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The cognitive and cultural foundations of moral behavior

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ARTICLE INFO

ABSTRACT

Does moral culture contribute to the evolution of cooperation? Here, we examine individuals' and communities' models of what it means to be good and bad and how they correspond to corollary behavior across a variety of socioecological contexts. Our sample includes over 600 people from eight different field sites that include foragers, horticulturalists, herders, and the fully market-reliant. We first examine the universals and particulars of explicit moral models. We then use these moral models to assess their role in the outcome of an economic experiment designed to detect systematic, dishonest rule-breaking favoritism. We show that individuals are slightly more inclined to play by the rules when their moral models include the task-relevant virtues of "honesty" and "dishonesty." We also find that religious beliefs are better predictors of honest play than these virtues. The predictive power of these values' and beliefs' local prevalence, however, remains inconclusive. In summary, we find that religious beliefs and moral models may help promote honest behavior that may widen the breadth of human cooperation.

1. Introduction

Many theories hold that socially learned moral norms are the lynchpin for the remarkable breadth of cooperation that humans uniquely exhibit (Bowles & Gintis, 2003; Boyd, 2018; Boyd & Richerson, 2009; Chudek & Henrich, 2011; Richerson et al., 2016). However, there are a few critical outstanding issues that make this view difficult to endorse with a confidence borne out by direct empirical evidence. First, it is not immediately obvious that individuals' and groups' moral prescriptions actually influence the behavior of those who espouse them (e.g., Graham, Meindl, Koleva, Iyer, & Johnson, 2015; Haidt, 2001; Perry, 2017; Smith, Blake, & Harris, 2013). When moral prescriptions and behavior are consistent with each other, moral prescriptions might simply be rationalizations of behavior rather than causes (e.g., Baumard, 2016; Haidt, 2001). Second, despite the fact that so many emphasize (or minimize) the importance of culture for human co-

operation, few actually measure its effects directly and model it as a distributed, superordinate property of social life (see Smaldino, 2014). Most empirical studies consider culture indirectly by either a) having participants in economic experiments make an allocation with money and then asking what the appropriate decision was (e.g., Gurven, Zanolini, & Schniter, 2008; Ensminger & Henrich, 2014; Henrich & Henrich, 2014, b) framing experimental introductions in locally salient ways (e.g., Brodbeck, Kugler, Reif, & Maier, 2013; Cohn, Fehr, & Maréchal, 2014; Cronk, 2007; Gerkey, 2013; Lesorogol, 2007; Stagnaro, Arechar, & Rand, 2017), or c) conducting studies across multiple groups, and concluding that cross-cultural variation in behavior reflects underlying variation in culture (e.g., Apicella, Marlowe, Fowler, & Christakis, 2012; Henrich, 2000; Henrich et al., 2004; Roth, Prasnikar, Okuno-Fujiwara, & Zamir, 1991). Third, many cross-cultural studies emphasizing the evolved psychology underlying morality rely heavily on theoretically-motivated scale designs (e.g., Curry, Chesters, & Van

Lissa, n.d.; Graham et al., 2011) that a) use items lacking in local relevance, b) are impractical for innumerate and/or nonliterate populations, c) presuppose that samples have the lexical equivalent of "moral," and d) do not link this data to quantitative behavior.

Here, we seek to overcome these limitations by measuring moral culture from a variety of societies and examine whether or not moral values and their distributions actually have an impact on the kind of broader cooperation typified by humans. We first briefly spell out our assumptions and introduce contemporary evolutionary perspectives on moral systems, followed by a more detailed assessment of the aforementioned limitations. We then introduce our two studies. The first consists of an analysis of systematically collected ethnographic data regarding what it means to be "good" and "bad" across eight different field sites. In doing so, we examine cross-cultural moral universals and local particulars. The second study uses this data to examine its contribution to corresponding behavior in an experimental game designed to distinguish dishonest favoritism from impartial, rule-following fairness. We conclude with a discussion of our studies' limitations and comment on avenues for further inquiry.

2. Background

2.1. Defining moral systems

We refer to "moral models" here as the content and structure of individuals' explicit representations of moral norms. If we adopt the view that "culture" is shared, socially transmitted information (cf. Boyd & Richerson, 1988; R. G. D'Andrade, 1981; Sperber, 1996), then moral culture is the shared, socially transmitted units that comprise individual moral models. Defined in this fashion, local prevalence of particular units of socially transmitted information indicates how "cultural" or "normative" those units are. In this view, then, directly assessing whether or not culture influences individual behavior requires 1) detailing individuals' models, 2) assessing how widespread the content of those models is in individuals' social groups, 3) examining the relationship between a behavioral trait and an individuals' models, and 4) examining the relationship between the trait and how prevalent specific informational units are in one's group. The first two requirements are descriptive, ethnographic accounts of moral culture. The latter most two allow us to disambiguate the relative impacts of individual and cultural models of morality on behavior. If moral culture predicts moral behavior, then the prevalence of moral models' constituent units in a group should covary with the target behavior.

We use "moral systems" here to refer to moral models, their psychological underpinnings, behavioral expressions, cultural prevalence, and the causal links between them (cf. Alexander, 1987; Haidt & Kesebir, 2010; Kiper & Sosis, 2014). Classical philosophical and contemporary social psychological views of moral systems emphasize universality and/or the view that morality is associated with abstract notions like "justice" and "rights" (Caton, 1963; Kant, 1997 [1785]; Turiel, 1983, 2006). In contrast, many evolutionary views boil down moral systems to the regulation of cooperative and/or mutualistic endeavors that generate individual- and/or group-level benefits (Alexander, 1987; Baumard, André, & Sperber, 2013; Barrett et al., 2016; Cosmides & Tooby, 2005; Cronk, 1994; Curry, 2016; Darwin, 1871; Greene, 2013; Fehr, Fischbacher, & Gächter, 2002; Haidt & Kesebir, 2010; Machery & Mallon, 2010; Mizzoni, 2009; Sripada & Stich, 2006; Trivers, 1971; Tomasello & Vaish, 2013). However, there is considerable variation in moral systems, variation that many suggest are inconsequential or run counter to such generalist theories (Baumard, 2016; Boehm, 1980; Buchtel et al., 2015; Fessler et al., 2015; Schwartz, 2007; Shweder, Much, Mahapatra, & Park, 1997; Smith, Smith, & Christopher, 2007). As we detail below, piecing together the constituent parts of moral systems in a cross-cultural empirical project remains a major challenge in the evolutionary literature.

2.2. Measuring components of moral systems

2.2.1. Evolutionary psychology of morality

Contemporary evolutionary psychological research focused on mapping the conceptual space of morality typically relies on scale items (Curry et al., n.d.; Graham et al., 2011) with prefabricated materials that are verified externally (i.e., using other scales). For example, seeking to better operationalize the moral domain with attention to cross-cultural validity, the popular "Moral Foundations" literature breaks down the evolutionary and cognitive "foundations" of morality into a few core dimensions. While the rubric itself has evolved (Graham et al., 2013), the most recent iteration includes (1) harm/care; (2) fairness/reciprocity; (3) ingroup/loyalty; (4) authority/respect, and (5) purity/sanctity as foundational to moral reasoning. The more recent "Morality-as-Cooperation" literature (Curry, 2016; Curry et al., n.d.) measures seven types of cooperation treated as the foundations for moral behavior: (1) family values; (2) group loyalty; (3) reciprocity; (4) dominance; (5) deference; (6) fairness; and (7) rights to property.

These rubrics were not designed to assess the relationship between moral culture and behavior. Rather, they seek to identify variation in moral reasoning as indicated by variation in how survey items load onto principal components and how mean values of scales vary across different groups. There are practical and methodological reasons to be reluctant to employ scale-based surveys in populations where they were not designed. First, many traditions lack the lexical equivalent of "morality." Second, some samples struggle with scale-based survey instruments. While convenient for researchers, in practice, scale items can be quite taxing and unintuitive for non-literate and/or innumerate participants (e.g., Gurven, Von Rueden, Massenkoff, Kaplan, & Lero Vie, 2013). Third, such instruments are often limited in local relevance. For example, the "Moral Foundations Questionnaire" (Graham et al., 2011) includes questions about whether or not "being good at math," having "love for one's country," being "denied rights," and "God's approval" are "relevant to [participants'] moral thinking" or to their sense of right and wrong. Such items and the notion of "moral relevance" are simply unintelligible in many contexts. Ideally, scale design in cross-cultural research begins with preliminary ethnographic inquiry to ensure that scale items are actually measuring target constructs (Bernard, 2011; Handwerker, 2001). Indeed, Smith et al. (2007) found that other theory-driven classification schemes inadequately captured the variation in folk-models of what it means to be "good" in seven different communities. Boehm (1980) imported a morality metric to Montenegro, but due to participants' initial off-target responses to the metric, he had to assess features of local moral behavior with open-ended questions.

2.2.2. Cultural evolutionary ecology of moral behavior

Those who emphasize culture's effects on cooperative behavior typically employ economic experimental games as an index of cooperation, but do not directly measure or model "culture." Some appeal to the importance of cultural institutions (i.e., shared pools of norms that constrain human interactions in specific, socially demarcated contexts; see D'Andrade, 2006; North, 1991; Searle, 1995) by manipulating the cultural relevance of experiments' instructions in the form of framing effects (Brodbeck et al., 2013; Cohn et al., 2014; Cronk, 2007; Lesorogol, 2007; Gerkey, 2013). Others conduct experiments and infer that culture contributes to the evolution of cooperation by virtue of statistical divergences between groups in experimental game outcomes (Apicella et al., 2012; Ensminger & Henrich, 2014; Henrich, 2000; Henrich et al., 2004; Roth et al., 1991). A burgeoning literature that actively measures variation in cultural information focuses on religious beliefs (McNamara, Norenzayan, & Henrich, 2016; Johnson, 2016; Purzycki et al., 2016a). This literature typically uses individuals' beliefs in punitive and knowledgeable deities to predict cooperative outcomes. However, the literature ignores the within-group distribution of religious beliefs–that is, groups' religious culture–as a factor in individual behavior.

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To the best of our knowledge, only a solitary study claims to assess the degree to which specifically *moral* culture has an effect in co-operation (Gurven et al., 2008; cf. Ensminger & Henrich, 2014; Henrich & Henrich, 2014, for more case studies from the same cross-cultural project). The study, which the authors characterize as "the first of its kind to show that local culture matters in explaining variation in pro-social behavior" (pg. 589), employed a variation of the Dictator Game in which participants were asked to identify "the morally correct offer to give in this...game" (3). While there were a few exceptions in their sample of nine Tsimane' (Bolivia) villages, in general there was a positive correlation between what people thought they should do in the game and how they actually allocated money. Note that the Tsimane' lack a word for "moral"; the researchers instead used *ruijsis* which "expresses the concept of appropriate behavior or action" (pg. 592). The authors "argue that local differences [in cooperation] are not necessarily due to strong norms *per se* that vary among villages, but due to local (unmeasured) effects that push and pull villages towards more or less pro-social sentiment" (pg. 589). Note, however, that this study elicited participants' views of the "appropriate" behavior for the experiment, not more general individual-level moral models or their distributions from which participants ostensibly drew.

In summary, while many argue about culture's role in the expansion of cooperation, and many examine a variety of important factors' contributions to this process, the cooperation literature does not directly probe the contribution of moral culture itself. Likewise, studies that have measured variation in moral culture do not link them to corresponding behavior. Here, we attempt to assess the relationship between individual moral models and cooperation directly, with an eye to the aspects of local culture—moral models' prevalence—that may serve as inputs to individual behavior. First, we assess the degree to which there are universals and particulars of moral culture by examining what people consider "good" and "bad" (Study 1). We then examine the respective roles of individual moral models and culture in the allocation of money using an experimental economic game designed to measure honest, impartial rule-following behavior towards anonymous others (Study 2).

3. Participants

We collected data in eight different field sites (see Table 1). These samples included (1) the Hadza of Tanzania; (2 and 3) inland and coastal villagers from Tanna, Vanuatu; (4) residents of Marajó island in Brazil; (5) Fijians from Yasawa island; (6) Indo-Fijians from Lovu; (7) Tyvan residents in Kyzyl, Tyva Republic; and (8) Indo-Mauritian residents of Porte aux Piment. Our sample is notably diverse; modes of subsistence range from the foraging Hadza and horticultural inland Tannese to the fully market-integrated economies of Kyzyl and Porte aux Piment.

This sample exhibits some of the considerable cross-cultural diversity known to cultural anthropology; our participants range from the fully market-integrated (e.g., Mauritians and Marajó Brazilians) to subsistence foragers and horticulturalists (e.g., the Hadza and Inland Tanna, respectively). Our sample thus includes people from traditional,

small-scale communities, whose means of living are subsistence-based with daily interactions consisting primarily with local familiars as well as urban samples where individuals regularly interact with anonymous others. Moreover, our samples are uniquely poised for consideration of our research questions and methods. No such work examining explicit moral models has been conducted among traditional, small-scale societies. Our methods (see below) are particularly useful for eliciting rich and comparable ethnographic data in innumerate and nonliterate samples often ignored or left out in studies relying on prefabricated scales and/or narrow samples.

4. Study 1: moral culture

While not every group has the lexical equivalent of "moral," some posit that the distinction between "good" and "bad" is a human universal (Brown, 1991; Wierzbicka, 1994). We can assess whether or not the content of these conceptual domains approximate morality simply by asking people what it *means* to be good and bad. To reliably capture moral models and culture, we assess freely-elicited data of what it means to be "good" and "bad" (see Buchtel et al., 2015; Purzycki, 2011, 2016; Smith et al., 2007, for precedent applications). This method allows individuals to answer on their own terms and avoids the aforementioned pitfalls associated with a lack of cultural relevance, the question of what measurement instruments actually measure, or the elicitation of rationalizations of behavior.

4.1. Methods

All materials were translated in local languages and back-translated into English for corroboration and subsequent edits. To obtain reliable, naturalistic, and culturally relevant data about morality, we asked participants to

- *Please list up to 5 behaviors that make someone a good/virtuous/moral person.*
- *Please list up to 5 behaviors that make a bad/immoral person.*

All free-list data were translated into English and subsequently submitted to Purzycki for compiling and coding. All original open-ended responses in English and the subsequently coded data are publicly available here https://github.com/bgpurzycki/Moral-Models-Moral-Behavior for re-assessment, further recoding, and analysis. See the Supplementary data for further materials, methodological notes, and per-site English translations of instructions of the free-list tasks.

4.1.1. Analysis

We analyzed the free-list data using the AnthroTools package (Jamieson-Lane & Purzycki, 2016; Purzycki & Jamieson-Lane, 2016) for R (R Core Team, 2016). This package calculates the cognitive salience of individual free-list items and tabulates their mean salience score (Smith's S). These scores can be calculated at the sample- and sub-sample (i.e., field site) levels. Individual item salience (i) is calculated with Eq. (1):

Table 1

Descriptive features of each field site. See Purzycki et al. (2016b) and the Supplementary data for further details.

Site/sample	Researcher	Sampling method	World religion	Economy
Coastal Tanna	Atkinson	Cluster sampling (census)	Christianity	Horticulture/market
Hadza	Apicella	Entire camps	None	Foraging
Inland Tanna	Atkinson	Entire community	None	Horticulture
Lovu, Fiji	Willard	Door-to-door	Hinduism	Market
Mauritians	Xygalatas	Random (street) sampling	Hinduism	Farming/market
Marajó, Brazil	Cohen	Random sampling (census)	Christianity	Market
Tyva Republic	Purzycki	Random and chain sampling (street)	Buddhism	Herding/market
Yasawa, Fiji	McNamara	Door-to-door	Christianity	Horticulture/market

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$$i = \frac{n + 1 - k}{n} \tag{1}$$

where n is the total number of items an individual listed, and k is the order in which an item was listed. Smith's S (Eq. (2)) is a sample's mean value of item type (Smith, 1993; Smith, Furbee, Maynard, Quick, & Ross, 1995; Smith & Borgatti, 1997):

$$S = \frac{\sum i_T}{N} \tag{2}$$

Here, we denote item type with i_T and N denotes the total sample or sub-sample size (i.e., the denominator is not limited only to those participants who listed a given item). Smith's S will therefore increase as a function of ubiquity and earlier placement in lists. In order to minimize inflated Smith's S values due to repeated items within lists, we used AnthroTools' "MAX" function which includes only the earliest-listed repeated item in its calculations.

It is important to note that our reported salience indices may reflect underestimations for three reasons. First, in terms of individual item salience, participants were encouraged to list up to only 5 items per sub-domain (i.e., "good" and "bad"). If these items would have been the earliest-listed in a task without such a constraint, all data considered here would have had much higher salience scores. Secondly, we retain items listed by only one individual in our analysis. Dropping such idiosyncratic items would decrease the denominator in Eq. (1) and therefore increase the salience values. Thirdly, for the sake of completeness, we include those individuals who simply answered "I don't know" (1 participant for the "good" list and 3 for the "bad"). Though negligible, these would inevitably have an item salience of 1 and contribute to a larger denominator in Eq. (2).

4.2. Results

4.2.1. Moral universals

What constitutes a "moral" or "good" person? Participants (N = 643) listed a total of 2478 items (M_{Listed} = 4.27, SD = 1.07) in this sub-domain. Table 2 and Fig. 1 show the salience of individually-listed items where S ≥ 0.10. We use this cut-off to minimize table lengths. Many participants listed various items that simply re-expressed the question (e.g., good people have "good hearts" or exhibit "good behavior"). For the purposes of analysis, these items were given the same code. After this, the most salient item for participants was "generosity" or "sharing," followed by "helpfulness" and "honesty."

For the sake of reference and discussion, we include a *post hoc*

Table 2

Sample salience scores ≥0.10 for what makes a good person (N = 643). Salience (M) is the average individual item salience among individuals who listed a given item, Smith's S is the individual item salience of the sample, and n is the number of participants listing the item. Foundation column indicates corresponding type in the "Moral Foundations" literature, while Cooperation type column denotes corresponding type in the "Morality-as-Cooperation" literature. Question marks indicate possible interpretations or lack of obvious correspondence. * denotes clustered items such as good conscience, good behavior, good nature, good heart.

Item	Foundation	Cooperation type	Salience (M)	Smith's S	n
Good*	–	–	0.73	0.22	195
Generous/ shares	Fairness/ reciprocity	Reciprocity	0.64	0.18	178
Helpful	Fairness/ reciprocity	Reciprocity	0.59	0.17	183
Honest	Honesty/ deception	?	0.69	0.14	129
Respectful	Authority/ respect	Group loyalty	0.56	0.13	144
Loving	Care/harm	?	0.61	0.11	113
Kind	Care/harm	?	0.73	0.10	88

coding of item types by their corresponding categories in the Moral Foundations (Graham et al., 2013, 2011) and Morality-as-Cooperation (Curry, 2016; Curry et al., n.d.) literatures. If we take these most salient items and apply their equivalent label in the Foundations and Co-operation typologies, it is clear that items in the "fairness/reciprocity" domain are the most salient. This suggests a greater cultural stability for this "foundational" category. While "honesty" appears in the Foundations typology and ranks among the items with the highest salience in the present free-lists, there is not a broad consensus about honesty in the literature; others simply include honesty as another moral sub-domain (Ashton, Lee, & de Vries, 2014; Blasi, 1980; Hofmann, Wisneski, Brandt, & Skitka, 2014) of the greater repertoire of moral foundations and the Morality-as-Cooperation literature bypasses it. Regardless, these results are consistent with what we would expect given the evolutionary literature's view of morality as a system regulating social exchange and cooperation (Alexander, 1987; Curry et al., n.d.): fairness and reciprocity loom large in mental models of what it means to be good. "Loving" and being kind are also included. While the Foundations literature considers this as part of the Care/Harm foundation, it is not immediately clear how these fall within the scope of the Cooperation typology, a limitation acknowledged in Curry et al. (n.d.).

What makes an "immoral" or "bad" person? In this sub-domain, participants (N = 650) listed 2728 items (M = 4.20, SD = 1.14). Table 3 details the top five items where S ≥ 0.10. Fig. 1 illustrates the content of these models by salience. Much like the "good" data, many participants reiterated the question in their responses (e.g., bad people exhibit "bad behavior"). Also consistent with the evolutionary literature, "theft" is the most salient item listed across cultural groups (the antithesis of generosity), followed by "deceit" and "violence." Notably—and not often considered in much of the evolutionary literature (cf. Kurzban, Dukes, & Weeden, 2010; Rozin, 1999)—the use and abuse of drugs, alcohol, and other substances are among the chief items listed in what makes a "bad" person. It may be that people really do see the consumption of drugs and alcohol as bad in and of itself, but they also may view intoxicants as the source of bad behavior and therefore indicative of immoral conduct. Here too, the Foundations literature has a little more coverage than the Morality-as-Cooperation literature.

Cross-culturally, the most salient components of individuals' mental models of morality revolve around the provisioning of material resources in the form of generosity, helpfulness, and theft. We might interpret honesty and dishonesty as facets of material goals as well insofar as it is virtuous to be honest about how much others stand to gain or lose in interactions (per Ashton et al., 2014; Fischbacher & Föllmi-Heusi, 2013, see below). However, as is made clearer in our examination of site-specific moral models, there is also some variation that is not immediately related to cooperation.

4.2.2. Moral particulars

While we presently have neither the room to contextualize each site's specific results nor the means to make confident inferences about why cross-cultural variation exists (i.e., we only have 8 groups and cross-sectional data), the analysis of moral particulars does indicate that patterns in the global sample are not merely artifacts of a few groups driving the results. For the sake of concision, we present the most salient item listed by site. Table 4 details the items with the highest salience scores by site for the "good" free-list data. Table 5 details the items with the highest salience scores by site for the "bad" list. More exhaustive tables are available in the Supplementary materials (Tables S2 and S3).

Across the most salient items of what constitutes good people, we find some curious idiosyncrasies. For instance, Indo-Mauritians listed "speaks well" (i.e., polite and considerate as opposed to rude and obscene) earlier and more often in lists than did other groups. Notably, Indo-Fijians (Lovu, Fiji) likewise ranked "speaks well" highly (S = 0.10) while all other sites ranked it lower when listed at all (S values were ≤0.04). This suggests a distinct cultural lineage; both are
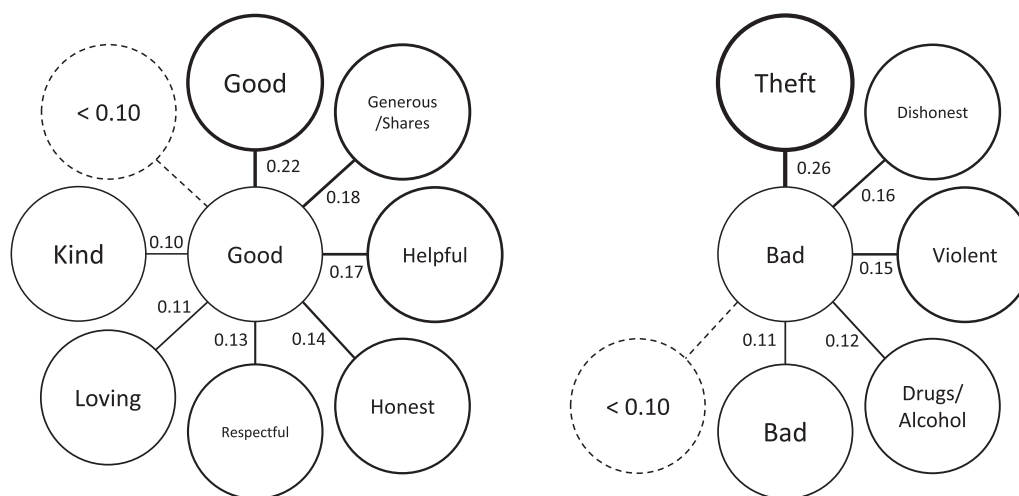
Fig. 1. Universal moral models. Center circle represents the domain. The most salient items in these domains are on top with item connection weights (Smith's S values) descending clockwise.

Table 3

Sample salience scores ≥ 0.10 for what makes a bad person (*N* = 650). Salience (M) is the average individual item salience among individuals who listed a given item, Smith's S is the individual item salience of the sample, and *n* is the number of participants listing the item. Foundation column indicates corresponding type in the "Moral Foundations" literature, while Cooperation type column denotes corresponding type in the "Morality-as-Cooperation" literature. Question marks indicate possible interpretations or lack of obvious correspondence. * denotes clustered items such as bad conscience, bad behavior, bad nature, bad heart.

Item	Foundation	Cooperation type	Salience (M)	Smith's S	*n*
Theft	Fairness/reciprocity	Property rights	0.71	0.26	235
Dishonest	Honesty/deception	?	0.66	0.16	156
Violent	Care/harm	?	0.65	0.15	153
Drugs/alcohol	Purity/sanctity (?)	?	0.70	0.12	108
Bad*	–	–	0.71	0.11	101

Indian diaspora populations that may have common-source value systems. Going to church was the most salient item for Fijians from Yasawa. This particular value does not obviously fit in the Moral Foundations or Morality-as-Cooperation rubrics and was not ranked highly at any other site. We nevertheless suggest "foundations" or "cooperation type" into which these might be classified in Tables 4 and 5. Likewise, in Marajó, "ignorance/arrogance" has the highest salience, although the small Smith's S suggests minimal consensus at this site.

This term *ignorante* is locally nuanced, and refers to one who ignores others' opinions and holds their own as superior. This is also not obviously a component of the Moral Foundations rubric. Note that for half of the sites, "theft" had the highest salience for what constitutes a bad person; for the other half, save Marajó, group-level salience for theft was > 0.10: Hadza (S = 0.31); Mauritius (S = 0.15); Tyva Republic (S = 0.13). Again, we refer readers to the more thorough tables in the Supplementary materials.

4.2.3. Discussion

Cross-culturally, the most salient indicators of good people are generosity and sharing, helpfulness, and honesty. The most salient indicators of bad people are theft, dishonesty, and violence. Theft is notable insofar as it might be construed as the antithesis of cooperation; Baumard (2016) characterizes it as "violating the logic of balanced interests" (126). These items largely correspond to rubrics offered by the Foundations and Cooperation literatures, but a closer look at site-specific moral models appear to complicate those rubrics insofar as articulateness, religious piety, drug and alcohol use and abuse, and ignorance and arrogance are not consistently considered. Aside from illustrating their limited breadth and narrow focus, our data pose little problem for the approaches; we are explicitly measuring representational models of morality rather than moral reasoning or judgment of a particular behavior. That said, it does suggest that the methods used in this literature have not captured some potentially informative variation found in cultural representations of what it means to be (im)moral.

While the above results map cross-cultural models of morality for eight populations, one remaining question is whether or not the content

Table 4

Per-site items with highest salience scores for what makes a good person. Salience (M) is the average individual item salience within individuals who listed a given item and Smith's S is the individual item salience of the sub-sample. Sample size (*n*) is site-specific sample size for sub-domain. Foundation column indicates corresponding type in the "Moral Foundations" literature, while Cooperation type column denotes corresponding type in the "Morality-as-Cooperation" literature. Question marks indicate possible interpretations or lack of obvious correspondence.

Site	Item	Foundation	Cooperation type	Salience (M)	Smith's S	*n*
Coastal Tanna	Generous/shares	Fairness/reciprocity	Reciprocity	0.74	0.40	44
Hadza	Loving[a]	Care/harm	?	0.62	0.40	69
Inland Tanna	Hospitable	Care/harm	Group loyalty (?)	0.74	0.45	74
Lovu, Fiji	Honest	Honesty/deception	?	0.73	0.38	79
Mauritius	Speaks well	Authority/respect (?)	Deference (?)	0.84	0.33	82
Marajó, Brazil	Helpful	Fairness/reciprocity	Reciprocity	0.70	0.18	77
Tyva Republic	Honest[a]	Honesty/deception	Reciprocity (?)	0.74	0.28	115
Yasawa, Fiji	Goes to church	Purity/sanctity (?)	Group loyalty (?)	0.68	0.39	103

[a] Second highest salience within sample after the lumped "good" category (see above).

Table 5

Per-site items with highest salience scores for what makes a bad person. Salience (M) is the average individual item salience within individuals who listed a given item and Smith's S is the individual item salience of the sub-sample. Sample size (*n*) is site-specific sample size for sub-domain. Foundation column indicates corresponding type in the "Moral Foundations" literature, while Cooperation type column denotes corresponding type in the "Morality-as-Cooperation" literature. Question marks indicate possible interpretations or lack of obvious correspondence.

Site	Item	Foundation	Cooperation type	Salience (M)	Smith's S	*n*
Coastal Tanna	Theft	Fairness/reciprocity	Property rights	0.76	0.46	44
Hadza	Murder	Care/harm	?	0.52	0.34	69
Inland Tanna	Theft	Fairness/reciprocity	Property rights	0.76	0.37	78
Lovu, Fiji	Theft	Fairness/reciprocity	Property rights	0.82	0.36	79
Mauritius	Violence	Care/harm	?	0.65	0.30	84
Marajó	Ignorance/arrogance	Authority/respect (?)	Deference (?)	0.69	0.14	76
Tyva Republic	Dishonest	Honesty/deception	?	0.70	0.35	117
Yasawa, Fiji	Theft	Fairness/reciprocity	Property rights	0.80	0.33	103

and ubiquity of moral models affect behavior. To assess this, we examined the effects of the presence and cognitive salience of honesty or dishonesty on a behavioral economic experiment that measured systematic and partial allocations. We predicted that in a game that measures dishonest favoritism indicative of systematic rule-breaking, the cognitive salience of "honesty" and "dishonesty" should predict fairer play. In other words, by measuring whether an individual's moral model includes honesty and dishonesty, we can assess his or her resistance to the opportunity to cheat. To assess the impact of moral culture, we also modeled group-level cultural prevalence of these components.

5. Study 2: moral behavior

5.1. Methods

5.1.1. Economic experiment

To measure honest behavior, we had participants play an economic game designed to detect dishonest favoritism (Cohn et al., 2014; Fischbacher & Föllmi-Heusi, 2013; Hruschka et al., 2014; Jiang, 2013; McNamara et al., 2016; Purzycki et al., 2016a). In this experiment, participants have a stack of 30 coins, a fair 6-sided, 2-colored die, and two cups designated for a specific individual. They think of which cup they want to put a coin into and then they roll the die. If one pre-designated color appears, they are supposed to put the coin into the cup they thought of. If the other color appears, they are supposed to put the coin into the cup opposite the one they thought of. They repeat this until all 30 coins are in cups. They make these decisions alone without any outside observers. Regardless of individual decisions, coins should be randomly allocated to either cup if participants follow instructions. However, since participants play alone, they can allocate more coins to the cup of their preference.

In our study, participants played two counterbalanced games, each with two cup dyads. The "Local Community Game" included one cup reserved for an anonymous co-ethnic, co-religionist in the participant's local community and one was for an anonymous, geographically distant co-religionist who was also a co-ethnic by default. In the "Self Game," one cup was reserved for the player and the other cup for another anonymous co-ethnic, co-religious individual in the same specified geographically distant region. Players got to keep the money that went into their own cups and we distributed all allocations to randomly-selected individuals designated by the other cups. Here, the geographically distant players function as an index of the kind of broader cooperation that is unique to humans; as participants are not likely to ever interact with these distant players, playing according to the rules indicates an unwillingness to favor themselves or their community.

Show-up fees for participation were ~25% of the average daily wage in our field sites. We set aggregate stakes at roughly a single day's wage (x) where individual die rolls were worth the closest coin in value to x/number of games played/30 coins. Coins were real currency in

each site except for the Hadza who played with tokens each worth 8 oz. (~226.80 g) maize. All participants were tested for game comprehension and knew that all coins would be distributed to those designated by the cups, including themselves. Only participants who passed the comprehension questions are included in this data set.

After experiments, participants answered a host of interview questions, including the aforementioned free-list tasks. Note that in experiments were predominantly those who completed free-list tasks, but there a few who did not complete free-lists or cases where individuals who participated in free-list tasks did not participate in experiments. They were also asked what they thought the experiment was about; their open-ended responses were coded for whether they mentioned cheating, fairness, or honesty. Participation took a total of ~90 min, with the free-list task typically taking place ~15 min after the game. Briefly, there are at least five reasons why this ordering had no effect on free-list outcomes: 1) free-list tasks were after demographic surveys, 2) the game check question is not correlated with listing (dis)honesty, 3) some sites simply did not list (dis)honesty frequently, 4) previous research (Smith et al., 2007) not using experiments in this fashion shows that listing "honest" is quite prevalent cross-culturally, and 5) comparing the data from one site with and without the experiment shows no indication of games having an effect (see Section 3.4 of the Supplementary data for more details).

All methods, materials, and data are available online at https://github.com/bgpurzycki/Moral-Models-Moral-Behavior.

5.1.2. Does moral culture matter?

If moral models contribute to the expansion of cooperation, listing (dis)honesty should predict playing by the rules. Participants who mention (dis)honesty will be more likely to allocate coins to the cup benefiting the recipient more socially distant from themselves—that is, someone non-local (as opposed to someone local), or someone other than the participant him- or herself. If the cognitive accessibility of task-relevant components of moral models is also important to the expansion of cooperation, we should see that salience of listing (dis)honesty increasing the chances of allocating coins as well. If moral culture contributes to the expansion of cooperation, then within-sample ubiquity of (dis)honesty in moral models should also have an effect on individual behavior. In other words, while an individual's moral model may induce fairer behavior, living in a context where more people share similar moral values–along with the expected repercussions of violating those values–should also contribute to the likelihood of playing honestly. Conversely, if moral culture evolves in response to local problems, it may actually be associated with *more* self-interested behavior. Previous work we build upon shows that individual-level beliefs about morally concerned gods' punishment and knowledge breadth (i.e., omniscience) predicted allocations to the distant play (Purzycki et al., 2016a). By the same logic, then, the more one's community claims that morally concerned deities know and punish people, the more likely individuals should behave fairly (or not). In sum, in addition to individuals' moral

Table 6
Summary statistics for individuals per site who participated in the experiment and listed "honest" and "dishonest" in the good and bad list respectively. *N* denotes number in sub-sample, *n* denotes those who listed "honest" and "dishonest," and Prop. refers to proportion of sub-sample listing these items. Means (M) and standard deviations (SD) are of item salience.

| Site | *N* | Honesty in good list | | | Dishonesty in bad list | | |
		n	Prop.	M(SD)	*n*	Prop.	M(SD)
Coastal Tanna	44	7	0.16	0.75 (0.20)	6	0.14	0.69 (0.22)
Hadza	68	8	0.12	0.52 (0.29)	10	0.15	0.59 (0.29)
Inland Tanna	76	1	0.01	0.25[a] (–)	2	0.03	0.71 (0.06)
Lovu, Fiji	76	40	0.53	0.73 (0.31)	41	0.54	0.65 (0.26)
Mauritius	91	4	0.04	0.57 (0.34)	4	0.04	0.55 (0.34)
Marajó	77	16	0.21	0.65 (0.31)	11	0.14	0.51 (0.35)
Tyva Republic	79	24	0.30	0.83 (0.20)	38	0.48	0.74 (0.28)
Yasawa, Fiji	72	4	0.06	0.40 (0.16)	18	0.25	0.72 (0.26)
Total	583	104	0.18	0.70 (0.29)	130	0.22	0.67 (0.28)

[a] Note that this value reflects the salience score of the single individual.

models and religious beliefs, within-sample ubiquity of (a) (dis)honesty in moral models, as well as (b) beliefs about moralistic gods' omniscience and (c) punishment, should predict fair play above and beyond the content of an.

To test whether moral models affect game play, we coded whether or not participants listed honesty or dishonesty in their free-lists and used the summation of these two indices as a predictor with possible values of 0, 1, and 2. As such, participants who did not answer free-list tasks or answered with "I don't know" are not considered in this analysis. Note that the odds of mentioning honesty and dishonesty are related; a logistic regression shows that the odds of listing dishonesty increase by 7.10 [95% CI = 4.48, 11.25] when participants list honesty.

5.1.3. Participants

Table 6 reports the summary statistics for experimental participants who listed "honesty" in the "good" list (*n* = 104, 51 women, mean age = 37.26) or "dishonesty" in the bad list (*n* = 130, 49 women, mean age = 39.32). Note the considerable variability in the number of participants who listed honesty or dishonesty across these eight populations. Ten individuals listed multiple items coded as "honest" for the "good" list and 9 individuals listed two items coded as "dishonest" for the "bad" list. Again, these individuals are treated as listing each only once.

5.1.4. Model

Again, elsewhere (Purzycki et al., 2016a, 2016b), we found that individuals' beliefs about morally concerned deities' punishment and knowledge breadth contributed to fairer play in a wide variety of model specifications. We also found that the more children people had, the more likely they were to allocate more coins to themselves and local communities. As some participants in the present study played in a treatment condition using various religious primes (with no overall effects detected), we hold this and game order (Local Community Game first = 1) constant in the regressions (see the Supplementary data for further details). In order to hold constant any effects for recognizing what the game was about, we created an indicator variable where values of 1 denote when participants thought the experiment was about fairness, honesty, and/or cheating (*n* = 31; 5% of the sample).

Here, we build upon the "Reduced models" in Purzycki et al. (2018). These reduced models were the result of backward-selected full models, had the lowest variance inflation factors, and largest sample sizes of any other model specification. We develop these models and their application in a few important ways. First, we incorporate moral models and culture as predictor variables at individual and group levels, respectively. Here, the group level refers to within-sample ubiquity. Second, we take group-level variation into account using varying effects. Rather

than hold intercultural variation constant, we incorporate it into our modeling structure (Gelman, 2006; Nezlek, 2010; Pinheiro & Bates, 2000). Third, we formally develop statistical models (see the Supplementary data) in a Bayesian framework. Fourth, using prior defined distributions, we impute our missing data.

Our outcome variable is the binomially distributed count of allocating coins to the socially distant cup. As mentioned above, this offers the strongest test of fairer play as the chances of allocating a coin to geographically distant people better approximates to playing fairly than do allocations to self- or local community (Hruschka et al., 2014; Purzycki et al., 2016a). The log-odds of each allocation is defined as a linear combination of

1. Varying intercepts for individual and group
2. Varying slopes by group for individual-level responses to moral models, moralistic gods' punishment, and moralistic gods' knowledge breadth
3. Fixed slopes by group for group-level average responses to moral models, moralistic gods' punishment, and moralistic gods' knowledge breadth
4. Simple effects for religious prime condition, order, game understanding check, game type, and number of children

The group-level responses are given their own statistical models, as they are not observed but rather must be inferred from the individual responses at each site. Rather than use simple fixed indices of group-level variation (e.g., the mean value for the cultural variables in each site), we infer them from the sample of individual statements. Then we simultaneously use the posterior distribution of each in the model. This retains all uncertainty so that we do not limit ourselves to point estimates that may lead to misleadingly false precision where there is actually a distribution of values within communities. For each set of beliefs—moral models, moralistic gods' punishment and knowledge breadth—we simultaneously estimate a varying intercept representing the average of each site's individual responses and use this intercept, with all associated uncertainty, as a predictor in the main model. This is analogous to a measurement error model, in which the group-level predictors are measured with error. In principle, then, our model is four simultaneous regressions: a main binomial regression predicting coin assignments and three varying intercept regressions predicting individual responses by field site. Formal details of the model are included in the Supplementary materials.

With one exception, each individual played both games. We therefore restructured the data set to include two duplicate participant-by-variable matrices and included a binary variable denoting which game it represents ("Self Game" = 1). We included all values for coins to distant co-religionists in a single vector and the cups designated for the local co-ethnic and participants in another single vector. The Hadza were not asked the game understanding check question, so we marginalized over these and imputed other missing values (see script for details, and the Supplementary data for alternate imputation strategies).

We fit this model using the R package rethinking (version 1.71) (McElreath, 2016, 2017) and rstan version 2.17.3 (Stan Development Team, 2017). We assessed chain convergence by inspecting traceplots, $\widehat{R}$ values, and the number of effective samples, and encountered no problems in sampling. The Supplementary materials include further analyses in a frequentist statistical framework and analyses considering the effects of item salience.

5.2. Results

5.2.1. Individual-level effects

Table 7 reports the main models. Values are exponentiated mean estimates (OR) and 95% credibility intervals (CI). We have highlighted the individual-level effects in Fig. 2. As indicated by the intercept,

Table 7

Exponentiated mean estimates (OR) and 95% credibility intervals (CI) of chances of allocating a coin to geographically distant co-religionists. The left-most model is the full model, the center model removes all moral variables, and the right-most model includes only individual-level moral models.

|	OR [95% CI]	OR [95% CI]	OR [95% CI]
(Dis)honesty summation	1.03 [0.96, 1.12]	–	1.03 [0.97, 1.09]
Moralistic gods' punishment	1.09 [0.93, 1.29]	1.10 [0.95, 1.26]	1.10 [0.96, 1.25]
Moralistic gods' knowledge	1.25 [1.03, 1.53]	1.25 [1.04, 1.51]	1.23 [1.02, 1.51]
Number of children	0.88 [0.70, 1.08]	0.86 [0.70, 1.06]	0.87 [0.70, 1.08]
Condition (treatment = 1)	0.97 [0.90, 1.05]	0.97 [0.89, 1.04]	0.96 [0.89, 1.04]
Local game played first = 1	1.02 [0.96, 1.09]	1.02 [0.96, 1.09]	1.02 [0.95, 1.10]
Game about honesty? (yes = 1)	1.00 [0.85, 1.20]	1.02 [0.87, 1.22]	1.02 [0.86, 1.20]
Game (self game = 1)	0.97 [0.93, 1.02]	0.97 [0.93, 1.02]	0.97 [0.94, 1.01]
Group-level moral models	1.30 [0.51, 3.59]	–	–
Group-level gods' punishment	1.65 [0.34, 6.25]	2.15 [0.59, 6.46]	2.23 [0.59, 6.55]
Group-level gods' knowledge	1.10 [0.29, 4.13]	1.18 [0.36, 4.01]	1.13 [0.38, 3.41]
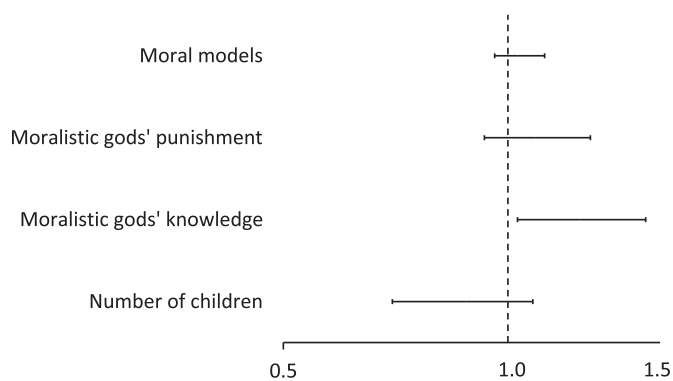
Fig. 2. Exponentiated 95% credibility intervals of mean estimates of individual-level effects of full model from Table 7. Horizontal axis is on a logarithmic scale. The dotted vertical line indicates the threshold of no effect where variables with no reliable effects would have error symmetry around 1.0. Effects to the right of 1.0 predict greater odds of allocating a coin to geographically distant players whereas effects to the left indicate decreased odds in such allocations.

individuals predictably bias allocations in favor of themselves and their local community across the eight sampled populations. As suggested by the Game variable, people favor themselves slightly more than they favor their local communities (i.e., the odds and range of the effect is trending towards values < 1.00). Moreover, the effect of the number of children people have is trending towards favoritism for the players themselves and their local communities.

Our focal individual-level variables—moral models, deities' punishment and knowledge breadth—all contribute to increasing the

chances of allocating a coin to the geographically distant players. Note here that the strongest effect is gods' attributed knowledge breadth; the more individuals claim gods know, the more likely they are to allocate to the distant cup. Gods' punishment also has an effect in the same direction, though not as obviously strong. Previous results (Purzycki et al., 2016a) indicated that punishment predicted larger allocations than knowledge. However, these previous models treated field site as a simple effect and did not allow any variables to have differential effects across sites. Moreover, they considered only complete cases. Here, we allow these factors to have differential effects across sites while estimating the effects of individual-level factors on fair behavior.

The content of moral models influences game play; individuals who listed (dis)honesty are more likely to play fairly (i.e., there is a 3% greater chance of allocating a coin to distant players). Note, however, while the bulk of the probability mass is > 1, this effect is notably slight by comparison to religious beliefs. As indicated by the relatively narrower intervals, it is, however, better estimated by the model. In the Supplementary data, among a variety of other model specifications, we show that salience of (dis)honesty has a similar relationship to behavioral outcome; individuals who list (dis)honesty earlier in lists are more likely to allocate coins to the distant players.

5.2.2. Group-level effects

Table 7 also includes the average contribution of moral and religious culture on allocations. Fig. 3 illustrates a projection of these group-level effects, assuming participants have no children and answered all questions at the half-way mark (in this case 0.5). This includes the free-list summations, which are inverse logit transformed to put them on the same scale as the other cultural variables. Group-level beliefs in moralistic gods' punishment (OR = 1.69, 95% CI = [0.39,
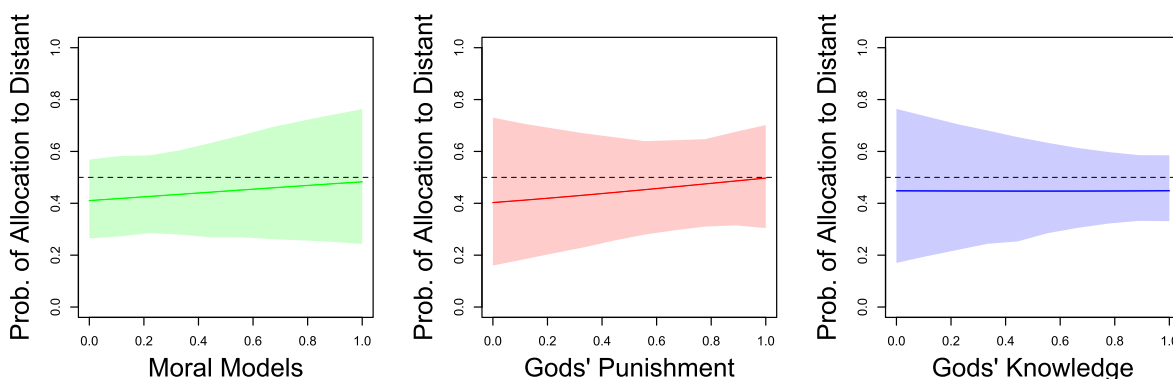

Fig. 3. Projected effects of cultural prevalence of (dis)honesty (green), gods' punishment (red), and gods' knowledge (blue) on probability of allocating a coin to distant players. Results are from full model in Table 7. Shading is 95% percentile intervals. Reference line is at the 50% mark indicating fair play. Across projections, number of children are held at zero, and all other values are held at 0.5 (the halfway point for each variable, including the inverse logit transformed values for moral models), varying only the group level values between 0 and 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

6.68]) exhibits the clearest positive trend (red in Fig. 3). In other words, the ubiquity of beliefs that gods punish in an individual's community positively predicts his or her fair behavior in the game (albeit with a range of error). Cultural ubiquity of (dis)honesty in moral models (green in Fig. 3) and gods' knowledge breadth (blue in Fig. 3) show no reliable effect on allocations (i.e., their credibility intervals are more symmetrical around 1.00).

The strongest conclusion to be drawn from the main results is that—as indicated by the wide intervals—these are poorly estimated factors. While the odds ratios (exponentiated mean estimates) appear to be high, the 95% credibility interval width is quite broad and it is difficult to conclude that culture–the prevalence of certain kinds of information within a community–has a systematic effect on individual behavior cross-culturally. Using more liberal-but-standard analyses, however, we cautiously show that for populations where (dis)honesty is infrequently listed, models predict that increasing its cultural prevalence brings allocations to distant players in this sites to baseline, cross-site allocation levels (Section 5.2.2 of the Supplementary data, Fig. S1). While individually held cultural information predicts individual outcomes, it remains less clear as to how cultural prevalence of that information does.

6. Discussion

The studies presented here give new insight into the relationship between morality and the kind of broad cooperation unique to humans. Among our diverse samples, the most salient and ubiquitous components of moral culture revolve around reciprocity, cooperation, honesty, and dishonesty. This cross-cultural ethnographic data empirically confirm that moral culture is more associated with the costs and benefits of social life (Alexander, 1987; Fessler et al., 2015; Greene, 2013; Tomasello & Vaish, 2013; Trivers, 1971) than with concerns of "justice" and "rights" (Turiel, 1983, 2006). We also found that individuals' moral models predict honest behavior towards geographically distant individuals, but their effects were not as strong as the effects of religious beliefs. As participants exhibited this behavior towards individuals they would never likely meet, our results also confirm the important role that individuals' beliefs and values have on human sociality by restraining selfish behavior. Group-level moral and religious culture, however, are *not* clearly associated with individuals' moral behavior. Below, we discuss various facets of the moral system in light of these results.

6.1. Morality in mind

While we found an individual-level effect of moral models on honest, rule-following behavior, the effect itself was quite small. This may have been due to the kind of data our methods elicit; open-ended questions require categorization for analysis, which may have introduced bias. However, field researchers collected and translated our ethnographic data which was checked multiple times for quality and consistency across research assistants. Moreover, our models exhibited considerable precision in estimating (dis)honesty's effect on behavior. We also considered other notions beyond (dis)honesty that we might assume to be task-relevant. However, moral model components such as "cheating," "disobedience," or "fairness" were either concentrated in a few communities or rarely listed at all, thus making it difficult to reliably assess their effect on behavior in a global cross-cultural study such as ours. Using the data presented here to design scales for measuring individuals' moral models would strike a balance between universal applicability and local relevance (e.g., Boehm, 1979, 1980; Buchtel et al., 2015).

Moral models might be only as effective to the extent that an individual can implement them. Accordingly, measuring other critical individual-level factors (e.g., self-control; Blasi, 1980) to predict moral behavior might be also appropriate. One indication of this in the present study is the cognitive salience of (dis)honesty. In the Supplementary data, we show that the effects for individual-level salience of (dis)honesty are similar to those we find above; the *earlier* individuals list (dis)honesty, the greater the odds of allocating a coin to the distant participant (see the Supplementary data). In addition to accessibility, item salience may indicate how readily individuals can implement these values. This is consistent with the psychological literature that emphasizes the impact of quick moral intuitions over slow moral judgments (Baumard, 2016; Cone & Rand, 2014; Haidt, 2001; Lotz, 2015), suggesting that deeper motivational forces are at work.

Fair play had a stronger association with religious beliefs than with moral models. The effect of being watched and potentially punished by a transcendent being may have played a larger role in our expanded sociality than moral cultivation. It also raises questions as to whether or not human moralistic punishment is powerful enough to offset the costs of defecting on social expectations (cf. Dawkins, 2016; De Waal, 2013; Johnson, 2016). In other words, not only moral models but additional institutional and environmental factors are likely required to stabilize wider, more predictable cooperation. The secularization literature (e.g., Norris & Inglehart, 2012) and some of the aforementioned experimental work (e.g., Cronk, 2007; Gerkey, 2013) suggest that this is the case.

6.2. Moral behavior

Some argue that the evolutionary function of moral behavior is to maintain individuals' reputations in reciprocal interactions (Baumard, 2016; Baumard et al., 2013; Sperber & Baumard, 2012). Our result that gods' knowledge has the strongest and most reliable association with giving more coins to distant players is consistent with this view insofar as one's reputation matters in the eyes of a god. Beliefs about morally concerned deities that know about and punish people for immoral behavior might predict moral behavior more reliably because they harness–among other things–psychological systems responsible for reputation management and punishment avoidance (Johnson, 2016; Purzycki et al., 2016a). If concern of one's reputation in his or her community was strong enough to overcome both the anonymity afforded by these experiments and that target recipients were in no position to reciprocate, we should have seen a relationship between moral *culture* and honest allocations. That is, individuals should have been more likely to play honestly if it meant breaching widely held values (Baumard, 2016, p. 131, n. 13). We found no such association. It may be, however, that moral culture functions in ways not captured by such games (see below).

Ongoing concerns revolve around the ecological validity of economic experiments (Baumard & Sperber, 2010; Gervais, 2017; Gurven & Winking, 2008; Wiessner, 2009; Winking & Mizer, 2013). In small-scale societies, the anonymity afforded by these experiments is not always available. Our study takes advantage of the rarely-offered anonymity by examining whether or not participants exploit the experimental context for their own gains. Moreover, recall that target recipients were geographically distant individuals with whom participants are unlikely to interact; we assessed whether or not cultural content can induce impartial and honest behavior in interactions we know are not happening regularly in our study sites. Other options for assessing interactions are likely to miss these rare encounters (Pisor & Gurven, 2016). As our religious belief measures showed a relatively strong association with allocation, this suggests that we cannot easily dismiss the value of using such games *in toto*.

6.3. Moral culture

Consistent with the precedent study examining cultural variation (Gurven et al., 2008), our results are inconclusive as to whether or not moral culture actually corresponds to individual behavior. As indicated by the wide credible intervals of our model estimates, group-level moral or religious commitments within a community do not reliably predict

individual behavior. It may be the case that there are unmeasured, contextual factors that may be responsible for this model uncertainty. For instance, we do not know the relationship between moral culture and the threat of punishment for moral violations in each sample (Boyd & Richerson, 1992). We also do not have a reliable sense of moral culture's relationship with socioecological factors such as material security (Hruschka et al., 2014) or environmental harshness (Gelfand et al., 2011). As our sample is limited to eight field sites, more attention to group-level measures such as these in a larger sample would facilitate a more reliable assessment of these factors' relative contributions.

However, it may be the case that behaviors that correspond to moral virtues occur too context-specifically or situationally to be reliably evoked in experimental games (Fessler et al., 2015; Gerkey, 2013; North, 1991). We do not have a precise grasp of the components of individuals' moral models that become salient when they operate in different contexts (or whether or not they do). At the group level, rather than having a direct, measurable effect on our behavior, cultural ubiquity and institutions may only facilitate learning the rules and norms for successfully navigating social life (cf. Brodbeck et al., 2013; Cohn et al., 2014; Cronk, 2007; Gerkey, 2013; Lesorogol, 2007; Smaldino, 2014), thus making them more salient *in situ*. While our results suggest that the composition of mental models predicts cooperative behavior that transcends what might otherwise be parochial boundaries (e.g., Hruschka et al., 2014; Pisor & Gurven, 2016), examining *when*, and *where*, and *to whom* participants claim these moral prescriptions apply would be a logical next step for future inquiry (cf. Fessler et al., 2015).

6.4. Evolution of moral systems

Social systems have long been held to structure human interactions, but their mechanics are rarely detailed with empirical data. We assessed some components of moral systems here by focusing on individual models, local culture, and their contribution to honest behavior between members of disparate communities. Like any social system, moral systems are the aggregate output of the complex interactions between deeper cognitive adaptations and our socioecological environments (Barrett, 2014; Kiper & Sosis, 2014). Further consideration of deeper psychological systems (Cosmides & Tooby, 2005; Curry, 2016; Graham et al., 2011) and their relationship to culture and institutions (Gerkey, 2013; Stagnaro et al., 2017) is necessary to further assess the dynamism between moral systems and human cooperation.

As is true with all cross-sectional and correlational research, we cannot satisfactorily explain variation or account for the causal links and feedback between facets of moral systems. The variability we see in moral culture may reflect variation in the challenges people collectively face together, but whether or not it contributes to the resolution of those challenges remains an open question (Alexander, 1987; Curry, 2016; Greene, 2013; Haidt & Kesebir, 2010). As is the case for most traits, uncovering the genesis of moral systems is a difficult-if not impossible-task, but longitudinal research on the topic would be better able to address the links between cognitive adaptations, culture, and environment by tracking individual- and group-level moral models and behavior, including how they change, from which sources they appear to develop, and the forces at work in their selective retention.

Author contributions

B.G.P. conceived, initiated, and managed this project, wrote the bulk of the manuscript, supplementary data, and R code, performed analysis and contributed to model development. A.P. contributed to writing the manuscript, supplementary data, and R code. R.M. contributed to main model development, its description, corollary R code, and group-level plots. C.A., Q.D.A., E.C., R.A.M., B.G.P., A.K.W., and D.X. collected data and contributed to protocol design with J.H. and A.N. All authors provided feedback.

Research ethics

This project was initially approved by the University of British Columbia's Behavioural Research Ethics Board (#H13-00671) and subsequently approved by the ethical review boards at the home university of each researcher who collected the data.

Competing interests

We declare that we have no competing interests.

Acknowledgments

Appendix A. Supplementary data

Supplementary materials including data, R scripts, and methods protocols to this article can be found online in https://github.com/bgpurzycki/Moral-Models-Moral-Behavior and at Purzycki et al. (2016b, 2017). Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2018.04.004.

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