The Genetic Basis of Altruistic Behavior: Evidence from Quantitative Genetics and Molecular Genetics

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Abstract

Altruistic behavior refers to actions wherein individuals expend their own resources to help others. In recent years, researchers have focused on the genetic basis of altruistic behavior. Employing two research methodologies—quantitative genetics and molecular genetics—they have investigated the heritability of altruistic behavior, confirmed that altruistic behavior is indeed influenced by genetics, and identified four categories of candidate genes for altruism, including dopamine receptor genes, serotonin transporter genes, oxytocin receptor genes, and vasopressin receptor genes. Building upon this foundation, they have discussed the role of environment in the genetic influence on altruism. On the one hand, genes and environment are interrelated, jointly influencing altruistic behavior, which is known as gene-environment correlation; on the other hand, the effects of genes are moderated by environment, which is known as the differential susceptibility model. Future research should expand exploration of neurobiological systems, emphasize genome-wide studies, meta-analyses, and mechanistic investigations, and conduct systematic environmental intervention practices.

Full Text

The Genetic Basis of Altruistic Behavior: Evidence from Quantitative and Molecular Genetics

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Abstract

Altruistic behavior refers to actions in which individuals expend their own resources to help others. Recent research has examined the genetic underpinnings of altruism through two primary approaches: quantitative genetics and molecular genetics. Studies have investigated the heritability of altruistic behavior, confirming that genetics indeed influence altruism, and have identified four categories of candidate genes: dopamine receptor genes, serotonin transporter genes, oxytocin receptor genes, and vasopressin receptor genes. Building upon this foundation, researchers have explored how environmental factors moderate genetic influences on altruism. On one hand, genes and environments are correlated, jointly shaping altruistic behavior—this is known as gene-environment correlation. On the other hand, the expression of genetic effects is contingent upon environmental conditions, as described by the differential susceptibility model. Future research should expand exploration of neurobiological systems, emphasize genome-wide association studies, meta-analyses, and mechanistic investigations, and develop systematic environmental intervention practices.

Keywords: altruistic behavior, gene, gene-environment correlation, differential susceptibility

Introduction

The ancient adage "In times of crisis, put others before oneself" expresses high praise for altruistic behavior. Definitions of altruism range from narrow to broad. The narrow definition characterizes altruism as behavior that seeks no personal gain and aims solely to enhance others' welfare (Kaiser, 2017). However, altruistic actions often bring reputational and reciprocal benefits to the helper. For instance, evolutionary biologist Robert Trivers proposed the concept of reciprocal altruism, wherein individuals benefit mutually through cooperation (Trivers, 1971). Consequently, many researchers endorse a broader definition of altruism as behavior in which individuals expend their own resources to help others (Li et al., 2020; Wang et al., 2020), encompassing helping, cooperation, resource sharing, charitable donations, and volunteer activities (Batson, 2012; Hu, 2017).

Altruism is widely valued because of its profound social significance, promoting harmonious interpersonal relationships and social cohesion. Biologist Edward O. Wilson's multilevel selection theory posits that individual altruism enhances group adaptability, making altruistic groups more likely to survive and thrive during crises (Wilson & Wilson, 2007). Moreover, extensive recent research reveals that altruism also benefits the helper. Psychologically, altruistic behavior enhances well-being (Hui et al., 2020) and boosts self-efficacy (Crocker et al., 2017). Physiologically, altruism generates internal utility gains (Xie et al., 2017), such as alleviating acute and chronic pain (Wang et al., 2020) and reducing the risk of cardiovascular disease and mortality (Burr et al., 2018).

Given altruism's importance, identifying its determinants is essential. Despite

its significance for groups and individuals, substantial evidence demonstrates individual differences in altruistic behavior (e.g., Chong et al., 2019; Li et al., 2020; Zahn-Waxler et al., 1992). For example, research shows that infants as young as 14 months provide varying degrees of help and comfort to distressed individuals (Zahn-Waxler et al., 1992). At this young age, infants have likely not yet undergone socialization, suggesting these behavioral differences may stem from physiological factors, particularly genetic influences. However, no systematic review of the genetic basis of altruism has been conducted to date. This paper provides a comprehensive overview of the genetic foundations of altruistic behavior, reviewing evidence from quantitative and molecular genetics, analyzing environmental influences, and discussing future research directions.

2. Genetic Basis

Genetic research employs two primary methodologies: quantitative genetics and molecular genetics. Quantitative genetics uses research designs to disentangle environmental and genetic effects on behavior, yielding the proportion of variance attributable to genetics—heritability. Molecular genetics examines potential "altruism genes" at the molecular level.

2.1 Quantitative Genetics

The traditional approach to investigating the genetic basis of altruism involves estimating heritability. Behavioral variance in heritability can be estimated through twin studies, adoption studies, and stepfamily genetic designs. Twin studies, for example, compare correlations between monozygotic and dizygotic twins to decompose variance into genetic effects, shared environmental effects, and non-shared environmental effects, thereby determining whether a behavior is genetically influenced and, more importantly, the magnitude of that influence (Nes & Røysamb, 2017).

summarizes recent quantitative genetic studies examining the heritability of altruism and related constructs such as empathy. These studies consistently demonstrate that altruistic behavior is genetically influenced. Matthews et al. (1981) pioneered this approach by investigating 230 twin pairs aged 42-57, finding high heritability for empathic concern (0.72)—a key mechanism underlying altruism (de Waal, 2008). Subsequent research has examined altruism heritability across diverse cultures, age groups, and socioeconomic strata using various measurement methods, yielding rich evidence (e.g., Knafo et al., 2015; Hur et al., 2017; Rushton et al., 1986; Wang & Saudino, 2015). For instance, Rushton et al. (1986) administered the Self-Report Altruism Scale to 1,400 twin pairs aged 19-60, reporting a heritability estimate of 0.60 for altruism, with minimal variance explained by shared environment; non-genetic variation was primarily attributed to non-shared environmental influences (or measurement error).

Meta-analysis of altruism heritability studies reveals considerable variation in

estimates (ranging from 0 to 0.87), suggesting that heritability may be moderated by several factors. First, longitudinal studies demonstrate that altruism heritability increases with age (Knafo & Plomin, 2006; Scourfield et al., 2004). For example, genetic effects on altruism increased from an average of 0.32 at age 2 to 0.61 at age 7, while shared environmental effects decreased from 0.47 to 0.03 (Knafo & Plomin, 2006). This pattern indicates strengthening genetic influences as children mature and experience increasingly diverse social environments, reducing shared environmental impact—a finding replicated by Scourfield et al. (2004).

Second, measurement methods may affect heritability estimates. Self-report questionnaires are most common, suitable for large samples (e.g., Krueger et al., 2001; Rushton et al., 1986). For young children, parents and teachers provide ratings (e.g., Hur & Rushton, 2007; Knafo et al., 2015). While some studies find high agreement between parent and teacher ratings (Knafo & Plomin, 2006), others report higher heritability from teacher ratings (0.78) than parent ratings (0.52) (Scourfield et al., 2004). Alternative methods include behavioral observations (Knafo et al., 2011; Volbrecht et al., 2007) and experimental tasks (Van IJzendoorn et al., 2010). For example, mothers and experimenters simulated distress (pretending to pinch a finger in a suitcase) while coding children' s altruistic responses from video recordings (Zahn-Waxler et al., 1992). Different measurement approaches introduce varying degrees of error, affecting heritability estimates.

Third, culture and family environment represent important moderators. Studies have examined populations across the United States, Netherlands, United Kingdom, South Korea, Sweden, and Israel. Comparisons using identical measurement methods reveal differences—for instance, between South Koreans (0.55) and British participants (0.61) (Hur & Rushton, 2007; Gregory et al., 2009). However, limited research precludes definitive conclusions about cross-cultural differences in altruism heritability, necessitating more rigorous designs and additional evidence.

Family environmental factors such as socioeconomic status (SES) may also play a role. The Scarr-Rowe hypothesis proposes a Gene × SES interaction, suggesting that genetic potential for adaptive functioning is more fully expressed in enriched environments, resulting in higher heritability among individuals from high (versus low) SES backgrounds (Scarr-Salapatek, 1971; Tucker-Drob & Bates, 2016). Given that altruism requires expending personal resources, resource-rich childhood environments may facilitate genetic expression of altruistic tendencies.

In summary, quantitative genetic methods provide substantial evidence for the heritability of altruism, confirming that human altruistic behavior is genetically influenced. However, heritability estimates vary across studies, likely due to age, measurement methods, and environmental factors. Systematic investigation of these moderators is lacking, warranting future longitudinal and large-sample studies to replicate findings, conduct meta-analyses, and examine po-

tential moderators such as SES. Most heritability studies have relied on twin designs, with only one using a stepfamily genetic design (Deater-Deckard et al., 2003)—a method that helps disentangle genetic and environmental variance confounds (Deater-Deckard et al., 2003). Diversifying methodological approaches represents an important future direction.

Twin studies partition environmental influences into shared and non-shared components. The reviewed studies indicate minimal or zero direct effects of shared environment on altruism (e.g., Knafo et al., 2015). This may reflect children' s increasing exposure to non-familial settings (e.g., schools) that amplify sibling differences, as well as parents' differential treatment of children. Significant non-shared environmental effects support the importance of unique experiences —such as distinct parenting styles, birth order, life events, and medical histories—in shaping sibling differences. While quantitative genetics has limitations (e.g., examining genetic influences only at the statistical level) and findings require further investigation, this body of work provides a crucial foundation for understanding genetic influences on altruism.

2.2 Molecular Genetics

Recent technological advances have enabled molecular-level investigation of "altruism genes." Genes are DNA sequences that store hereditary information governing biological processes. Researchers have employed candidate gene studies, examining associations between altruism and variations in or near genes with known functions. Over the past decades, research has focused on four neurobiological systems: the dopamine system (executive function, learning, reward), the serotonin system (emotion and inhibition), and the oxytocin and vasopressin systems (social cognition and behavior). provides a summary of these findings.

2.2.1 Dopamine Receptor Genes Dopamine (DA) is a catecholamine neurotransmitter associated with reward-seeking; its release accompanies feelings of excitement and pleasure (Skuse & Gallagher, 2009). Animal research links dopamine to impulsivity and risky decision-making (Huang et al., 2016). In humans, helping behavior activates dopaminergic reward centers—specifically, the ventral striatum shows enhanced activity when individuals support loved ones (Inagaki & Eisenberger, 2012). Given dopamine' s central role in reward processing, examining related candidate genes is crucial for understanding altruistic motivation.

Dopamine receptor genes have been implicated in altruism (Li et al., 2020). The dopamine D4 receptor (DRD4) gene, located on chromosome 11p15.5, contains five exons and four introns. A 48bp variable number tandem repeat (VNTR) in exon 3 exhibits 2-8 or 10 repeats, with longer repeats reducing dopamine binding efficiency. Longer repeats (6-8) associate with increased risk-taking behaviors; for example, DRD4-7R correlates more strongly with novelty-seeking and ADHD than DRD4-4R (Rettew & McKee, 2005). This VNTR also predicts altruism (Anacker et al., 2013; Bachner-Melman et al., 2005; Reuter et al.,

2013). Bachner-Melman et al. (2005) found DRD4-4R significantly associated with scores on an unselfishness scale measuring tendencies to neglect personal needs in service of others. The balance between DRD4-4R and 7R may reflect evolutionary demands for behavioral diversity: 4R may underlie altruistic, prosocial traits, while 7R carriers may exhibit novelty-seeking, aggression, or antisocial behavior (Anacker et al., 2013; Bachner-Melman et al., 2005; Rettew & McKee, 2005). This provides a neurochemical basis linking reward and altruism—individuals may be "rewarded" by dopamine pulses when doing good, suggesting that natural selection may have favored polymorphisms that reinforce altruism through dopaminerg pathways (Bachner-Melman et al., 2005).

Recent research reveals that DRD4 polymorphisms' effects on altruism are moderated by environmental factors such as religious belief and family environment (Wang et al., 2020; Jiang et al., 2015; Sasaki et al., 2013). For instance, DRD4-4R carriers show higher altruistic tendencies only in family environments that openly express aggression (Wang et al., 2020), demonstrating environment' s crucial role in gene-behavior relationships.

2.2.2 Serotonin Transporter Gene Serotonin (5-hydroxytryptamine) is an inhibitory neurotransmitter involved in emotion and behavioral regulation. Elevated serotonin levels increase cooperation in Prisoner' s Dilemma games (Tse & Bond, 2002), while depleted serotonin reduces cooperation (Wood et al., 2006). Based on altruism' s definition, cooperation in such games qualifies as altruistic behavior (Bhogal et al., 2017; Gallotti & Grujić, 2019; Smith, 2003; Wang et al., 2020; Li et al., 2020), as individuals sacrifice personal interests for others' benefit. These findings confirm that serotonin influences altruism and justify investigating "altruism genes."

The serotonin transporter gene (SLC6A4), located on chromosome 17q11.1-12 with 14 exons, regulates serotonin reuptake from the synaptic cleft, thereby modulating synaptic serotonin concentration and receptor activation (Lesch, 2007). The most studied polymorphism is the serotonin transporter gene-linked polymorphic region (5-HTTLPR). Although empathy—considered a key mechanism underlying altruism (de Waal, 2008)—shows no significant association with 5-HTTLPR (Huetter et al., 2020), this does not preclude a direct gene-altruism link. 5-HTTLPR has two alleles: long (L) and short (S). Stoltenberg et al. (2013) found L carriers more likely to help others than S carriers, with this effect mediated by S carriers' tendency to perceive social situations as threatening. Thus, S carriers may exhibit less altruism because they experience higher emotional arousal in potentially risky social contexts, reducing willingness to sacrifice personal resources. Overall, research on the serotonin transporter gene and altruism remains limited, requiring further replication.

2.2.3 Oxytocin Receptor Gene Oxytocin (OT) is a nine-amino-acid neuropeptide (Shang & Su, 2016; Zhang et al., 2018). Initially recognized for its role in female lactation, childbirth, and maternal attachment (Smith et al., 2010),

oxytocin is secreted by both sexes and influences diverse social behaviors (Zhang et al., 2018), earning it the moniker "love hormone." Intranasal oxytocin administration increases charitable donations compared to placebo (Barraza et al., 2011), and individuals with higher oxytocin levels engage more frequently in social interactions and helping behaviors while reporting greater positive affect (Isgett et al., 2017). Oxytocin's effects on altruism are moderated by factors such as group membership (Daughters et al., 2017).

The most extensively studied oxytocin system gene is the oxytocin receptor gene (OXTR), located on chromosome 3p25, spanning approximately 17kb with four exons and three introns. The single nucleotide polymorphism (SNP) rs53576 in OXTR relates to altruism: individuals carrying more G alleles (GG genotype) are more likely to help others than A allele carriers (AG, AA) (Verbeke et al., 2013). The Dictator Game, which involves allocating "found money" to others (Israel et al., 2009), aligns with altruism's definition (Wang et al., 2020; Li et al., 2020) and is widely used to measure altruism alongside similar measures like the Social Value Orientation (SVO) task (e.g., Israel et al., 2009; Jiang et al., 2015; Knafo et al., 2008). Israel et al. (2009) examined relationships between altruism and 15 OXTR SNPs using these paradigms, identifying three SNPs (rs1042778, rs2268490, rs237887) significantly associated with altruism, with rs1042778 showing the strongest relationship. Moreover, individuals carrying the "kindness gene" can be identified by observers: Kogan et al. (2011) found that observers watching silent 20-second clips of individuals describing painful life experiences could distinguish GG carriers from A carriers based on more altruistic behavior.

Despite substantial evidence linking OXTR to altruism, some studies report null findings (Apicella et al., 2010; Bakermans-Kranenburg & van IJzendoorn, 2014; Nave et al., 2015). For example, Apicella et al. (2010) found no association between nine OXTR SNPs (including rs53576 and rs237887) and performance in Dictator or Trust games among 684 Swedish twins. The authors proposed several explanations, including environmental differences between Swedish and Israeli samples, suggesting that external environments may moderate OXTR's effects on altruism. This is supported by evidence that OXTR's influence on altruism is moderated by environmental factors such as threat and recipient identity (Poulin et al., 2012; Shang et al., 2017; Wu & Su, 2018). Thus, the OXTR-altruism relationship is not simply correlational but involves complex environmental interactions.

2.2.4 Vasopressin Receptor Genes Arginine vasopressin (AVP) is a neuroendocrine hormone structurally similar to oxytocin, composed of nine amino acids with differences at positions 3 and 8 (Wu et al., 2019). Extensive research demonstrates vasopressin's roles in cognitive processing (auditory processing, attention, face recognition, memory) and social interaction (Wu et al., 2019). Compared to placebo, intranasal vasopressin increases cooperation among male participants in Prisoner's Dilemma games, while females show increased coop-

eration specifically after partners' defection (Feng et al., 2015).

Humans have at least three vasopressin receptor types (V1a, V1b, and V2R). The vasopressin receptor 1a (AVPR1a) gene, located on chromosome 12q14-15 with two exons, contains three polymorphic repeats (RS1, RS3, and GT25). AVPR1a RS3 promoter repeat length predicts altruism in the Dictator Game: longer repeats (327-343 bp) correlate with higher hippocampal AVPR1a mRNA levels and greater monetary allocations to others compared to shorter repeats (308-325 bp) (Knafo et al., 2008). However, some findings are contradictory: children carrying the AVPR1a RS3 (327bp) allele exhibited less altruism (Avinun et al., 2011). Additionally, the vasopressin receptor 1b (AVPR1b) gene, located on chromosome 1q32 with two exons, also explains individual differences in altruism (Wu et al., 2015). Using the revised Prosocial Tendencies Measure (PTM-R) altruism subscale, Wu et al. (2015) found that AVPR1b rs28373064 was significantly associated with altruistic tendencies, mediated by emotional empathy. Overall, researchers have identified SNPs in both vasopressin receptor genes associated with altruism.

3. Genetics and Environment

Both quantitative and molecular genetic studies provide robust evidence for genetic influences on altruism. However, it is crucial to recognize that environmental factors affect not only heritability estimates (e.g., Tucker-Drob & Bates, 2016) but also play a critical role in gene-to-behavior pathways (e.g., Wang et al., 2020). As environmental influences are paramount and humans are products of both genetic and environmental forces, environmental factors must be integrated into investigations of altruism' s genetic basis. Researchers have primarily examined two mechanisms of gene-environment interplay: gene-environment correlation, where genes influence the environments individuals experience, and gene-environment interaction, where environments modulate genetic expression.

3.1 Genes Select Environments: Gene-Environment Correlation

When using quantitative genetic methods to disentangle genetic and environmental influences on altruism, a critical consideration is that genes and environments may not be independent—they can be correlated. Gene-environment correlation theory (Perlstein & Waller, 2022; Scarr & McCartney, 1983) posits that genes drive experiences, meaning genotypes determine or select the environments individuals encounter, creating correlations between genes and environments. For example, first-grade children with genetic predispositions for prosocial leadership have more friends (Rivizzigno et al., 2014). While supporting the gene-environment correlation hypothesis, such studies cannot specify the precise mechanisms of interaction.

Scarr and McCartney (1983) identified three types of gene-environment correlations. First, *passive* correlation occurs when children passively receive both

genes and environments from parents, which are correlated. Genetically altruistic parents not only transmit altruism-related genes but also create environments that foster altruistic behavior, jointly promoting children' s altruism. Second, *evocative* correlation arises when individuals' genotypes elicit specific responses from others; altruistic individuals are more likely to receive altruistic feedback. For instance, when randomly paired unfamiliar children played together, 5-year-olds genetically predisposed to altruism and extraversion evoked more altruistic and easy-going behavior from their peers (DiLalla et al., 2015). Third, *active* correlation involves individuals actively creating or selecting environments that match their genetic predispositions, such as choosing similar friends and partners (Wu et al., 2017). Consequently, altruistic individuals tend to select altruistic friends and partners. Scarr and McCartney (1983) proposed developmental shifts: passive correlations decline from infancy through adolescence, while evocative and active correlations increase.

Gene-environment correlation theory demonstrates that genotypes shape the environments individuals inhabit, with both jointly influencing altruism. This framework helps explain why genetic effects on altruism strengthen with age (Knafo & Plomin, 2006; Scourfield et al., 2004). Based on gene-environment correlation, individuals experience environments that match their genotypes, which in turn shape behavior. Over development, these systematic processes accumulate, amplifying genetic effects. Furthermore, this theory challenges quantitative genetic analytic methods: if environmental variation partially originates from genetic variation, statistical models estimating genetic effects on behavior must account for this confound (Knoblach et al., 2019).

3.2 Environment Influences Gene Expression: The Differential Susceptibility Model

Twin studies estimate heritability by assuming monozygotic twins share identical genomes, attributing any behavioral differences between them to environmental factors (Hur & Rushton, 2007). However, recent research reveals that monozygotic twins exhibit genetic differences from early embryonic development, averaging 5.2 early developmental mutations, meaning their genomes are not truly identical (Jonsson et al., 2021). Moreover, even with identical genes, expression patterns may differ (Zhang & Zheng, 2016). The differential susceptibility model (Zhao et al., 2017; Hartman & Belsky, 2016) proposes that environments affect gene expression. Rather than directly encoding social-emotional behaviors, genes likely encode enzymes that, under specific environmental conditions, influence brain physiology and neurohormonal system patterns. These factors subsequently shape behavioral, cognitive, and emotional responses to others' suffering, thereby affecting altruism. Thus, carriers of certain genotypes are more susceptible to environmental influences—both adverse effects of negative environments and beneficial effects of supportive environments—with external contexts affecting behavior development in a "for better or for worse" manner.

In dopamine receptor genes, DRD4-2R and 7R are considered susceptibility genes, potentially influenced by family environment, peer relationships, and religious beliefs (Wang et al., 2020; Sasaki et al., 2013; Schlomer et al., 2020). For example, individuals carrying DRD4 susceptibility genes show increased volunteering intentions after implicit religious priming, whereas non-carriers are unaffected (Sasaki et al., 2013). A study of Chinese university students found a significant interaction between DRD4 polymorphisms and family environment on altruism: DRD4-2R(7R) carriers exhibited lower altruism than non-carriers in families with openly expressed aggression, but higher altruism in less aggressive families (Wang et al., 2020). Other research examined whether DRD4 moderates positive emotional benefits from altruism. Using experience sampling with nurses, one study found DRD4-2R carriers experienced significantly increased positive affect and reduced physical fatigue after altruistic acts, effects not observed in non-carriers (Zhuang, 2017). However, some studies fail to find susceptibility effects for DRD4-7R, such as non-significant interactions between parenting style and DRD4-7R on children' s self-reported altruism (Bersted, 2016).

Similar findings emerge for oxytocin receptor genes. OXTR SNP rs53576 is widely considered a susceptibility gene: among individuals perceiving greater environmental threat (e.g., believing evil outweighs good in the world), AA homozygotes and AG carriers exhibit less charitable behavior, whereas threat perception does not predict charity in GG carriers (Poulin et al., 2012). Other OXTR SNPs (e.g., rs13316193, rs1042778, rs237887, rs2254298) show relationships with altruism moderated by recipient identity, altruism cost, and gender (Shang et al., 2017; Wu & Su, 2018). Furthermore, post-altruism emotions are moderated by OXTR susceptibility genes. In a six-week loving-kindness or mindfulness intervention, rs1042778 GG carriers showed significantly increased positive affect after loving-kindness training, whereas TT/TG carriers and other SNP carriers (rs2254298, rs53576) showed no improvement (Isgett et al., 2016). However, other studies found no moderation of positive emotional benefits from altruism by OXTR SNPs (rs53576, rs2268498, rs2254298) (Whillans et al., 2020).

The differential susceptibility model emphasizes that while traits and behaviors may be genetically influenced, this influence is constrained by environmental contexts—genes operate through environments. This provides an alternative framework for understanding gene-environment interactions in altruism, garnering increasing research attention. However, literature searches reveal that some studies fail to find susceptibility gene-environment interactions (e.g., Bersted, 2016; Isgett et al., 2016; Whillans et al., 2020). This may reflect that specific genotypes are sensitive only to particular environmental factors; when environments vary, genetic effects on behavior change accordingly, consistent with the differential susceptibility model. Nevertheless, these null findings caution against overestimating small effects and potential publication bias (Whillans et al., 2020).

4. Summary and Outlook

In conclusion, extensive research on altruism heritability confirms genetic influences on altruistic behavior, with heritability estimates moderated by multiple factors. Molecular genetics and gene detection technologies have identified four categories of candidate genes, providing rich evidence for "altruism genes." Moreover, environmental factors must be integrated into genetic models, both through gene-environment correlations (where genes shape experienced environments) and gene-environment interactions (where environments modulate genetic expression). Despite substantial progress, future research should pursue several directions:

4.1 Expand Neurobiological System Exploration and Emphasize Genome-Wide Research

With over 20,000 human genes, identifying specific altruism-related genes is challenging. Current approaches successfully narrow candidate gene pools based on known physiological mechanisms, yielding rich findings. However, this strategy is speculative and limited by incomplete knowledge, potentially overlooking relevant genes. For example, in the oxytocin system, most research focuses on OXTR while neglecting other genes. A recent study found that the oxytocin-neurophysin I gene (located on chromosome 20p13, encoding oxytocin ligand) also predicts altruistic traits: AA homozygotes for SNP rs2770378 reported higher altruism than G carriers (Chong et al., 2019). Over the past decade, genome-wide association studies (GWAS) have become the standard for identifying common genetic variants associated with complex behaviors and diseases. Future research should expand neurobiological system investigation and adopt GWAS approaches to generate more comprehensive findings.

4.2 Emphasize Large-Sample and Meta-Analytic Research to Address Reproducibility

A major concern is the low reproducibility of candidate gene studies. For example, while OXTR may partially explain human altruism, findings are inconsistent and effect sizes are small (Bakermans-Kranenburg & van IJzendoorn, 2014; Benjamin et al., 2012). Small sample sizes may inflate associations between altruism and common genetic variants. Moreover, genes operate in complex, probabilistic rather than deterministic ways, necessitating cautious interpretation of findings. Additionally, most studies examine single genes within one neurobiological system, yet evidence suggests altruism is likely determined by multiple systems and gene segments acting in concert. Future research requires large samples, meta-analyses examining potential moderators, and investigation of multi-system, multi-gene effects (Zhang et al., 2018; Israel et al., 2015; Nave et al., 2015).

4.3 Strengthen Mechanistic Exploration of Altruism' s Genetic Basis

Researchers have begun exploring mechanisms underlying genetic influences on altruism. For example, Stoltenberg et al. (2013) found that 5-HTTLPR S carriers help less because they perceive social situations as threatening. Wu et al. (2015) demonstrated that AVPR1b rs28373064 G carriers show greater emotional empathy, promoting altruism. Recently, researchers have combined functional magnetic resonance imaging (fMRI) with genetic designs, using brain structure and function as mechanistic pathways explaining genetic effects on behavior (Qian et al., 2018). Future research should integrate physiological and psychological perspectives with imaging genetics to elucidate mechanisms linking genes to altruism.

4.4 Strengthen Gene-Environment Interaction Research and Conduct Environmental Intervention

The differential susceptibility model has expanded research on gene-environment interactions in altruism. Current investigations focus primarily on dopamine and oxytocin receptor genes, with less attention to serotonin and vasopressin systems. Even within dopamine receptor genes, different environmental factors (e.g., parenting, peer environment) and altruism types (e.g., donations, sharing, cooperation) yield inconsistent results. For example, DRD4-7R shows susceptibility effects in some studies but not others (Bakermans-Kranenburg & van IJzendoorn, 2011; Bersted, 2016). Future research should comprehensively examine interactions between various genes and environmental factors. Additionally, while genes themselves cannot be ethically manipulated, the differential susceptibility model offers new avenues for intervention: tailored environmental interventions for different genotypes could cultivate altruistic tendencies, enhancing social welfare and building harmonious societies.

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