RESEARCH ARTICLE



Do Monozygotic Twins Have Higher Genetic Quality than Dizygotic Twins and Singletons? Hints from Attractiveness Ratings and Self-Reported Health

Satoshi Kanazawa¹ · Nancy L. Segal²

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Abstract

Evolutionary theories generally concur that sexual reproduction and genetic recombination evolved to maximize genetic variability. Thus, the existence of monozygotic (MZ) twins, which do not take advantage of genetic recombination for each offspring, poses a puzzle. Evolutionary logic of inclusive fitness suggests that parents with high-quality genes may be more likely to produce MZ twins. Analyses of data from the National Longitudinal Study of Adolescent to Adult Health show that MZ twins were significantly more physically attractive and healthier than dizygotic (DZ) twins and singletons. These results suggest that MZ twins may possess higher-quality genes than DZ twins and singletons, and support one of the first evolutionary theories of MZ twinning that specifies its ultimate functions.

Keywords Twin research · Monozygotic twin conception · Add Health

Researchers have identified several factors associated with an increased probability of dizygotic (DZ) twin conceptions, such as later maternal age, African ancestry, greater coital frequency, use of assisted reproductive technologies, and even consumption of white yams (Segal 2000, 2017). Yet researchers have not made comparable advances in identifying factors associated with monozygotic (MZ) twinning. With the possible exceptions of left-handedness (Boklage 1981) and use of assisted reproductive technologies that increase MZ twinning to some extent, albeit less than DZ twinning (Aston et al. 2017; Segal 2017), researchers have not identified parental characteristics reliably associated with a higher likelihood of MZ twinning. In particular, although researchers have determined that the tendency to have MZ twins may be heritable in a subset of families and in specific populations in places like India and Iran (Segal 2017), with only a few exceptions, no one has proposed an evolutionary theory of MZ twinning or identified its *ultimate functions*. Gleeson et al. (1994) explain the emergence of genes for cloning (MZ twinning) in the context of parent-offspring conflict and show that such a gene can evolve in a haploid species if the benefits of increased frequency of the genotype outweigh the cost of reduced survival chances given limited parental resources. Craig et al. (1997) propose that polyembryony evolved in species as a routine or obligate means of reproduction when either the embryo has better information about the optimal clutch size in a given environment than the mother does or the mother is limited in the number of eggs she can produce. However, neither of these theories explain *individual differences* in the tendency to have MZ twins. *Which parents* are more likely to have MZ twins, and *why*?

Given their costs, why sexual reproduction and genetic recombination initially evolved and continued to be maintained is one of the persistent and unresolved puzzles in evolutionary biology (Otto and Lenormand 2002). There are a large number of hypotheses for the evolution and maintenance of sexual reproduction and genetic recombination (Kondrashov 1993). However, "most of the evolutionary hypotheses for sex stem from the idea that sex generates greater variability because chromosomal segregation and recombination break down genetic associations. It is therefore thought that modifier alleles that increase the frequency of sex and recombination are favoured because they improve the ability of a population

Satoshi Kanazawa S.Kanazawa@lse.ac.uk

¹ Department of Management, London School of Economics and Political Science, Houghton Street, London WC2A 2AE, UK

² Department of Psychology, California State University-Fullerton, Fullerton, USA

to evolve by increasing the genetic variation on which natural selection acts" (Otto and Lenormand 2002, p. 255).

Genetic variability of offspring has benefits not only for the population as a whole but for the offspring's parents as well. For example, the Aphid-Rotifer Model of the evolution of sexual reproduction "proposes that there is normally a survival of the literally 'fittest,' and that prospects may be highly unfavorable for the merely typically fit. Sexual reproduction increases variation in fitness and thereby increases the number of extraordinarily fit offspring" (Williams and Mitton 1973, p. 553). What are parents to do when one of their offspring turns out to be "extraordinarily fit," with the highest genetic quality as measured by the absence of deleterious mutations in the genome, as a chance result of random recombination of parental genomes? One fitnessmaximizing strategy parents can pursue to take advantage of chance production of such "extraordinarily fit" offspring is to clone them and create MZ twins.

This reasoning suggests that MZ twins may be more likely to be "extraordinarily fit," carrying higher-quality genes than DZ twins (who do not result from cloning and are genetically no different from full siblings) and singletons. Conversely, parents who already have higher-quality genes, who are statistically more likely to produce "extraordinarily fit" offspring as a result of random genetic recombination, may be more likely to have MZ twins than parents with relatively low-quality genes. While offspring of high-quality parents are on average expected to be of higher genetic quality than offspring of low-quality parents, not all offspring of high-quality parents are of *equally* high quality, due to the random nature of genetic recombination. Our logic suggests that high-quality parents are more likely to clone offspring of particularly high genetic quality and produce MZ twins.

Two phenotypic indicators of genetic quality are physical attractiveness and health. Physical attractiveness, indexed by bilateral symmetry, averageness, and markers of secondary sexual characteristics (Mealey et al. 1999; Thornhill and Gangestad 1993), is a phenotypic indicator of genetic quality and health; beauty can be considered a "health certification" (Thornhill and Møller 1997, pp. 528–533). As a result, more physically attractive individuals appear to be healthier than less physically attractive individuals (Langlois et al. 2000). We would therefore expect that more physically attractive and healthier individuals, who likely carry higherquality genes, are more likely to have MZ twins than are less physically attractive and healthy individuals. Equivalently, we would expect MZ twins to be more physically attractive and healthier than DZ twins and singletons. We are not inherently interested in explaining individual differences in physical attractive and health; we only use them as empirical indicators of underlying genetic quality.

Empirical Analyses

Data

The National Longitudinal Study of Adolescent to Adult Health (Add Health) is a large, nationally representative, and prospectively longitudinal study of young Americans. A sample of 20,745 adolescents were personally interviewed in their homes in 1994–1995 (Wave I: mean age = 15.6 years), and they were subsequently interviewed in 1996 (Wave II), 2001–2002 (Wave III), and 2007–2008 (Wave IV). Additional details of sampling and study design are provided at http://www.cpc.unc.edu/projects/addhealth/design. We analyzed the data with SPSS Version 23. Table 1 presents the descriptive statistics separately by twin status.

Dependent Variable: Twin Status

Add Health assessed the twin status of each respondent during Wave I by asking the mother whether the respondent was a twin. If the mother said yes, then Add Health asked "In your opinion, are _____ and _____ identical twins or fraternal twins?" The mother could respond as follows: 1=definitely identical, 2=probably identical, 3=probably fraternal, or 4=definitely fraternal. We collapsed "definitely" and "probably" and created a binary measure of zygosity. There were 425 individual MZ twins (203 female, 222 male) and 950 individual DZ twins (418 female, 469 male). From this information, we created two dummies for MZ twin status (1 if MZ twin, 0 otherwise) and DZ twin status (1 if DZ twin, 0 otherwise). Add Health conducted DNA analysis at

Table 1 Descriptive statistics

	Full sample $(n=20,674)$	Singletons $(n=19,299)$	DZ twins $(n=950)$	MZ twins $(n=425)$
Physical attractiveness	3.56	3.55	3.57	3.74
	(0.867)	(0.868)	(0.821)	(0.912)
Health	0.0000	-0.0032	0.0172	0.1076
	(1.000)	(1.0083)	(0.8977)	(0.8174)

Main entries are the means

(Numbers in parentheses are standard deviations)

Wave III and discovered that only 9% (n=34) of the twins' zygosity was misclassified by mothers' self-report at Wave I (Harris et al. 2006, p. 992). Note that, unlike most studies in twin research (Frazier et al. 2014; Segal 2012), our sample contained only one twin in each pair, not both. While Add Health does have separate genetic samples of twins and siblings, we used the main sample. Thus all the twins (and singletons) in our sample were genetically unrelated.

Independent Variable: Physical Attractiveness

At the conclusion of the in-home interview at Wave I, the Add Health interviewer rated the respondent's physical attractiveness on a five-point ordinal scale (1 = very unattractive, 2 = unattractive, 3 = about average, 4 = attractive, 5 = very attractive). The Add Health measure of physical attractiveness has been shown to be very reliable, with very high interrater reliability across waves (mean Rwg = 0.7861; 95% CI 0.7815–0.7907) (Kanazawa and Still 2018, Table 1). Rwg (within-group interrater reliability) is a measure of interrater agreement, which varies from 0, when judges are in total lack of agreement, to 1.0, when judges are in perfect agreement. No measures of parents' physical attractiveness or health are available in Add Health.

Bilateral symmetry and averageness are two important determinants of physical attractiveness. Attractive faces are more symmetrical than unattractive faces (Gangestad et al. 1994; Mealey et al. 1999; Perrett et al. 1999) because fluctuating asymmetry increases with genetic disruptions such as mutations and inbreeding (Parsons 1990, 1992). Facial averageness also increases physical attractiveness. Faces with features closer to the population averages are more attractive than those with extreme features (Langlois and Roggman 1990; Rubenstein et al. 2002) because averageness results from the heterozygosity rather than homozygosity of alleles at loci; thus individuals with average faces are more resistant to a larger number of parasites and are less likely to be homozygous on deleterious alleles (Thornhill and Gangestad 1993). Thus the two determinants of physical attractiveness-bilateral symmetry and averageness-are both indicators of genetic quality.

Independent Variable: Health

Add Health measured the health of the respondents during Wave I by asking them how frequently they experienced 20 separate ailments during the last 12 months, such as headache, feeling hot all over suddenly for no reason, and stomach ache or upset stomach. For each question, the respondents could respond: 0=every day, 1=almost every day, 2=about once a week, 3=just a few times, 4=never. We performed a principal component analysis to extract a latent factor for health from these 20 responses. Factor loadings were moderately high, ranging from 0.379 to 0.646. The principal component analysis used the SPSS default values; the extraction method used the correlation matrix, the extraction criterion was a minimum Eigenvalue of 1.0, and no rotation was used. The latent factor explained 31.4% of the variance. The extracted factor correlated very highly with the sum (r=0.995) and the median (r=0.851) of the 20 raw indicators. The latent factor for health had a mean of 0 and a standard deviation of 1. Multiple-indicator model and principal component analysis are designed to eliminate random measurement errors (Costner 1969). However, given the recent concerns with the use of the best linear unbiased prediction in evolutionary biology (Hadfield et al. 2010; Houslay and Wilson 2017), caution is necessary in interpreting the coefficient for this variable.

Statistical Method

We analyzed the data with binary logistic regression, with the twin status as the dependent variable, and physical attractiveness and health simultaneously entered as independent variables. For the graphical presentation in the figures, we performed one-way ANOVAs, comparing the three subsamples (singletons, DZ twins, MZ twins).

Results

Table 2, Column (1), shows that both physical attractiveness (b=0.249, SE=0.057, p<0.001) and health (b=0.136, p<0.001)SE = 0.059, p = 0.020) were independently positively associated with MZ twin status in a binary logistic regression, demonstrating that, relative to all others (DZ twins and singletons), MZ twins were significantly more physically attractive and healthier. In sharp contrast, Column (2) shows that DZ twin status was not at all associated with physical attractiveness (b = 0.016. SE = 0.038, p = 0.677) or health (b = 0.015, SE = 0.035, p = 0.666). DZ twins were therefore no more physically attractive or healthier than everyone else (MZ twins and singletons). Further, in a limited sample of twins only, Column (3) shows that MZ twins were significantly more physically attractive (b = 0.235, SE = 0.070, p < 0.001) and marginally significantly healthier (b = 0.125, SE = 0.071, p = 0.076) than DZ twins. Although women are significantly more attractive than men (Kanazawa 2011), and MZ twins are more likely to be female (Loos et al. 1998; Segal 2017), controlling for sex or race did not alter the main results presented in Table 2 at all. The results of these binary logistic regression analyses supported the prediction.

Figure 1 presents the results graphically for physical attractiveness, showing that MZ twins were more physically attractive (M=3.7) than either DZ twins (M=3.6) or singletons (M=3.6) [F(2, 20,671)=9.467, p < 0.001]. Similarly, Fig. 2 shows that MZ twins were healthier (M=0.11) than

Table 2Associations betweentwin status and indicators ofgenetic quality

	(1)	(2)	(3)
	MZ twin (vs. everyone else)	DZ twin (vs. everyone else)	MZ twin (vs. DZ twin)
Physical attractiveness	0.249***	0.016	0.235***
	(0.057)	(0.038)	(0.070)
Health	0.136*	0.015	0.125^{\dagger}
	(0.059)	(0.035)	(0.071)
Intercept	-4.778	-3.090	-1.671
	(0.220)	(0.141)	(0.264)
$\chi^2 (df=2)$	24.517***	0.365	14.747***
Number of cases	20,674	20,674	1,375

Main entries are unstandardized regression coefficients

(Numbers in parentheses are standard errors)

 $^{\dagger}p < 0.10, *p < 0.05, **p < 0.01, ***p < 0.001$

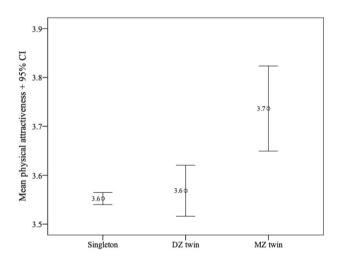


Fig. 1 Mean physical attractiveness, by twin status

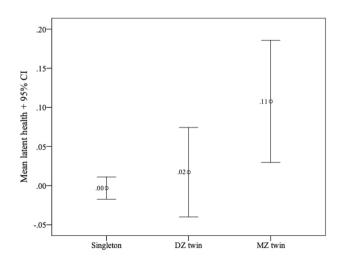


Fig. 2 Mean health, by twin status

either DZ twins (M = 0.02) or singletons (M = 0.00) [F(2, 20,742) = 2.701, p = 0.067].

Discussion

The analyses of Add Health data showed that MZ twins were significantly more attractive and healthier than either DZ twins or singletons, while DZ twins were no different from singletons. Because both physical attractiveness and health are phenotypic indicators of genetic quality, the results suggested that MZ twins and their parents had higher-quality genes than DZ twins and singletons. The results were consistent with the suggestion that parents might clone "extraordinarily fit" embryos of exceptionally high genetic quality and parents of particularly high genetic quality might be more likely to have MZ twins because they are statistically more likely to produce "extraordinarily fit" offspring as a consequence of random genetic recombination.

There are some important limitations in our study that require caution in interpreting our results. Both of our measures of genetic quality (physical attractiveness and health) are very indirect. Further, the physical attractiveness measure is based on one rating by one interviewer, and the health measure is based on self-report, rather than measured by a physician. In addition, the effect sizes, even when statistically significant, are often very small.

While the empirical results are consistent with our suggestion that parents are more likely to clone "extraordinarily fit" embryos of exceptionally high genetic quality, there may be alternative explanations for our finding that MZ twins have higher genetic quality than DZ twins and singletons. First, while our suggestion is that it is the parents that "decide" to clone offspring of exceptionally high genetic quality (that is, parents might be evolutionarily selected to possess the genetic tendency to clone embryos of extraordinarily high genetic quality), it is also possible that it is the "extraordinarily fit" embryos themselves that "decide" to clone themselves (that is, embryos might be evolutionarily selected to possess the genetic tendency to clone themselves when they are of extraordinarily high genetic quality). However, this explanation encounters at least two immediate difficulties. It is not only the genes inside "extraordinarily fit" embryos that have genetic interest in cloning themselves to maximize inclusive fitness, but all genes in all embryos. And how are the genes in the embryos to assess their genetic quality *in comparison to* all past and future offspring of the same parents (Craig et al. 1997)? Parents, who are aware of their own genetic quality, are in a better position to "assess" how "extraordinarily fit" a given embryo may be.

An evolutionary explanation that can potentially overcome these difficulties is that parents might produce MZ twins randomly with respect to the genetic quality of the embryos, but only cloned embryos of extraordinary genetic quality can survive the process of cloning and the common hazards of a subsequent MZ twin pregnancy, in particular, the two-thirds of MZ twins who are monochorionic (Dube et al. 2002). This explanation, however, has difficulty explaining how relatively low-quality DZ twins can survive the twin pregnancies, even though DZ twins (albeit with rare exceptions) do not share their chorion (Souter et al. 2003). Because of the particular circumstances of their gestation, both MZ and DZ twins often suffer from premature birth, low birth weight, and other early health complications. However, the two-thirds of MZ twins who are monochorionic are at potential risk for twin-to-twin transfusion syndrome and many (though not all) studies find that MZ twins are more likely to be born with structural anomalies than DZ twins (Rustico et al. 2005; but see; Sperling et al. 2007), perhaps explaining why MZ twins would have to be of exceptionally high genetic quality to survive the pregnancy.

It is conceivable that there exist non-evolutionary, nongenetic explanations for how life experiences as an MZ twin might increase MZ twins' physical attractiveness and health, independent of their genetic quality. The life experience of growing up as an MZ twin is very different from that of growing up as a DZ twin or singleton. MZ twins generally share a much closer social relationship with each other and grieve to a greater extent than DZ twins do when one cotwin passes away (Segal 2011). The minority of MZ twins who regularly attend twin festivals may be especially alike in appearance and invested in being a twin. These twins, who are not representative of MZ twins in general, may intentionally enhance their physical similarities and, consequently, their visual interest but not necessarily their physical attractiveness. However, both physical attractiveness and health are highly heritable, with shared environments having little effects (Mitchem et al. 2014; Thornhill and Møller 1997). It therefore seems unlikely that growing up as an MZ twin can substantially enhance these measures. One way to test this hypothesis would be to compare MZ twins raised together with those raised apart and with those whose cotwin died in infancy. Another way is to compare attractiveness and health between MZ twin pairs whose members intentionally did or did not highlight their similar appearance.

As noted earlier, a possible limitation of the present study is that twins' physical attractiveness was assessed by a oneitem measure of overall appearance. While the Add Health measure of physical attractiveness has been shown to be highly reliable (Kanazawa and Still 2018), research shows that physical attractiveness may vary as a function of the body parts of interest, body movements and possibly the sex of the rater (Nedelec and Beaver 2011). Nevertheless, our results are of interest and, to the best of our knowledge, ours is the first evolutionary theory of MZ twinning that explains individual differences in the tendency to bear MZ twins. If correct, the theory generates other empirical implications. For example, the embryo quality hypothesis of pregnancy sickness (Forbes 2017) posits that higher-quality embryos produce larger amounts of human chorionic gonadotropin, which induce their mothers to experience more severe episodes of pregnancy sickness. If true, then the evolutionary theory of MZ twinning would suggest the testable hypothesis that mothers of MZ twins may experience more severe pregnancy sickness than mothers of DZ twins or singletons.

While the preliminary empirical analyses were consistent with the theoretical prediction, further research is necessary to replicate our finding that MZ twins are on average more physically attractive and healthier than DZ twins or singletons, suggesting that parents of MZ twins may have higher-quality genes than those of DZ twins and singletons. (Unfortunately, most twin studies that include physical attractiveness measures fail to report twin group means; see, for example, McGovern et al. 1996; Mitchem et al. 2014.) The finding that MZ twins outlive DZ twins for both genetic and experiential reasons further supports our result (Christensen et al. 1995; Hjelmborg et al. 2006; Sharrow and Anderson 2016), although some researchers have challenged this finding. Our theory can also explain why there are more female than male MZ twins (Loos et al. 1998; Segal 2017). There is evidence that male embryos with low genetic quality are selectively spontaneously aborted (Catalano et al. 2009, 2012). Future studies should examine the genomes of the parents of MZ twins directly to establish, among other things, that they may possibly have lower mutation loads than the genomes of the parents of DZ twins and singletons.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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