LEBS
Vol. 17 No. 2 (2026) 55–58
Letters on Evolutionary Behavioral Science

Oxytocin Receptor Polymorphism rs9840864 and Childhood Parental Attentiveness in Relation to Moral Foundations

Keiko Ishii[1,*], Masahiro Matsunaga[2], Yasuki Noguchi[3], Hidenori Yamasue[4], Yohsuke Ohtsubo[1]

[1]The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-0033, Japan

[2]Aichi Toho University, 3-11 Heiwagaoka, Meito-ku, Nagoya 465-0097, Japan

[3]Kobe University, 1-1 Rokkodai-cho, Nada-ku, Kobe 657-8501, Japan

[4]Hamamatsu University School of Medicine, 1-20-1 Handayama, Chuo-ku, Hamamatsu 431-3125, Japan

[*]Author for correspondence (ishiik@l.u-tokyo.ac.jp)

Previous research suggests that the distinctive frequency of the OXTR rs9840864 C allele in East Asia may reflect selection pressure exerted by cultural tightness. Building on this possibility, the present study reanalyzed Japanese data to examine whether this polymorphism is associated with individual differences in moral foundations and whether it interacts with childhood parental attentiveness to shape moral concern. Data were drawn from 416 Japanese undergraduates who completed measures of moral foundations and parental attentiveness and whose OXTR rs9840864 genotype was assessed. Main effects of OXTR were generally weak. However, lower parental attentiveness was associated with reduced concern for fairness overall, and for care specifically the detrimental effect of lower parental attentiveness emerged only among GG participants. These findings provide limited preliminary evidence that OXTR rs9840864 may moderate the association between childhood family environment and care-related moral concern.

Keywords
OXTR rs9840864, cultural tightness, moral judgment, parental attentiveness

Introduction

Theories of gene-culture coevolution propose that social and cultural environments exert selective pressure on the intergenerational transmission of genes, and that, as the frequency of a given genotype rises within a population, the defining features of that environment are correspondingly reinforced (Feldman & Laland, 1996; Richerson & Boyd, 2005). A representative example is regional variation in lactose tolerance among adults. In cultural environments where pastoral (dairying) practices have developed, individuals carrying the gene that enables adults to digest milk (i.e., the lactase persistence gene) may obtain more calories than non-carriers and, as a result, live longer and leave more offspring. Under such conditions, the lactase persistence gene confers relatively high fitness, making it more likely to be passed on to subsequent generations. As the proportion of carriers increases, milk consumption itself rises within the region, and the culture evolves accordingly.

Building on this framework, prior research has examined how genotype proportions at a given genetic polymorphism vary across countries and regions, relating these proportions to the norms and behavioral patterns that predominate in each area, an approach that has produced a range of suggestive findings. For example, the frequency of the short allele of the serotonin transporter polymorphism (5-HTTLPR), which has increased against the backdrop of historical pathogen prevalence, is associated with greater collectivism and lower anxiety and rates of mental disorder at the global level (Chiao & Blizinsky, 2010). Additionally, the frequency of the short allele of 5-HTTLPR is associated with the justifiability of morally relevant behavior (Mrazek et al., 2013) via cultural tightness-looseness (Gelfand et al., 2011), a cultural dimension that shapes individuals' psychological and behavioral tendencies over time. A notable limitation of this approach, however, is that the pathway linking genotype to norms and behavioral patterns remains unclear, given the inherent complexity of the latter.

To address this gap, Lee et al. (2022) introduced the concept of "neuroendophenotypes," which infers intermediate brain-based phenotypes of a set of genes from the extent to which their polymorphisms are expressed in specific brain regions. To demonstrate this process of gene-culture coevolution using neuroendophenotypes, they estimated oxytocin receptor (OXTR) expression in specific brain regions and examined whether it varied as a function of cultural tightness-looseness (Gelfand et al., 2011). Oxytocin is a peptide hormone whose receptors are expressed not only in peripheral tissues such as the uterus and mammary glands but also in brain regions including the amygdala, hippocampus, nucleus accumbens, and prefrontal cortex, where they regulate emotional functions (e.g., reducing anxiety and fear) and social behaviors (e.g., empathy and trust). According to Gelfand et al. (2011), regions exposed to greater ecological threat, including pathogens, high population density, resource scarcity, and intergroup territorial conflict, tend to develop tighter social norms and lower tolerance for deviant behavior. This tightness is thought to reflect the need for collective defense in such regions: collectivist traits such as ethnocentrism and conformity likely functioned as

doi: 10.5178/lebs.2026.139
Received 21 August 2026.
Accepted 05 September 2026.
Published online 14 September 2026.

effective means of ensuring survival under threat.

Lee and colleagues examined 70 OXTR polymorphisms across 10 brain regions (e.g., anterior cingulate cortex, prefrontal cortex, caudate nucleus). Comparing OXTR expression levels across five world regions (Africa, East Asia, South Asia, Europe, and the Americas), they found the clearest regional differences in the anterior cingulate cortex, where OXTR expression correlated positively with both country-level ecological threat and tightness of norms. While the two polymorphisms most closely associated with this anterior cingulate cortex expression showed no regional variation, a polymorphism (rs9840864) in linkage disequilibrium with them did: its minor C allele had, in fact, become the major allele in East Asia (China, Japan, Vietnam). This suggests that the OXTR genotype has undergone positive selection in East Asian populations, reflecting ecological threat and the tightness of social norms.

The Present Research

If the distinctive frequency of the OXTR rs9840864 C allele in East Asia reflects a selection pressure exerted by cultural tightness, does this genetic variation also correspond to individual differences in psychological tendencies related to the tightness of social norms? To address this question, the present study reanalyzed Japanese data collected as part of our broader research project on the association between psychological traits and gene polymorphisms (Ishii et al., 2021). We focused on the relationship between OXTR rs9840864 and moral foundations, one of the measures in that project most conceptually related to the tightness of norms.

In addition, we examined parental attentiveness during childhood as a related variable. Childhood neglect has been associated with Machiavellianism (Láng & Lénárd, 2015), a trait characterized by deceptive and manipulative tendencies and reduced moral concern, including weaker endorsement of moral foundations (Karandikar et al., 2019). Attachment avoidance, which has also been linked to lower caregiver sensitivity (Madigan et al., 2024), is associated with weaker moral concern for care and fairness (Koleva et al., 2014). In addition, recent evidence suggests that parental warmth plays an important role in the development of morality (Wilke & Rademacher, 2025). Accordingly, we expected lower parental attentiveness to be associated with weaker moral intuitions. For exploratory purposes, we also examined whether the detrimental effects of parental attentiveness were moderated by OXTR rs9840864. Given prior findings on gene × environment interactions (e.g., Zheng et al., 2020), we speculated that these effects might be stronger in individuals carrying the OXTR rs9840864 G allele, which is relatively rare in Japan.

Methods

Participants and Procedure

Japanese data were drawn from Ishii et al. (2021), which consist of 416 undergraduates at Kobe University (217 females and 198 males, one unidentified; M_{age} = 19.47, *SD* = 1.24). They were recruited through a psychology subject pool. One participant who withdrew from the study due to illness and did not complete the parental attentiveness questionnaire was excluded from the following analysis. The current research was reviewed and approved by the ethics committee at Graduate School of Humanities, Kobe University and adhered to the Declaration of Helsinki and the relevant guidelines and regulations. It was not pre-registered. Data are posted in https://osf.io/qn6e4.

The participants provided a written informed consent at the beginning of the study. All responses were confidential. As reported in Ishii et al. (2021), participants completed questionnaires with a wide range of topics, such as self, emotion, cognition, and interpersonal behaviors. Measures used were translated and backtranslated between Japanese and English to ensure cross-cultural equivalence. The following measures were relevant to this research.

Moral Foundations

Participants completed the moral foundation questionnaire (Graham et al., 2011), consisting of 15 moral relevance items and 15 moral judgment items related to the five domains of morality (care, fairness, loyalty, authority, and purity). For the moral relevance items, the participants were asked to indicate using a six-point Likert-type scale the extent to which each statement was relevant to their decision about whether something was right or wrong (0 = "not at all" to 5 = "extremely"). For the moral judgment items, the participants were asked to indicate using a six-point Likert-type scale the extent to which they agreed (0 = "strongly disagree" to 5 = "strongly agree") with each statement. Descriptive statistics and internal consistency for each foundation were as follows: care (M = 3.36, SD = 0.68, α = .64), fairness (M = 3.25, SD = 0.59, α = .58), loyalty (M = 2.44, SD = 0.65, α = .55), authority (M = 2.66, SD = 0.68, α = .63), and purity (M = 2.32, SD = 0.60, α = .49).

Parental Attentiveness

Participants also reported the degree to which their father and mother, respectively, had paid attention to them during childhood (1 = not at all, 6 = very much).

Genotyping

We extracted genomic DNA from nail samples using ISOHAIR kits (Nippon Gene Co., Ltd., Tokyo, Japan). We genotyped the SNP marker for OXTR rs9840864 using TaqMan SNP Genotyping Assays (Thermo Fisher Scientific Inc., Waltham, Massachusetts). We conducted all polymerase chain reactions (PCR) and allelic discrimination reactions by using the StepOne Plus™ Real-Time PCR System (Thermo Fisher Scientific, Inc.).

Results

The distribution of OXTR rs9840864 polymorphism was not deviant from that based on the Hardy-Weinberg equilibrium, 176 participants were CC homozygotes, 191 were CG heterozygotes, and 42 were GG homozygotes, $\chi^2(1) = 0.88$, $p = .35$. Six participants whose genotype could not be determined were excluded from the analyses reported below.

For each moral foundation, we conducted a multiple regression analysis with two dummy-coded variables representing OXTR rs9840864 genotype (OXTR1: CG [1] vs. GG [0]; OXTR2: CC [1] vs. GG [0]), mean-centered

parental attentiveness (averaged across the two parent-report items), and sex (male = 0, female = 1) entered as predictors at Step 1. At Step 2, we entered the two genotype × parental attentiveness interaction terms to test whether genotype moderated the association between parental attentiveness and moral foundations. The overall model was significant only for care and fairness at both steps (see Supplemental Materials for the full regression results). The significance level was set at 0.01 based on the five separate analyses conducted to test the effect of parental attentiveness.

No significant main effects of OXTR1 or OXTR2 emerged for either care or fairness. Participants who reported lower parental attentiveness also reported lower care (b = .11, p = .02) and lower fairness (b = .13, p < .001), although only the latter association was statistically significant (Tables S1 and S2). When the genotype × parental attentiveness interaction terms were added, only the model predicting care indicated a moderating effect of genotype (OXTR1 × attentiveness: b = −.35, p = .03; OXTR2 × attentiveness: b = −.40, p = .01). Simple slope analyses indicated that the association between parental attentiveness and care was significant only among GG participants (b = .45, p = .003), and not among CG (b = −.07, p = .43) or CC (b = −.12, p = .24) participants.

Discussion

This study examined whether OXTR rs9840864, a polymorphism whose C allele has become the majority variant in East Asian populations, corresponds to individual differences in moral foundations and interacts with childhood parental attentiveness to shape moral concern. Lower parental attentiveness was associated with reduced concern for fairness overall, but for care, this association emerged only among GG participants; CG and CC participants showed no such dependence.

The results suggest that GG participants may be particularly vulnerable to the adverse effects of low parental attentiveness on the development of care-related moral values, whereas the C allele, the major allele in this and other East Asian samples, may be protective against such effects. This pattern raises the possibility that C allele carriers develop moral concern for others through pathways that are less contingent on the immediate family environment, including other parenting-related factors such as disciplinary strategies and broader contextual influences such as school, religious, and political affiliations. Specifically, if moral development in tighter cultural contexts is scaffolded more by strong, pervasive social norms than by parenting sensitivity alone, individuals whose genotype is more prevalent in such contexts (i.e., the OXTR rs9840864 C allele) may be comparatively buffered against variation in parental attentiveness. However, this possibility also suggests that future research should examine not only parental attentiveness but also these other factors, as well as their combined effects with OXTR rs9840864 genotype on morality.

Although this interaction pattern offers partial support for the broader gene-culture coevolution account proposed by Lee et al. (2022), who linked OXTR expression in the anterior cingulate cortex to the tightness of social norms against a backdrop of ecological threat, the main effects of OXTR were generally weak, and model fit for loyalty, authority, and purity was poor. Nevertheless, there was a tentative indication that CG individuals scored higher on purity than GG individuals (Table S5), although this pattern should be interpreted with considerable caution given the weak overall evidence. Because purity is widely classified as one of the binding moral foundations, reflecting concerns about sanctity, tradition, and conformity to shared norms rather than concerns centered on individual welfare (Graham et al., 2011), and because historical pathogen prevalence has also been linked to moral purity (Atari et al., 2022), future research should examine more directly whether the allele's population-level association with cultural tightness, itself shaped by ecological threat such as pathogen prevalence, corresponds to individual-level moral intuitions tied to norm maintenance. More direct evidence is also needed for the neuroendophenotype pathway proposed by Lee et al. (2022), in which OXTR expression differences linked to cultural tightness manifest behaviorally as norm-oriented moral cognition.

These findings should be interpreted with several caveats. The design was correlational and cross-sectional, drawing on a single reanalyzed dataset of Japanese undergraduates; accordingly, no causal claims about gene-environment influences on moral development can be made, and the direction of any developmental process remains speculative. In addition, the alternative possibility that individuals with stronger adherence to the care foundation may recall or perceive their parents as having been more attentive cannot be ruled out. Moreover, reflecting the characteristics of the sample, which may have received relatively greater parental investment, overall levels of parental attentiveness were high. This skewed distribution and limited variability may have attenuated the effects of childhood adversity on moral foundations. In addition, this study examined a single SNP among many possible functional variants in the OXTR gene. Although the neuroendophenotype framework offers a plausible mechanistic account linking this variant to cultural tightness, it does not resolve the broader question of how this polymorphism interacts with other genetic or epigenetic factors that may jointly shape moral attitudes. Finally, because the sample was restricted to Japanese undergraduates, it remains unclear whether these associations would generalize to other East Asian populations. Despite these limitations, this research points to a novel behavioral link between a neuroendophenotype-based candidate gene and moral judgment. This possibility warrants further testing in larger and more diverse samples, ideally incorporating cross-national comparisons that directly examine whether the association between genotype and moral foundations varies with a population's level of cultural tightness.

Acknowledgments

This study was financially supported by JSPS KAKENHI 22H01074.

Author contribution

Keiko Ishii: Conceptualization, Data curation, Funding acquisition, Investigation, Project administration, Writing – original draft, Writing – review and editing. **Masahiro Matsunaga:** Conceptualization, Data curation, Investigation. **Yasuki Noguchi:** Conceptualization, Investigation. **Hidenori Yamasue:** Conceptualization, Supervision. **Yohsuke Ohtsubo:** Conceptualization, Investigation, Project administration.

Ethical statement

The current research was reviewed and approved by the ethics committee at Graduate School of Humanities, Kobe University (No. 2014-10).

Data accessibility & program code

Data are posted in https://osf.io/qn6e4.

Supplementary material

Electronic supplementary materials are available online.

References

Atari, M., Reimer, N. K., Graham, J., Hoover, J., Kennedy, B., Davani, A. M., Karimi-Malekabadi, F., Birjandi, S., & Dehghani, M. (2022). Pathogens are linked to human moral systems across time and space. *Current Research in Ecological and Social Psychology*, *3*, Article 100060. https://doi.org/10.1016/j.cresp.2022.100060

Chiao, J. Y., & Blizinsky, K. D. (2010). Culture–gene coevolution of individualism–collectivism and the serotonin transporter gene. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1681), 529–537. https://doi.org/10.1098/rspb.2009.1650

Feldman, M. W., & Laland, K. N. (1996). Gene-culture coevolutionary theory. *Trends in Ecology & Evolution*, *11*(11), 453–457. https://doi.org/10.1016/0169-5347(96)10052-5

Gelfand, M. J., Raver, J. L., Nishii, L., Leslie, L. M., Lun, J., Lim, B. C., Duan, L., Almaliach, A., Ang, S., Arnadottir, J., Aycan, Z., Boehnke, K., Boski, P., Cabecinhas, R., Chan, D., Chhokar, J., D'Amato, A., Subirats Ferrer, M., Fischlmayr, I. C., … Yamaguchi, S. (2011). Differences between tight and loose cultures: A 33-nation study. *Science*, *332*(6033), 1100–1104. https://doi.org/10.1126/science.1197754

Graham, J., Nosek, B. A., Haidt, J., Iyer, R., Koleva, S., & Ditto, P. H. (2011). Mapping the moral domain. *Journal of Personality and Social Psychology*, *101*(2), 366–385. https://doi.org/10.1037/a0021847

Ishii, K., Masuda, T., Matsunaga, M., Noguchi, Y., Yamasue, H., & Ohtsubo, Y. (2021). A reexamination of the effects of culture and dopamine D4 receptor gene interaction on social orientation. *Psychologia*, *63*(2), 137–150. https://doi.org/10.2117/psysoc.2021-B014

Karandikar, S., Kapoor, H., Fernandes, S., & Jonason, P. K. (2019). Predicting moral decision-making with dark personalities and moral values. *Personality and Individual Differences*, *140*, 70–75. https://doi.org/10.1016/j.paid.2018.03.048

Koleva, S., Selterman, D., Iyer, R., Ditto, P., & Graham, J. (2014). The moral compass of insecurity: Anxious and avoidant attachment predict moral judgment. *Social Psychological and Personality Science*, *5*(2), 185–194. https://doi.org/10.1177/1948550613490965

Láng, A., & Lénárd, K. (2015). The relation between memories of childhood psychological maltreatment and machiavellianism. *Personality and Individual Differences*, *77*, 81–85. https://doi.org/10.1016/j.paid.2014.12.054

Lee, M., Lindo, J., & Rilling, J. K. (2022). Exploring gene-culture coevolution in humans by inferring neuroendophenotypes: a case study of the oxytocin receptor gene and cultural tightness. *Genes, Brain and Behavior*, *21*(3), Article e12783. https://doi.org/10.1111/gbb.12783

Madigan, S., Deneault, A. -A., Duschinsky, R., Bakermans-Kranenburg, M. J., Schuengel, C., van IJzendoorn, M. H., Ly, A., Fearon, R. M. P., Eirich, R., & Verhage, M. L. (2024). Maternal and paternal sensitivity: Key determinants of child attachment security examined through meta-analysis. *Psychological Bulletin*, *150*(7), 839–872. https://doi.org/10.1037/bul0000433

Mrazek, A. J., Chiao, J. Y., Blizinsky, K. D., Lun, J., & Gelfand, M. J. (2013). The role of culture–gene coevolution in morality judgment: Examining the interplay between tightness–looseness and allelic variation of the serotonin transporter gene. *Culture and Brain*, *1*(2–4), 100–117. https://doi.org/10.1007/s40167-013-0009-x

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. The University of Chicago Press.

Wilke, J., & Rademacher, A. (2025). True intraindividual change in moral self: The role of parental warmth in moral development during middle childhood. *International Journal of Behavioral Development*. Advance online publication. https://doi.org/10.1177/01650254251368791

Zheng, S., Masuda, T., Matsunaga, M., Noguchi, Y., Ohtsubo, Y., Yamasue, H., & Ishii, K. (2020). Oxytocin receptor gene (OXTR) and childhood adversity influence trust. *Psychoneuroendocrinology*, *121*, Article 104840. https://doi.org/10.1016/j.psyneuen.2020.104840