

Altruistic Behavior among Twins Willingness to Fight and Self-Sacrifice for their Closest Relatives

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Abstract According to kin selection theory, indirect reproductive advantages may induce individuals to care for others with whom they share genes by common descent, and the amount of care, including self-sacrifice, will increase with the proportion of genes shared. Twins represent a natural situation in which this hypothesis can be tested. Twin pairs experience the same early environment because they were born and raised at the same time and in the same family but their genetic relatedness differs depending on zygosity. We compared the degree of willingness to fight and sacrifice for the co-twin among monozygotic (MZ) and dizygotic (DZ) pairs in a sample of 1443 same-sex and opposite-sex twins. We also analyzed the effect of the subject's gender and that of the co-twin on those altruistic behaviors. Results partly supported the postulated explanation. MZ twins (who share nearly their entire genome) were significantly more likely than DZ twins (who on average share half of their segregating genes) to self-sacrifice for their co-twins, but zygosity did not affect willingness to fight for him/her. The genders of the subject and of the co-twin, not genetic relatedness, were the best predictors of aggressive altruistic intentions.

Keywords Altruism · Self-sacrifice · Twins · Genetic relatedness · Kin selection theory

Because of its paradoxical character, altruistic behavior has historically been an object of interest and controversy in evolutionary science. Behaviors beneficial to others at the

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expense of oneself cannot be easily explained by classical evolutionary models. The main attempt to account for the evolution of this pattern of behavior is Hamilton's kin selection theory (1964), which explains it in terms of inclusive fitness. Hamilton's rule ($C < rB$) predicts that we can expect actors to show self-sacrificing behaviors for recipients provided the reproductive cost to the actor (C) is less than the additional reproductive benefit to the recipient (B), r being the degree of relatedness between actors and recipients. Ultimately, these costs and benefits are measured in terms of inclusive fitness, which includes direct and indirect fitness. That is, there would be two ways in which an individual can boost the presence of copies of its genes into the next generation: via offspring or indirectly through giving aid to other relatives (Kurland and Gaulin 2005; Workman and Reader 2008). According to this explanation, sharing genes with the recipient of an action would increase the probability of behaving altruistically. In other words, individuals may be more likely to care for others who share genes by common descent, and the amount of care they give will increase, as does the proportion of these genes shared (Workman and Reader 2008).

Research tends to support this explanatory frame by focusing on different kinds of behaviors (Burnstein 2005). Thus, there seems to be a relationship between helping behavior and genetic relatedness, especially in life-or-death situations (Burnstein et al. 1994) or when the costs associated with the help increase (Stewart-Williams 2008), and people are more prone to provide social or emotional support to their full- or half-siblings than to non-genetically-related siblings, such as adopted or step-siblings (Mikkelsen et al. 2011). This association between altruism and genetic relatedness extends to financial support, social discounting, and money allocation studies (Osiński 2009; Webster 2003, 2004; Webster et al. 2008). Individuals are also more willing to self-sacrifice, enduring increasingly intense physical pain, as long as they benefit close genetic relatives rather than distant ones or those who are unrelated (Madsen et al. 2007).

Behaviors other than helping or self-sacrifice have been studied under this paradigm. Some researchers have focused on the aggressive component inherent in some altruistic behaviors (Webster et al. 2012). For example, people appear more prone to retaliate when close kin are insulted (Fitzgerald and Ketterer 2011). Similarly, Gesselman and Webster (2012) studied aggressiveness in response to insults to strangers or distant or close relatives. Consistent with their predictions, perceived genetic relatedness influenced aggressive responses, which were stronger when insults were directed toward kin rather than non-kin.

In general, all of these behavioral patterns have been explained in terms of indirect reproductive advantages of benefiting the closer kin. However, these attempts have been hampered by the difficulty of disentangling social from genetic relatedness. Twins provide a unique opportunity to compare relatives who differ in terms of genetic relatedness but have a similar degree of social relatedness. They experience the same early environment by being born and raised at the same time and in the same family, and they can be categorized according to genetic closeness. Monozygotic twins (MZ) share 100% of their genetic makeup, while dizygotic (DZ) twins share, on average, 50% of their genes.

Comparison of the degree of altruistic behaviors between MZ and DZ twins may offer relevant information, as well as a direct test of the nepotistic altruism hypothesis.

This premise maintains that, because of their greater genetic relatedness, MZ twins should exhibit greater levels of self-sacrifice and motivation to fight for their twin (Segal et al. 2003). Our aim is to test this hypothesis by analyzing the reported willingness to perform altruistic behaviors in a large sample of adult twins. Additionally, since evolutionary arguments attribute different features to males and females, we aim to explore possible gender differences in these behaviors.

Materials and Methods

The sample comprised 503 MZ (43.5% males) and 940 DZ (50.1% males) individuals born between 1940 and 1966; all are participants in the Murcia Twin Registry (MTR) (Ordoñana et al. 2013). Mean age at data collection was 56.1 (SD = 6.8; range = 47–73). The MTR is a population-based registry of adult multiples in the region of Murcia (Spain). The general goal of this initiative was to create a basic research tool for the analysis of the relative contribution of genetic and environmental factors to the development of complex phenotypes, with a focus on health and health-related behaviors. Participation in the MTR is voluntary, subjected to informed consent, and not remunerated. Twin zygosity was ascertained by a 12-item questionnaire which included questions on whether twins were similar in eye color, hair color, and facial color and form. This zygosity-based questionnaire corresponds well with zygosity as determined by DNA testing, with an agreement in nearly 96% of cases (Ordoñana et al. 2013). More detailed information about recruitment procedures and data collection is provided in Ordoñana et al. (2006, 2013). The MTR data collection and analytical procedures have been approved by the Committee of Research Ethics of the University of Murcia and meet the legal requirements of confidentiality and personal data protection.

The MTR periodically collects information from the twins. Data for this study were collected in the 2013 wave by trained personnel through a telephone interview. Subjects answered demographic and health-related questions. For this study, subjects responded to a questionnaire about willingness to fight and die for others (Swann et al. 2009; Gómez and Vázquez 2015) adapted to the specific circumstances of twins. The questionnaire consists of four questions with answers ranging from 0 (completely disagree) to 10 (completely agree): “I would hit anyone who threatened my twin,” “I would hit anyone that would insult or laugh at my twin,” “Hurting another person to protect my twin is admissible,” and “I would sacrifice my life to save my twin’s life.” The first three questions formed a scale on willingness to *fight* ($\alpha = .89$), while the last is a measure of disposition for *self-sacrifice*.

The associations between *zygosity* and *gender* as predictors, and *self-sacrifice* and *fighting* for kin as the outcomes, were examined using the generalized estimating equations (GEE) regression procedure in IBM SPSS Statistics 19. Twin pairs cannot be assumed to be independent, so GEE was used to control for the clustering of twins within a pair. GEE algorithms are based on Zeger and Liang (1986) and Diggle et al. (2002).

An exchangeable correlation matrix showed the best fit in each analysis based on the lowest values for the quasi-likelihood under the independence model criterion (QIC);

therefore it was chosen as the working correlation matrix. The working correlation matrix describes how the observations of each cluster are related to one another (Katz 2011). Age was included as a covariate in all analyses, and all significance tests were two-tailed.

One limitation of the GEE procedure is that, if the sample size is not high enough, the robust standard errors tend to be downward-biased and the type I error inflates. However, previous simulation studies have shown that this problem arises when data from less than 40 clusters are analyzed (Murray et al. 2004). In the present study, this situation is prevented by having data from more than 500 independent pairs for each analysis.

Results

Correlation between fight and self-sacrifice was moderate ($r = .42$), which indicates that they relate to different concepts and can be analyzed separately (Swann et al. 2009). Mean scores for self-sacrifice and fight by zygotity and gender are depicted in Fig. 1. Because same-sex and opposite-sex twins appeared to behave distinctively, differences among groups were compared for statistical significance following several steps.

The first analysis included only same-sex DZ and MZ pairs. The first GEE model included age, zygotity, and gender main effects, and the interaction between the last two variables. Since the interaction (zygotity \times gender) was not significant for either self-sacrifice or fight (Self-sacrifice: $\chi^2_{(1)} = 0.415$, $p = .519$; Fight: $\chi^2_{(1)} = 0.243$, $p = .622$), it was dropped from the final model. Results are shown in Table 1.

We found significant effects of zygotity on willingness to self-sacrifice. Being monozygotic increased the mean score of the self-sacrifice measure ($M_{MZ} = 7.91$,

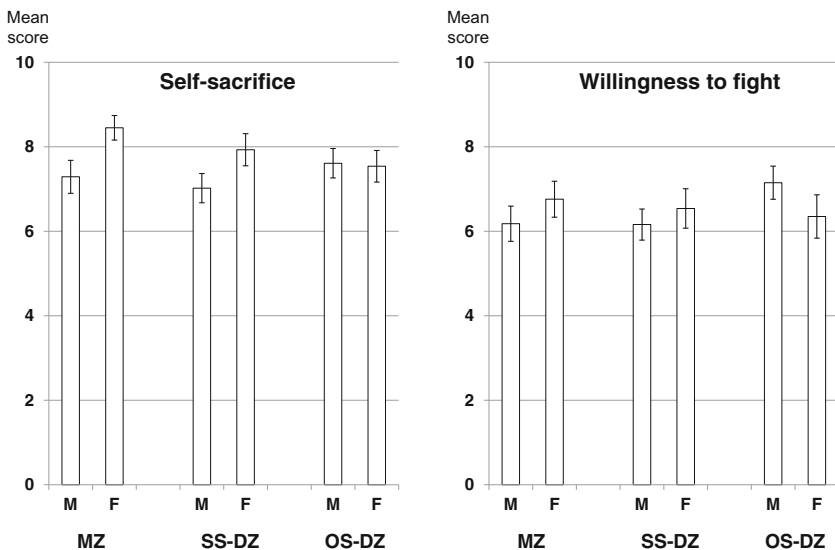


Fig. 1 Mean scores (and 95% Confidence Intervals) for self-sacrifice and willingness to fight, stratified by zygotity and sex (M: Male; F: Female; MZ: Monozygotic; SS-DZ: Same-sex dizygotic; OS-DZ: Opposite-sex dizygotic)

Table 1 Effect of age, zygosity, and gender on self-sacrifice and willingness to fight for the co-twin

Response	Predictors	β [95% CI]	SE	Wald χ^2 (df)	<i>p</i>
Self-sacrifice	Age	0.02 [-0.01, 0.05]	0.01	2.45 (1)	.127
	Zygosity (SS-DZ) ^a	-0.42 [-0.81, -0.04]	0.20	4.60 (1)	.032
	Gender (♀) ^a	1.04 [0.65, 1.43]	0.20	27.81 (1)	<.001
Fight	Age	0.07 [0.04, 0.10]	0.02	17.07(1)	<.001
	Zygosity (SS-DZ) ^a	-0.17 [-0.64, 0.30]	0.24	0.48(1)	.488
	Gender (♀) ^a	0.50 [0.03, 0.96]	0.24	4.36(1)	.037

Generalized estimating equations (GEE) coefficients (opposite-sex dizygotic twins not included)

^a Reference category

SD = 2.7; $M_{DZ} = 7.44$, SD = 2.8). Gender also had a statistically significant impact on willingness to self-sacrifice, as well as on willingness to fight for the sibling. Being female increased the mean scores for both, self-sacrifice ($M_{Female} = 8.21$, SD = 2.6; $M_{Male} = 7.14$, SD = 2.8) and fight ($M_{Female} = 6.66$, SD = 3.51; $M_{Male} = 6.17$, SD = 3.04). Age as a covariate only had a significant effect on fight response.

As an additional check, we were able to obtain self-sacrifice scores between correctly (i.e., twins raised according to true zygosity) and incorrectly (i.e., MZ twins labeled as DZ by their family and vice versa) labeled twins in same-sex pairs. Some of the MZ subjects ($n = 152$) had been mislabeled as DZ by their family, and vice versa; some of the DZ twins believed they were MZ ($n = 28$). The highest scores were obtained from MZ twins regardless of their zygosity assignment ($M_{MZ-MZ} = 8.03$, SD = 2.7; $M_{MZ-DZ} = 7.86$, SD = 2.4), and the lowest by DZ twins irrespective of their beliefs about their zygosity ($M_{DZ-DZ} = 7.48$, SD = 2.7; $M_{DZ-MZ} = 7.68$, SD = 2.8).

The same analysis was then conducted including opposite-sex dizygotic pairs (OSDZ). When OSDZ twins were added, an interaction between zygosity and gender was found for both the self-sacrifice ($\chi^2_{(1)} = 5.832$, $p = .016$) and fight ($\chi^2_{(1)} = 4.959$, $p = .026$) variables. Those who were both dizygotic and male behaved differently from the other groups (Fig. 1).

This deviation from the original results was coherent with the unusually high means for OSDZ males, who tended to report greater willingness to fight or to sacrifice for their sisters than males in same-sex pairs. They actually showed the highest score on willingness to fight for their sibling. Therefore, the effect of sex of the sibling on self-sacrifice and fight attitudes was analyzed.

As a consequence, two parallel analyses that only included DZ pairs were performed in order to assess the impact of sibling's sex on willingness to sacrifice and to fight. MZ twins were excluded, so that zygosity would not become a confounding variable. The results of these analyses are shown in Table 2. The interaction between own and sibling's gender was not significant in any case (Self-sacrifice: $\chi^2_{(1)} = 0.237$, $p = .626$; Fight: $\chi^2_{(1)} = 1.080$, $p = .299$). Therefore, this interaction was dropped from the final models.

In this final analysis, a significant effect of both own and sibling's gender was found on willingness to sacrifice. That is, females' mean score was higher than that of males for self-sacrifice ($M_{Females} = 7.74$, SD = 2.7; $M_{Males} = 7.28$, SD = 2.7), while males showed a similar result but only when they had a sister ($M_{Males-Sister} = 7.61$, SD = 2.5;

Table 2 Effect of age, gender, and sibling sex on self-sacrifice and willingness to fight for the co-twin

Response	Predictors	β [95% CI]	SE	Wald $\chi^2_{(df)}$	<i>p</i>
Self-sacrifice	Age	0.01 [-0.02, 0.03]	0.01	0.28 (1)	.598
	Gender (♀) ^a	0.42 [0.06, 0.77]	0.18	5.34 (1)	.021
	Sibling Sex (♀) ^a	0.50 [0.15, 0.85]	0.18	7.79 (1)	.005
Fight	Age	0.07 [0.04, 0.10]	0.02	18.77 (1)	<.001
	Gender (♀) ^a	-0.21 [-0.65, 0.24]	0.23	0.84 (1)	.359
	Sibling Sex (♀) ^a	0.59 [0.16, 1.03]	0.22	7.05 (1)	.008

Generalized estimating equations (GEE) coefficients (monozygotic twins not included)

^a Reference category

$M_{\text{Males-Brother}} = 7.02$, $SD = 2.8$). Accordingly, having a sister yielded higher mean scores than having a brother ($M_{\text{Sister}} = 7.77$; $SD = 2.7$; $M_{\text{Brother}} = 7.25$, $SD = 2.7$). However, only sibling's gender had a statistically significant impact on willingness to fight, which was mainly dependent on the fact that the sibling was female ($M_{\text{Sister}} = 6.84$, $SD = 3.3$; $M_{\text{Brother}} = 6.25$, $SD = 3.3$). As in the first analysis, age as a covariate only had a significant effect on fight response.

Discussion

Our aim in this study was to analyze to what extent genetic relatedness in a sibling pair influences altruistic behavior toward the sibling, as predicted by the inclusive fitness model. The results partially confirm our predictions. Genetic relatedness significantly influenced disposition to sacrifice for the sibling; however, it did not show any effect on the willingness to fight for the twin, which was mainly driven by the gender of the subject and that of the sibling.

As expected, we found a stronger tendency to accept self-sacrifice for the sibling among MZ twins. This result is in accordance with the tenets of inclusive fitness, which posits that a greater genetic relatedness would facilitate behaviors that take a heavy toll on the individuals. From this standpoint, MZ twins should show greater within-pair altruism than DZ twins given that alleles influencing individuals to favor others likely to carry replicas of those alleles is an indirect means of achieving future representation (Segal et al. 2003). This ultimate evolutionary goal would relate to proximal mechanisms, such as phenotypic matching or emotional closeness, which may mediate between genetic relatedness and altruistic behavior (Fortuna et al. 2010; Korchmaros and Kenny 2006; Neyer and Lang 2003; Park and Ackerman 2011). For instance, positive and significant correlations between perceptions of physical resemblance and social closeness and familiarity have been reported among reunited twin pairs who had been reared apart. Consequently, reunited MZ twins showed greater perception of social closeness and familiarity than DZ ones (Segal et al. 2003). This is also consistent with the large body of literature showing that MZ twins exhibit a much closer relationship than DZ twins (Danby and Thorpe 2006; Foy et al. 2001; Loh and Elliott 1998; Neyer 2002a, 2002b; Segal 2000), even when raised apart (Segal et al. 2003). This close relationship also makes them miss their co-twin more than any other

relative (Segal et al. 1995), and they grieve the loss of their sibling more intensely (Segal and Ream 1998). Our results provide some evidence of sensitivity to precise degrees of relatedness as well, based on phenotypic matching. A negative result showing no difference between twins would have challenged the idea of phenotype matching as a kin-recognition mechanism and would favor alternative mechanisms such as familiarity or social closeness as main indicators of relatedness.

However, other mechanisms could account for the influence of zygosity on self-sacrifice scores. A classical assumption in twin studies, called the equal environments assumption (EEA), implies that MZ and DZ twins experience equivalent trait-relevant environmental exposures. If the EEA had not been met, the outcome of this study could have been produced by environmental forces impacting the twins' perceptions and beliefs. From this point of view, the greater behavioral resemblance between MZ twins could be the result of a social-upbringing effect rather than their greater genetic relatedness. MZ twins would experience more-equal treatment from their environment than DZ twins and, based on their physical similarity, could be encouraged to establish stronger bonds, all of which could facilitate altruistic attitudes. Even the simple belief of being genetically identical could push them to think that their social environment expects them to be emotionally closer and thus they act accordingly. However, the question of EEA has been extensively discussed and the general conclusion is that this assumption is reasonably met (Plomin et al. 2013). Moreover, in our sample, an additional check has found no evidence of EEA violation. Twins in our sample actually appear to behave according to their true zygosity.

Despite the significant relationship found between zygosity and self-sacrifice, the degree of genetic relatedness did not appear to affect the willingness to fight for the co-twin if threatened or insulted or to hurt someone to protect their sibling, suggesting that self-sacrifice and willingness to fight for the co-twin may depend on a different combination of factors. In fact, the evolutionary psychological perspective suggests that aggression is context-specific (Buss and Shackelford 1997). Hence, the aggressive component present in some altruistic behaviors may not depend mainly on genetic relatedness. Perhaps other contextual components (e.g., group membership, kind of aggression, or social roles), including perceived social closeness (Hackman et al. 2017), exert a strong influence on eliciting aggressive behavior, which would overcome that of precise genetic relatedness. Proximal mechanisms such as identity fusion (for a review see Gómez and Vázquez 2015) or identification with a group (Lickel et al. 2006; Yzerbyt et al. 2003) have been used to explain aggressive behavior when a member of a group is threatened. Moreover, Mediterranean countries are influenced by honor codes, which emphasize family values and respect and approve particular types of violence as a reaction to personal or collective affronts (Guerra et al. 2013; Rodríguez Mosquera et al. 2008). Thus, pertaining to the same group (i.e., family and twin pair), regardless of zygosity, may be sufficient to elicit an aggressive response of this kind. This explanation would not contradict the reports of more-intense reactions to offenses against kin than those against non-kin (Gesselman and Webster 2012) since the responses would be modulated by group closeness.

Apart from differences linked to zygosity, gender differences were also found in both disposition to self-sacrifice and willingness to fight for the co-twin. According to our results, females are generally more prone to fight or sacrifice for their co-twins than males. Recent research on fight and self-sacrificing behaviors that accounts for gender

differences usually reports that males show higher scores than females on these traits (Gómez et al. 2011), and most research on gender differences in aggression supports a male preeminence for these behaviors in a wide variety of situations (Bettencourt and Miller 1996; Eagly and Steffen 1986; Gesselman and Webster 2012), especially regarding physical aggression (Archer 2009; Giles and Heyman 2005; Salmivalli and Kaukiainen 2004). The difference in our results could be related to the subject of the threat. Whereas males are more prone to sacrifice for their country or group (Swann et al. 2014; Van Vugt 2009), females would be more inclined to sacrifice and show aggressive behaviors to protect relatives, which, by the way, is not exclusive to our species. Evolutionary premises support the adaptive character of a greater investment by females than males in close relatives (Neyer and Lang 2003), and that female aggression is modulated by the greater centrality of mothers to offspring survival (Campbell 2013). Importantly, our questions focused specifically on physical aggression, which is where the largest difference between males and females is found (Archer 2009); in other forms of aggression, such differences appear to be lower (i.e., verbal aggression) or inverted (i.e., indirect aggression). Hence, questions addressing other forms of aggression could have produced a different pattern of results.

We found only one exception in the altruistic behavior pattern related to gender: when males have a sister, their willingness to sacrifice and fight or die for their co-twin parallels that of females. Inclusive fitness helps to explain that, for both males and females, helping a female relative is always more efficient in evolutionary terms than helping a brother given that paternity carries some degree of uncertainty. Hence protecting a sister who can be a mother of future related offspring would be more likely than protecting a brother (Kenrick et al. 2003). Additionally, the probability of sharing genes with a sibling could also affect altruism by increasing the chance of one's own genes being propagated by kin (Grafen 2006). For instance, a female shares on average $\frac{3}{4}$ of X-linked genes with a sister but only $\frac{1}{4}$ with a brother, and both males and females share mitochondrial genes with their sister's offspring but not with their brother's. Processes studied from a social psychology standpoint could be regarded as the proximate causes of sex differences in social behavior, with social roles accounting for some inter- and intra-sex variability (Archer 2009). First, norms regulating help are different in female and male gender roles. Whereas the helping behavior expected from women consists of caring for others especially in close relationships, the sort of helping consistent with the male gender role occurs both in close relationships and with strangers and encompasses risky acts of rescuing others and courteous and protective behaviors often directed toward women (Eagly and Crowley 1986). Women's traditional social role implies that they ought to take care of family members (Eagly and Wood 1999), and the very concept of sacrificing for their family might cause them to feel more obliged to show altruistic behaviors toward relatives. This same social role would define them as weaker than men and deserving of protection, especially from their male relatives (Glick and Fiske 2001), who could feel social pressure to take care of their female co-twin. In this vein, Fitzgerald and Ketterer (2011) found that males were more predisposed to fight to defend a sister than a brother. Hence, a male role regarding female relatives could increase the perception of indirect aggression, defined as an attack/offense directed toward belongings, status, or relationships (Richardson

and Green 1999), which would produce the typical high reactivity in males when they are provoked (Bettencourt and Kernahan 1997). Moreover, although females in OSDZ pairs apparently take more responsibility and play a more active role than their male siblings (Pulkkinen et al. 2003), self-reported co-twin dependence seems to be more prevalent among girls in opposite-sex dyads (Penninkilampi-Kerola et al. 2005). Finally, another compatible explanation of the observed male variability in altruistic behavior could be the competitiveness and rivalry between members of same-sex male twin pairs (Mark et al. 2017), which could act by lowering the likelihood of behaving altruistically toward their male counterparts.

In summary, our results support the notion that genetic relatedness facilitates the development of non-aggressive altruistic behavior, supporting the inclusive fitness explanation for altruism, whereas aggression-related behavior appears to depend more heavily on social factors related to specific gender roles. However, our conclusions also need to take into account some limitations of this study and future directions. Although the sample is distinctive and includes appropriate comparisons in terms of genetic relatedness, incorporating other kinds of relatives would have allowed further insights. In addition, future research could widen the characterization of the studied behaviors to account for specific situations and kind of responses (e.g., forms of aggression assessed), as well as possible mediating variables between zygosity and altruistic behaviors. Furthermore, we could not include all the subjects in the same analysis since it would not be possible to control for the intervening variables. Although opposite-sex MZ twins are obviously impossible, other alternatives (e.g., analyzing DZ twins who vary in degree of genetic relatedness based on genome scans) could be explored. Finally, given the importance of social roles, cultural factors could also be studied, and replication from additional samples and with different characteristics (e.g., age) could be of great interest.

Despite these limitations, to the best of our knowledge this is the first study that analyzes self-sacrifice and aggressive altruistic behavior in twins. Using this kind of sample has allowed us to make a direct comparison of genetic relatedness and provide additional support for the inclusive fitness explanation of nepotistic altruism. Future research using twins could be instrumental in illuminating this area of research.

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Compliance with Ethical Standards

Ethical Approval MTR participants were contacted through postal letter invitation, which contained information regarding the objectives of the registry and study information. Twins were later contacted by telephone. Oral informed consent was obtained from all individual participants included in the study, prior to any data collection taking place. All MTR procedures, including informed consent and data collection for this study, was approved by the Murcia University Ethical Committee. National regulations regarding personal data protection were followed. All procedures performed in this study involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

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