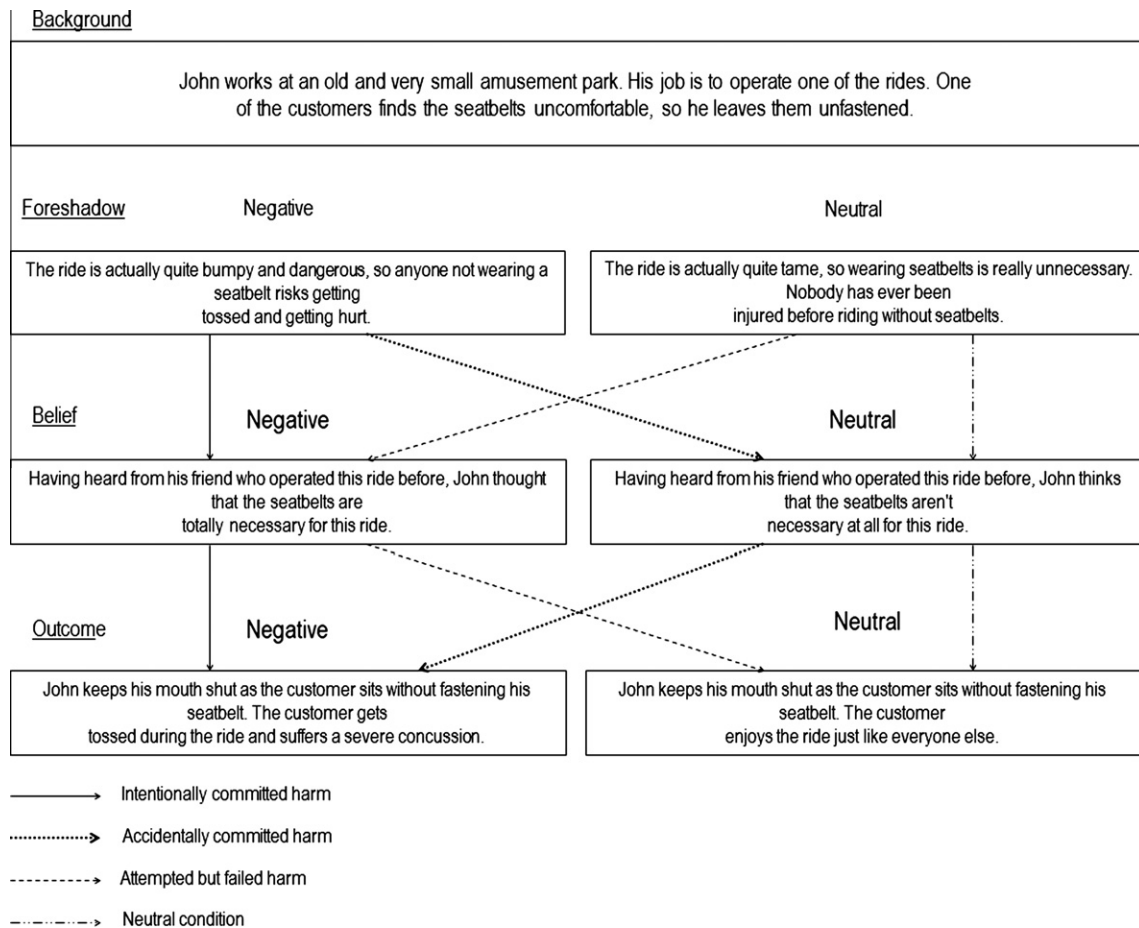


Fig. 1. Design of the four different kinds of moral dilemmas illustrated by an exemplary story (see Young and Saxe, 2009).

3.3. Effects of the OXTR rs2268498 on moral judgments

Three ANOVAs were conducted separately for the ratings of intentional harms, attempted but failed harms and accidental harms as dependent variables. The allelic groups of the OXTR rs2268498 (C+ vs. C− group) were entered as between-subject factor in each analysis.

The analyses yielded a significant effect of the rs2268498 allelic groups on the ratings of accidentally committed harms ($F_{(1,152)} = 11.49, p = .001, \eta^2 = .07$). Carriers of at least one C-allele (C+ group: CC and CT genotype carriers) rated accidentally committed harms as significantly more blameworthy than TT genotype carriers (C+: $M = 2.9, SD = .71$; C−: $M = 2.43, SD = .73$).

No further significant effects could be observed neither for intended and committed harm ($F_{(1,152)} = .045, p > .05, \eta^2 < .001$) nor for intended but failed harm ($F_{(1,152)} = .498, p > .05, \eta^2 = .003$).

The multivariate ANOVA with all three ratings of harm as dependent variables yielded an overall effect of OXTR rs2268498 (C+ vs. C−) on moral judgments ($F_{(3,150)} = 3.88, p = .011, \eta^2 = .072$). On a descriptive level there were no differences between C-allele carriers and non-carriers regarding the blameworthiness-ratings for intended and committed harm (C+: $M = 4.5, SD = .42$; C−: $M = 4.51, SD = .45$). C-allele carriers rated intended but failed harms descriptively as more blameworthy than non-carriers of the C-allele (C+: $M = 4.17, SD = .58$; C−: $M = 4.08, SD = .77$).

4. Discussion

The pivotal role of the neuropeptide oxytocin and the gene coding for the oxytocin receptor (OXTR) for social behavior has been

highlighted by pharmacological, knock-out and molecular genetic association studies. Individual differences in oxytocin and the OXTR functionality have been linked to a variety of social behaviors such as pair bond formation, affiliation, maternal care (reviewed by Young & Wang, 2004), trust (Kosfeld et al., 2005), gloating (schadenfreude) (Shamay-Tsoory et al., 2009), altruism (De Dreu et al., 2010), and mind-reading (Domes et al., 2007). Human morality has been shown to have its origin in emotional processes that lead people to care about the welfare of others (Greene & Haidt, 2002). Furthermore, the role of reasoning processes including the consideration of the agent's intention has been highlighted in moral decision making research (e.g. Knobe, 2005; Young et al., 2007). In the present study we were able to provide the first evidence for an oxytocinergic genetic contribution to moral judgments, especially to ratings of blameworthiness of accidentally committed harm. A recent brain-imaging study on moral judgment identified a specific brain area, the right temporo parietal junction, whose activation correlated significantly with the extent to which moral judgments for committed harm are mitigated by taking the agent's mental state into account (Young & Saxe, 2009). Thus, the authors demonstrated individual differences in moral judgments and were able to explain them due to differences in brain activation. With our present results we extend neuroscientific research on moral decision making by providing the first evidence for a genetic contribution to moral judgments. The polymorphism under investigation has previously been associated with trust (unpublished data of our own workgroup) and negative emotionality (Montag et al., 2011). The C allele has been linked to higher mRNA expression for the oxytocin receptor and in interaction with the short allele of the 5-HTTLPR polymorphism to higher Fear and Sadness scores of

the Affective Neuroscience Personality Scales as well as on the underlying factor negative emotionality. In this work it has been hypothesized that carriers of the TT-genotype, a variant associated with lower mRNA expression (potentially resulting in lower oxytocin receptor density), show a more efficient oxytocin signaling, because smaller numbers of receptors can be more easily occupied (Shankaran et al., 2007). In our present study, carriers of the C allele rated accidentally committed harm as significantly more blameworthy than homozygous T allele carriers. Given the association of this polymorphism with negative emotionality (Montag et al., 2011), the present findings suggest that the C-allele carriers rely more strongly on negative emotions when solving a moral dilemma dealing with accidental harm. Following this idea, carriers of the TT-genotype are less affected by the negative consequences of committed harm (hence negative emotions) and depend more on rational processes when being confronted with the same moral dilemma. The present interpretation of the results must be treated with caution, because the study by Montag et al. (2011) could not demonstrate a main effect of rs2268498 on negative emotionality.

The distinction between an emotional and a rational process plays a pivotal role in judging the blameworthiness of an agent in an accidentally committed harm scenario. In law tradition, a conviction is based on both a committed harm to another person and on the intention to harm (Young et al., 2007). In cases of accidentally committed harm, the intention to harm another person is absent. Those cases require a trade-off between the severity of the committed harm and the lack of volition/planning to harm. Therefore, emotionality and rationality need to be combined to come to a judgment in cases of accidentally harm.

As mentioned above, oxytocin is involved in a great variety of facets of social behavior. This might be due to its interplay with different hormones and neurotransmitters, like vasopressin, serotonin and dopamine within the brain (Skuse & Gallagher, 2009; Vacher, Frétier, Crémignon, Calas, & Hardin-Pouzet, 2002). In the present study we focused solely on the role of a functional variant of the OXTR gene, and we do not want to exclude the possibility of an interaction between different variants of the OXTR gene with variants of, for example, dopamine-relevant genes to explain more variance in individual differences regarding moral decision making. However, research on biological underpinnings of moral judgment and moral decision making is a very new field in the scope of cognitive, affective and social neuroscience. Considering the mounting evidence regarding oxytocin and its role for affective and social behavior relevant in the light of perspective taking and moral judgment it is quite reasonable to focus on variants of the OXTR gene as a starting point.

Behaviorally, we were able to replicate the results by Young and Saxe (2009) regarding moral judgments. In both studies subjects rated intentional harm as most blameworthy followed by attempted but failed harm. The lowest ratings were observable for accidental harm. Interestingly, we found a significant effect of the OXTR rs2268498 only on moral judgments regarding the blameworthiness of accidental harm. Ratings for intentional harm had the lowest variance and ranged only from 3 to 5 on the 5-point Likert scale. However, ratings for accidentally committed harm ranged from 1 to 5 with the highest variance. The consideration of the ratings' range and variances points to a general accordance of people to blame intentionally committed harm but to diverse views of how to treat agents causing harm accidentally and unknowingly. Should we exculpate a person for committing harm unknowingly and/or unintentionally? 'Ignorance is no excuse' is a popular response. Our results suggest that this answer will not be universally accepted by everyone. And a common variation on the OXTR gene can explain why some people agree while others do not.

Our study has some limitations. Most of our participants were female psychology students. Results from a recent study

demonstrated that moral judgments are at least partially gender dependent (Fumagalli et al., 2010). Although we found no gender differences, this can be due to our relatively small male subsample. Another point is that our present study focused only on a quite special aspect of moral judgment, namely the consideration of agent's mental state in the judgment of blameworthiness of committed harm. Further research is needed to investigate the effect of genetic variations on classical personal and non-personal dilemmas focusing on the trade-off between an emotional aversive committed (and intended) harm and a utilitarian maximization of aggregated welfare. As mentioned above, future research should also investigate interaction effects between genes relevant for different neurotransmitters, such as the interaction between oxytocin and dopamine or serotonin relevant genes. This is of importance, because complex phenotypes as investigated in the present study are influenced by a large number of genes with small effect sizes (Craig & Plomin, 2006). In the present study rs2268498 explained 7% of the variance of the blameworthiness ratings in the accidental harm condition, which can be considered a large genetic effect. Usually effect sizes of polymorphisms are much smaller (about 1–2%; Markett, Montag, & Reuter, 2011; Montag et al., 2010; Walter, Montag, Markett, & Reuter, 2011), but these numbers are also strongly influenced by the sample size, which is rather small in the current study. We assume that the real effect size of rs2268498 would decrease towards 1 or 2% if the sample size under investigation would have been considerably higher.

It should be pointed out that our study has some important strengths. We investigated a very homogenous sample with respect to age, education and cultural/ethnic background, which are factors that can have a strong impact on moral judgments (e.g. Chap, 1985–1986; Cohen & Rozin, 2001; Kim & Cohen, 2010; Proios & Doganis, 2006). Thus, it is noteworthy that we found individual differences in ratings regarding the blameworthiness of accidentally committed harm. Furthermore, we are able to partially explain those differences by one certain genetic variation on the OXTR gene. This finding may have strong implications for future research on moral decision making as well as for our everyday life. Just consider the saying 'ignorance is no excuse'.

Acknowledgments

We thank Smiljana Mutic and Alisa M. Klein for their help in data collection.

This study was supported by grants from the German Research Association to MR (Grant Nos. DFG-RE 1692/4-1).

References

- Avis, J., & Harris, P. (1991). Belief-desire reasoning among Baka children: Evidence for a universal conception of mind. *Child Development*, 62, 460–467.
- Cesarini, D., Dawes, C. T., Fowler, J. H., Johannesson, M., Lichtenstein, P., & Wallace, B. (2008). Heritability of cooperative behavior in the trust game. *PNAS*, 105(10), 3721–3726.
- Chap, J. B. (1985–1986). Moral judgment in the middle and late adulthood: The effect of age-appropriate moral dilemmas and spontaneous role-taking. *International journal of aging and human development*, 22(3), 161–172.
- Cohen, A. B., & Rozin, P. (2001). Religion and the morality of mentality. *Journal of Personality and Social Psychology*, 81, 697–710.
- Craig, I., & Plomin, R. (2006). Quantitative trait loci for IQ and other complex traits: Single-nucleotide polymorphism genotyping using pooled DNA microarrays. *Genes, Brain, and Behavior*, 5, 32–37.
- De Dreu, C. K., Greer, L. L., Handgraaf, M. J., Shalvi, S., Van Kleef, G. A., Baas, M., et al. (2010). The neuropeptide oxytocin regulates parochial altruism in intergroup conflict among humans. *Science*, 328(5984), 1408–1411.
- Decety, J., & Sommerville, J. A. (2003). Shared representations between self and other: A social cognitive neuroscience view. *Trends in Cognitive Sciences*, 7(12), 527–533.
- Domes, G., Heinrichs, M., Michel, A., Berger, C., & Herpertz, S. C. (2007). Oxytocin improves "mind-reading" in humans. *Biological Psychiatry*, 61(6), 731–733.

- Fisher-Shofty, M., Shamay-Tsoory, S. G., Harari, H., & Levkovitz, Y. (2009). The effect of intranasal administration of oxytocin on fear recognition. *Neuropsychologia*, 48(1), 179–184.
- Fumagalli, M., Ferrucci, R., Mameli, F., Marceglia, S., Mrakic-Spota, S., Zago, S., et al. (2010). Gender-related differences in moral judgments. *Cognitive processing*, 11(3), 219–226.
- Greene, J., & Haidt, J. (2002). How (and where) does moral judgment work? *Trends in Cognitive Sciences*, 6(12), 517–523.
- Greene, J. D., Nystrom, L. E., Engell, A. D., Darley, J. M., & Cohen, J. D. (2004). The neural bases of cognitive conflict and control in moral judgment. *Neuron*, 44(2), 389–400.
- Guastella, A. J., Einfeld, S. L., Gray, K. M., Rinehart, N. J., Tonge, B. J., Lambert, T. J., et al. (2009). Intranasal oxytocin improves emotion recognition for youth with autism spectrum disorders. *Biological Psychiatry*, 67(7), 692–694.
- Haidt, J. (2001). The emotional dog and its rational tail: A social intuitionist approach to moral judgment. *Psychological Review*, 108, 814–834.
- Higashida, H., Lopatina, O., Yoshihara, T., Pichugina, Y. A., Soumarokov, A. A., Munesue, T., et al. (2010). Oxytocin signal and social behavior: Comparison among adult and infant oxytocin, oxytocin receptor and CD38 knockout mice. *Journal of Neuroendocrinology*, 22(5), 373–379.
- Israel, S., Lerer, E., Shalev, I., Uzevovsky, F., Riebold, M., Laiba, E., et al. (2009). The oxytocin receptor (OXTR) contributes to prosocial fund allocations in the dictator game and the social value orientation task. *PLoS ONE*, 4, e5535.
- Kim, Y. H., & Cohen, D. (2010). Information, perspective, and judgments about the self in face and dignity cultures. *Personality and Social Psychology Bulletin*, 36(4), 537–550.
- 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(1), 53–67.
- Knafo, A., Zahn-Waxler, C., Van Hulle, C., Robinson, J. L., & Rhee, S. H. (2008). The developmental origins of a disposition towards empathy: Genetic and environmental contributions. *Emotion*, 8(6), 737–752.
- Knobe, J. (2005). Theory of mind and moral cognition: Exploring the connections. *Trends in cognitive sciences*, 9(8), 379–9.
- Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U., & Fehr, E. (2005). Oxytocin increases trust in humans. *Nature*, 435(7042), 673–676.
- Lee, H. J., Caldwell, H. K., Macbeth, A. H., & Young, W. S. 3rd., (2008). Behavioural studies using temporal and spatial inactivation of the oxytocin receptor. *Progress in Brain Research*, 170, 73–77.
- Lerer, E., Levi, S., Salomon, S., Darvasi, A., Yirmiya, N., & Ebstein, R. P. (2008). Association between the oxytocin receptor (OXTR) gene and autism: Relationship to Vineland adaptive behavior scales and cognition. *Molecular Psychiatry*, 13(10), 980–988.
- Markett, S., Montag, C., & Reuter, M. (2011). The nicotinic acetylcholine receptor gene CHRNA4 is associated with negative emotionality. *Emotion*, 11, 450–455.
- Montag, C., Fiebach, C. J., Kirsch, P., & Reuter, M. (2011). Interaction of 5-HTTLPR and a variation on the oxytocin receptor gene influences negative emotionality. *Biological Psychiatry*, 69, 601–603.
- Montag, C., Markett, S., Basten, U., Stelzel, C., Fiebach, C., Canli, T., et al. (2010). Epistasis of the DRD2/ANKK1 Taq 1a and the BDNF Val66Met polymorphism impacts novelty seeking and harm avoidance. *Neuropsychopharmacology*, 35, 1860–1867.
- Neumann, I. D. (2008). Brain oxytocin: A key regulator of emotional and social behaviours in both females and males. *Journal of Neuroendocrinology*, 20(6), 858–865.
- Proios, M., & Doganis, G. (2006). Age and education in moral judgment of participants in team sports. *Perceptual and motor skills*, 102(1), 247–253.
- Sabbagh, M. L., Xu, F., Carlson, S. M., Moses, L. J., & Lee, K. (2006). The development of executive functioning and theory of mind. A comparison of Chinese and US preschoolers. *Psychological Science*, 17(1), 74–81.
- Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in “theory of mind”. *Neuroimage*, 19(4), 1835–1842.
- Shamay-Tsoory, S. G., Fischer, M., Dvash, J., Harari, H., Perach-Bloom, N., & Levkovitz, Y. (2009). Intranasal administration of oxytocin increases envy and schadenfreude (gloating). *Biological Psychiatry*, 66(9), 864–870.
- Shankaran, H., Wiley, H. S., & Resat, H. (2007). Receptor downregulation and desensitization enhance the information processing ability of signaling receptors. *BMC Systems Biology*, 1, 48.
- Skuse, D. H., & Gallagher, L. (2009). Dopaminergic-neuropeptide interactions in the social brain. *Trends in Cognitive Sciences*, 13(1), 27–35.
- Vacher, C. M., Frétier, P., Crémion, C., Calas, A., & Hardin-Pouzet, H. (2002). Activations by serotonin and noradrenalin of vasopressin and oxytocin expression in the mouse paraventricular and supraoptic nuclei. *Journal of Neuroscience*, 22(5), 1513–1522.
- Walter, N. T., Montag, C., Markett, S. A., & Reuter, M. (2011). Interaction effect of functional variants of the BDNF and DRD2/ANKK1 gene is associated with alexithymia in healthy human subjects. *Psychosomatic Medicine*, 73(1), 23–28.
- Wimmer, H., & Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition*, 13(1), 103–128.
- Wu, S., & Keysar, B. (2007). The effect of culture on perspective taking. *Psychological Science*, 18(7), 600–606.
- Young, L., Cushman, F., Hauser, M., & Saxe, R. (2007). The neural basis of the interaction between theory of mind and moral judgment. *PNAS*, 104(2), 8235–8240.
- Young, L., & Saxe, R. (2009). Innocent intentions: A correlation between forgiveness for accidental harm and neural activity. *Neuropsychologia*, 47, 2065–2072.
- Young, L. J., & Wang, Z. (2004). The neurobiology of pair bonding. *Nature Neuroscience*, 7(10), 1048–1054.
- Yuill, N., & Perner, J. (1988). Intentionality and knowledge in children's judgments of actor's responsibility and recipient's emotional reaction. *Developmental Psychology*, 24(3), 358–365.
- Zelazo, P. D., Helwig, C. C., & Lau, A. (1996). Intention, act, and outcome in behavioral prediction and moral judgments. *Child Development*, 67, 2478–2492.