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In-group favoritism is ubiquitous in human societies (Bernhard, Fischbacher, & Fehr, 2006; LeVine & Campbell, 1972; Sumner, 1907). Competition for resources exacerbates in-group favoritism (Sherif, 1966; Sherif & Sherif, 1956); however, favoritism continues to exist even in the absence of such competition (Billig & Tajfel, 1973; Tajfel, 1982; Tajfel, Billig, Bundy, & Flament, 1971; Yamagishi & Mifune, 2008) and extends to arbitrary affiliations (Locksley, Ortiz, & Hepburn, 1980; Yamagishi & Mifune, 2008). Such observations, coupled with the survival and reproductive benefits of group membership (Baumeister & Leary, 1995), suggest that mechanisms fostering alignment with the in-group are likely to have been subject to positive selection in humans (Hammond & Axelrod, 2006).

If the selective benefits of in-group favoritism have been high while the cues for affiliation have been arbitrary (rather than limited to a small set of essentialist types), selection could have favored the development of a flexible central affiliation mechanism (CAM) that has access to the full range of perceptual information signifying group membership (Kurzban, Tooby, & Cosmides, 2001; Rand et al., 2009). If such a central mechanism underlies human in-group favoritism, then the drive to prefer own-group members may be high, and the chosen in-group will be relatively arbitrarily assembled on the basis of context and will be updatable over time. By contrast, a strong-specificity hypothesis suggesting that affiliation is based on a set of essentialist features, such as kinship, ethnicity, or shared beliefs, predicts that favoritism will be uncorrelated across domains, relatively hard to form from arbitrary cues, and relatively invariant to context (Gil-White, 2001; Hirschfeld, 1996). Although previous research has tended to favor either a CAM or an essentialist model of favoritism, it is also plausible that both a flexible CAM system and a set of essentialist mechanisms have evolved in humans.

Research suggests that group affiliation is relatively flexible for at least some features (Rand et al., 2009), although certain types of groupings appear to robustly retain special salience (Gil-White, 2001; Hirschfeld, 1996). Therefore, we predicted that a mixed model containing both a flexible CAM system and a set of essentialist mechanisms have evolved in humans.

Genetic Evidence for Multiple Biological Mechanisms Underlying In-Group Favoritism

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Abstract
In-group favoritism is ubiquitous and associated with intergroup conflict, yet is little understood from a biological perspective. A fundamental question regarding the structure of favoritism is whether it is inflexibly directed toward distinct, “essentialist” categories, such as ethnicity and race, or is deployed in a context-sensitive manner. In this article, we report the first study (to our knowledge) of the genetic and environmental structure of in-group favoritism in the religious, ethnic, and racial domains. We contrasted a model of favoritism based on a single domain-general central affiliation mechanism (CAM) with a model in which each domain was influenced by specific mechanisms. In a series of multivariate analyses, utilizing a large, representative sample of twins, models containing only the CAM or essentialist domains fit the data poorly. The best-fitting model revealed that a biological mechanism facilitates affiliation with arbitrary groups and exists alongside essentialist systems that evolved to process salient cues, such as shared beliefs and ancestry.

Keywords
in-group favoritism, ethnocentrism, religion, genetics, twins

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mechanism and specialized essentialist mechanisms would best explain human in-group favoritism. We tested these contrasting mechanisms using measures of in-group favoritism across three important social groupings—religion, ethnicity, and race. Favoritism according to these groupings was assessed in a large, genetically informative, and population-representative twin sample and analyzed using multiple-group multivariate structural modeling.

The three theoretical models make clear predictions about behavior and, in particular, about the patterns of correlation that should be observed between different types of favoritism. Multivariate behavior genetics research designs allowed us to discriminate among these theories through the predicted patterns of genetic and environmental influences on in-group favoritism. In particular, the common-pathway model was developed by Kendler, Heath, Martin, and Eaves (1987) as a powerful statistical tool precisely to distinguish among these types of competing theories (i.e., those with a common underlying mechanism for a given set of traits vs. those with a unique mechanism specific to each trait); in the research reported here, we applied the common-pathway model to in-group favoritism.

If a common brain or mental system underlies multiple behaviors (as is predicted by the CAM model of in-group favoritism), then environmental and genetic effects on these diverse behaviors must be mediated by this central (or common) pathway, as shown in the upper portion of Figure 1. However, if each behavioral domain reflects the operation of distinct, essentialist brain or mental systems, then each of these behaviors will result from its own unique genetic (A), shared-environment (or familial-environment; C), and unique-environment (E) effects (see the lower portion of Fig. 1). Finally, if the brain or mental systems underlying favoritism involve both a common flexible system and additional distinct, essentialist mechanisms, then a mixed model (i.e., one encompassing both parts of Fig. 1) would be required to explain the observed pattern of behavior.

We tested these competing theories of in-group favoritism by comparing three models: Model 1, the CAM model; Model 2, the essentialist model; and Model 3, the mixed

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**Fig. 1.** Predictions from the central affiliation mechanism (CAM) and essentialist theories of in-group favoritism. As illustrated in the upper portion of the figure, if there is a single neural or mental mechanism for affiliation across multiple behavioral domains, this would constrain genetic (A) and environmental (C, shared environment, and E, unique environment) influences on favoritism to be mediated through the CAM factor. However, as illustrated in the lower portion of the figure, if there are distinct, essentialist mechanisms (i.e., if each essential group-formation domain has its own evolved mechanism), different kinds of favoritism would have different sets of genetic and environmental influences.
model. Model 1 assumes that favoritism is not based on essentialist systems and allowed us to test the prediction that genetic and environmental effects operating solely via a single common favoritism factor fit the data well. Model 2 allowed us to test the prediction that only specific influences operating on each favoritism trait are required for the model to achieve a good fit to the data, and that there is no need for a common favoritism factor. Model 3, the full common-pathway model, allowed us to test the prediction that both a general favoritism mechanism and additional specific (essentialist) effects are required to provide an adequate fit to the data.

Method

Participants

Phenotypic data were available for 957 pairs of twins contacted by the MacArthur Foundation Survey of Midlife Development (MIDUS) in the United States (Kendler, Thornton, Gilman, & Kessler, 2000; Kessler, Gilman, Thornton, & Kendler, 2004). The pairs of twins were assessed for religious, ethnic, and racial in-group favoritism, among other behaviors. Of the monozygotic (MZ) pairs, 167 were male (mean age = 44.6 years, SD = 11.4) and 194 were female (mean age = 43.7 years, SD = 12.2). Of the dizygotic (DZ) pairs, 136 were male (mean age = 44.6 years, SD = 12.4), 210 were female (mean age = 45.8 years, SD = 12.6), and 250 were opposite-sex pairs (mean age = 45.9 years, SD = 11.8).

Measures of in-group favoritism

For each group type, we assessed three distinct elements of in-group favoritism: (a) strength of identification with the group, (b) preference for affiliating with in-group members, and (c) the importance placed on marrying within the group. For instance, religious in-group favoritism was assessed with the following items: “How closely do you identify with being a member of your religious group?” “How much do you prefer to be with other people who are the same religion as you?” and “How important do you think it is for people of your religion to marry other people who are the same religion?” The items for ethnic and racial in-group favoritism had the same wording as the items for religious in-group favoritism, except that the appropriate group type was substituted (e.g., “How closely do you identify with being a member of your racial group?”). All responses were made on 4-point Likert scales (from 1, very, to 4, not at all). Interitem correlations were high within each group type (ranging from .32 to .65, with all but one correlation greater than .40), and scale scores were calculated as the sum of item scores within a group type.

Analysis

Prior to conducting the analyses, we controlled for the effects of age and sex, and standardized residuals were used in subsequent analyses (McGue & Bouchard, 1984). A classical twin design was used. We used structural equation modeling to model the covariance of MZ twins in terms of additive genetic effects, shared-environment effects, and unique-environment effects. These models were estimated by full-information maximum-likelihood analysis using OpenMx (Boker et al., 2010, in press).

Results

Intraclass correlations indicated that MZ twins were significantly more similar to each other than were DZ twins for all three types of in-group favoritism, a pattern suggesting a genetic influence (see Fig. 2). For ethnic in-group favoritism, MZ correlations were more than twice the DZ correlations, suggesting nonadditive genetic variance. However, because of the clear theoretical importance of the shared environment for all three types of in-group favoritism, we tested models incorporating additive genetic and shared- and unique-environment influences (the classical ACE model) for each type rather than modeling genetic dominance effects. The full results of the univariate modeling for each type of in-group favoritism are presented in Univariate Modeling and Table S1 in the Supplemental Material available online.

The three theoretical models were compared with a standard baseline model—the Cholesky ACE decomposition incorporating all three favoritism traits (for fit statistics and comparison statistics for all models, see Table 1 and Table S2 in the Supplemental Material; for diagrams of the baseline and other models, see Path Diagrams Excluding Opposite-Sex Dizygotic Twin Pairs in the Supplemental Material).

The prediction that a CAM factor alone provides an adequate explanation of favoritism (Model 1) was tested first. This model, which includes a common-pathway mechanism but no genetic pathways specific to any domain of in-group favoritism, fit significantly worse than the baseline model, \( \Delta \chi^2(6) = 38.89, p < .01 \). Thus, contrary to the CAM-only theory, essentialist pathways are required to explain favoritism.

Next, we tested whether essentialist factors alone are sufficient to model in-group favoritism (Model 2). This model, lacking a CAM, also fit significantly worse than the baseline model, \( \Delta \chi^2(6) = 845.68, p < .01 \). Thus, contrary to the essentialist-only theory, a common or context-sensitive system is required to explain favoritism.

Finally, Model 3 (the mixed model) was tested. This model posited both a CAM system and essentialist factors, including correlated unique-environment pathways at the essentialist level. This model fit the data with no significant decrement from the fit of the baseline model, \( \Delta \chi^2(1) = 0.60, p = .44 \). This finding strongly supports the idea that both the CAM and essentialist genetic effects are required to explain variation in favoritism. We conducted chi-square comparisons...
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as a rigorous and direct test of Model 3 against nested Models 1 and 2. These comparisons indicated that both Model 1, $\Delta \chi^2(3) = 21.65, p < .01$, and Model 2, $\Delta \chi^2(3) = 222.49, p < .01$, showed a significant loss of fit compared with Model 3, our preferred model. This indicated again that both the CAM and essentialist genetic effects are required to explain variation in favoritism.

We then examined whether Model 3 could be further simplified without significant loss of fit. No genetic paths could be removed without significantly worsening fit. A marginal exception was the essentialist genetic path to religious favoritism. Dropping this path (Model 3a) did not cause a nominally significant decrease in fit, $\Delta \chi^2(1) = 3.60, p = .058$ (see Fig. S5 in the Supplemental Material); however, the model demonstrated an inferior fit relative to Model 3 according to Akaike’s information criterion (AIC; AIC increased to 3,338.42 from 3,336.82), and this path was therefore retained.

Exploring the role of environments on favoritism, we examined the significance of the shared- and unique-environment effects. It was possible to drop all shared-environment paths without significant loss of fit (Model 3b), $\Delta \chi^2(4) = 3.47, p = .48$. In a final step, we examined unique-environment influences. This step revealed that there were no significant effects from the common unique-environment influence on racial in-group favoritism, nor from the specific unique-environment influence on ethnic in-group favoritism: In Model 3c, the common unique-environment path was removed, $\Delta \chi^2(1) = 2.73, p = .10$, and in Model 3d, the specific unique-environment path was removed, $\Delta \chi^2(1) = 0.04, p = .84$. The final reduced model is shown in Figure 3.

### Table 1. Fit Statistics and Comparison Statistics for All Models

<table>
<thead>
<tr>
<th>Model</th>
<th>No. of parameters</th>
<th>$-2LL$</th>
<th>AIC</th>
<th>Reference model</th>
<th>$\Delta \chi^2$</th>
<th>$\Delta df$</th>
<th>$p$</th>
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<tbody>
<tr>
<td>Baseline</td>
<td>21</td>
<td>12,968.22</td>
<td>3,340.22</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1</td>
<td>15</td>
<td>13,007.11</td>
<td>3,365.11</td>
<td>Baseline</td>
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<td>6</td>
<td>&lt;.01</td>
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<tr>
<td>2</td>
<td>15</td>
<td>13,813.90</td>
<td>4,171.90</td>
<td>Baseline</td>
<td>845.68</td>
<td>6</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>3</td>
<td>20</td>
<td>12,968.82</td>
<td>3,336.82</td>
<td>Baseline</td>
<td>0.60</td>
<td>1</td>
<td>.44</td>
</tr>
<tr>
<td>3a</td>
<td>19</td>
<td>12,972.42</td>
<td>3,338.42</td>
<td>3</td>
<td>3.60</td>
<td>1</td>
<td>.058</td>
</tr>
<tr>
<td>3b</td>
<td>16</td>
<td>12,972.29</td>
<td>3,332.27</td>
<td>3</td>
<td>3.47</td>
<td>4</td>
<td>.48</td>
</tr>
<tr>
<td>3c</td>
<td>15</td>
<td>12,975.02</td>
<td>3,333.02</td>
<td>3b</td>
<td>2.73</td>
<td>1</td>
<td>.10</td>
</tr>
<tr>
<td>3d (final model)</td>
<td>14</td>
<td>12,975.06</td>
<td>3,331.06</td>
<td>3c</td>
<td>0.04</td>
<td>1</td>
<td>.84</td>
</tr>
</tbody>
</table>

Note: Model 1 models the common affiliation mechanism, Model 2 is an essentialist model, and Model 3 is the mixed model. Model 3a excludes the essentialist genetic path to religious favoritism, Model 3b excludes all shared-environment paths, Model 3c excludes the common unique-environment path (to racial in-group favoritism), and Model 3d excludes the specific unique-environment path (to racial in-group favoritism). $\Delta \chi^2$ is the change in $-2$ log likelihood ($-2LL$), and $\Delta df$ is the change in the degrees of freedom, relative to the reference model. AIC = Akaike’s information criterion.
Discussion

This study is the first, to our knowledge, to provide genetic evidence that in-group favoritism, at least at the level of religion, ethnicity, and race, is underpinned by both a CAM and essentialist favoritism systems, each with significant genetic and environmental components. These results are compatible with recent behavioral research and game-theoretic modeling (Baumeister & Leary, 1995; Hammond & Axelrod, 2006) and suggest that human in-group favoritism is best understood in terms of a multicomponent architecture supporting both essentialist domains (Gil-White, 2001; Hirschfeld, 1996) and a flexible CAM supporting dynamic group affiliation (Cosmides, Tooby, & Kurzban, 2003). With regard to the relative influences of the CAM system and the essentialist systems on each of the favoritism traits, squaring the factor loadings demonstrates that the CAM accounts for 35%, 69%, and 21% of variation in religious, ethnic, and racial favoritism, respectively. These data indicate that the CAM only partially mediates religious, ethnic, and racial favoritism, and that substantial influences on favoritism also occur at the essentialist-system level.

Our results indicated that the shared environment does not exert significant influences on favoritism. Although our choice of final model reflected the most parsimonious interpretation of the data, our study was not sufficiently powered to detect small shared-environment effects. Further research is recommended to address this potentially important, albeit likely modest, source of variation in in-group favoritism. Conversely, although our final model contained an essentialist genetic influence on religious favoritism, removing this path only marginally worsened the model’s fit to the data. Therefore, further research is recommended to clarify whether the genetic influences on religious in-group favoritism are wholly mediated through the CAM or act in tandem with it.

Perhaps the most interesting environmental effect was that elements of the unique environment acting at the essentialist level exerted effects countervailing environmentally mediated religious favoritism, such that elevated levels of religious favoritism were associated with lowered levels of ethnic favoritism. This may reflect the influence of religious teachings, which may increase ethnic tolerance, or the possibility that religion became superordinate to coalitions based on ethnicity.
Although the three group types we studied tap commonly studied and relevant bases of in-group favoritism, future research could fruitfully be extended to additional domains—for instance, loyalty to military, political, and sports coalitions; employer and workplace affiliation; and detailed close-kin affiliations. Cross-cultural studies would also be useful to determine the extent to which our results generalize across societies. Such research could further understanding of the extent to which the reported common factor influences the full range of in-group favoritism behaviors and could reveal whether favoritism in other group domains reflects the specialized systems in our final model or additional specialized systems.

In conclusion, this study provides evidence that in-group favoritism possesses both a CAM and additional, specific affiliation mechanisms, each with a distinct genetic architecture and distinct responses to unique environments. These findings have significant implications for theories addressing the evolution of, and the mechanisms underpinning, human group behavior.

Declaration of Conflicting Interests
The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Supplemental Material
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