

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/319470470>

The devoted actor's will to fight and the spiritual dimension of human conflict

Article in *Nature Human Behaviour* · September 2017

DOI: 10.1038/s41562-017-0193-3

CITATIONS

117

READS

3,048

9 authors, including:



Angel Gómez

National Distance Education University

161 PUBLICATIONS 5,972 CITATIONS

[SEE PROFILE](#)



Lucía López-Rodríguez

Universidad de Almería

68 PUBLICATIONS 968 CITATIONS

[SEE PROFILE](#)



Hammad Sheikh

The New School

27 PUBLICATIONS 792 CITATIONS

[SEE PROFILE](#)



Jeremy Ginges

The New School

72 PUBLICATIONS 3,628 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Predictors of Success [View project](#)



God Values the Lives of My Out-Group More Than I Do: Evidence From Fiji and Israel [View project](#)

The devoted actor's will to fight and the spiritual dimension of human conflict

Ángel Gómez^{1,2}, Lucía López-Rodríguez^{1,3}, Hammad Sheikh^{1,4}, Jeremy Ginges^{1,4}, Lydia Wilson¹, Hoshang Waziri¹, Alexandra Vázquez¹, Richard Davis^{1,5,6} and Scott Atran^{1,5,7,8*}

Frontline investigations with fighters against the Islamic State (ISIL or ISIS), combined with multiple online studies, address willingness to fight and die in intergroup conflict. The general focus is on non-utilitarian aspects of human conflict, which combatants themselves deem 'sacred' or 'spiritual', whether secular or religious. Here we investigate two key components of a theoretical framework we call 'the devoted actor'—sacred values and identity fusion with a group—to better understand people's willingness to make costly sacrifices. We reveal three crucial factors: commitment to non-negotiable sacred values and the groups that the actors are wholly fused with; readiness to forsake kin for those values; and perceived spiritual strength of ingroup versus foes as more important than relative material strength. We directly relate expressed willingness for action to behaviour as a check on claims that decisions in extreme conflicts are driven by cost-benefit calculations, which may help to inform policy decisions for the common defense.

In September 2014, US president Barack Obama endorsed the declaration of his national intelligence director: “We underestimated ISIL and overestimated the fighting capability of the Iraqi army ... It boils down to predicting the will to fight, which is an imponderable”¹. Willingness to fight may be more comprehensible if we pay more attention (see briefings and reports to NSC, DoD and U.S. Senate Armed Services available at <http://www.artisinternational.org/>) to the spiritual (non-material), non-utilitarian dimension of human conflict^{2,3}. Although most analyses focus on relative material prowess among conflicting parties, ever since World War II, insurgent groups have in general prevailed with as little as ten times less firepower and manpower than state forces⁴. One plausible reason resides in the motivations of combatants: when group interests become sacred and non-negotiable, spiritual considerations trump material ones⁵.

To examine this dimension of conflict, we developed analyses based on ethnographic fieldwork and interviews with combatants fighting against the Islamic State (ISIS, ISIL), including members of the Kurdistan Worker's Party (PKK), and other frontline fighters in northern Iraq in February–March 2015, as well as captured ISIS fighters. Next, we tested and refined these analyses with large-sample online studies in Spain to understand the willingness of people to make costly sacrifices for their groups and their values. We carried out a quantitative field study in February–March 2016 on the same frontline with Peshmerga (Kurdish Regional Government forces), Iraqi army Kurds and Arab Sunni militia. Further online studies then examined cognitive mechanisms underlying frontline results.

This research is theoretically informed by a devoted actor framework, which integrates research on sacred values (values people refuse to trade-off for material or monetary compensation)⁶ and

identity fusion (feelings of inseparable connection between self and group)⁷. It was initially developed based on case studies of extremists (for example, the 2004 Madrid train bombings)⁸, then extended to larger-scale conflict (for example, Israel–Palestine)⁹. Within this framework people most willingly engage in costly sacrifices and extreme actions when motivated to protect non-negotiable sacred values^{10–12}—whether religious (for example, holy law) or secular (for example, democracy)—and such values are associated with a group to which they feel viscerally connected and that imbues them with a collective sense of invulnerability¹³.

We found evidence of devoted action in the battle for the village of Kudilah, the first engagement in the offensive to retake Mosul, the largest ISIS-controlled city. Some ninety ISIS fighters fought several hundred coalition forces of Peshmerga, Iraqi army and Arab Sunni militia. More than half of ISIS's fighters died, including more than a dozen suicide attackers. Study 1 on the frontline examined the will to fight among the three anti-ISIS groups who fought at Kudilah, which many veteran fighters claimed to be the fiercest battle of their lives.

Studying frontline fighters is challenging and samples are relatively small. Thus, our research involves a dynamic relationship between theory development and method, using insights from fieldwork to create and refine operational analyses in online studies with large samples of non-combatants where statistical power and validity can be tested. For online studies we chose Spain, a recurrent target of jihadis vowing to recover Al-Andalus, Western Europe's last Muslim polity, which fell in 1492. This was an explicit motivation for the 2004 Madrid train bombings, one of Europe's worst terrorist attacks, along with grievances pertaining to Western involvement in ongoing conflicts in Muslim lands, as with the August 2017 attack

¹Artis International, 6424 East Greenway Parkway, Suite 100-498, Scottsdale, AZ 85254, USA. ²Departamento de Psicología Social y de las Organizaciones, Universidad Nacional de Educación a Distancia, UNED, C/ Juan del Rosal, No. 10, 28040 Madrid, Spain. ³Departamento de Psicología, Universidad de Almería, Cañada de San Urbano s/n, 04120 Almería, Spain. ⁴Department of Psychology, New School for Social Research, 66 West 12th Street, New York, NY 10011, USA. ⁵Centre for the Resolution of Intractable Conflicts, CRIC, Department of Politics and International Relations and Harris Manchester College, University of Oxford, Mansfield Road, Oxford, OX1 3TD UK. ⁶School of Politics and Global Studies, Arizona State University, Coor Hall, 975 South Myrtle Avenue, Tempe, AZ 85287, USA. ⁷Centre National de la Recherche Scientifique, Institut Jean Nicod—Ecole Normale Supérieure, 29 Rue d'Ulm, 75005 Paris, France. ⁸Gerald Ford School of Public Policy and Institute for Social Research, University of Michigan, Ann Arbor, MI 48109, USA. Ángel Gómez and Scott Atran contributed equally to this work. *e-mail: satran@umich.edu

in Barcelona that occurred subsequent to our study. Strikingly, the frontline and online studies converge on key determinants of willingness to make costly sacrifices.

Results

Devoted actors on the ISIS frontline. Previous online and field studies have shown that commitment to sacred values and identity fusion independently affect willingness to make costly sacrifices, but their interaction maximizes such willingness under real or perceived threat¹⁴. We first analysed these aspects of the devoted actor framework with frontline and online participants.

In initial field interviews in Iraq, we identified a plausible set of sacred values for each group of actors, based on indicators of such values tested in our previous studies (in Israel, Palestine, Indonesia, Iran, Nigeria, Guatemala and the United States): immunity to material tradeoffs, insensitivity to discounting, blindness to exit strategies, resistance to social pressure¹⁵. Values considered sacred for Peshmerga and Iraqi Army Kurds were mainly 'Kurdeity' (a cultural concept denoting a sense of Kurdish language, heritage and land, which were 63% and 41%, respectively) and Independent Kurdistan (a political goal, of 26% and 47%, respectively). For Sunni Arab fighters, maintaining the integrity of the Iraqi nation (a political goal, 55%) and Arabness (a cultural concept, 20%) were considered sacred. The different groups with which Peshmerga, Iraqi Army Kurds and Arab Sunni militia participants might be fused were: family (95%, 94%, 100%, respectively), kin-like group of friends (95%, 82%, 94%), Muslim Ummah (26%, 19%, 39%), Iraqi People (0%, 12%, 61%) and own group (79%, 100%, 56%) (study 1).

All combatants were fused with at least one group whose members were perceived to be sharing at least one sacred value. All were constantly under threat and were putting their lives on the line, as evident from the fact that more than half of frontline participants had been wounded in battle (Table 1). Those who had been wounded expressed greater willingness to make costly sacrifices, indicating convergence between stated and actual willingness for costly sacrifices on the front (study 1, $n = 56$).

Study 2 ($n = 816$) tested our analyses of sacred values and fusion online. Participants responded to measurements of fusion with country (Spain) and democracy as a sacred value. Under an explicit threat condition highlighting the 2004 Madrid train bombings, an interaction of identity fusion and sacred values characteristic of devoted actors appeared: devoted actors in the threat condition displayed the strongest willingness for costly sacrifice (three-way interaction, $F_{1,808} = 13.74$, $P < 0.001$, $\eta^2_p = .02$; see Supplementary Information for pairwise comparisons and further details).

A difficult choice of value versus group. From a material and evolutionary perspective, one should prioritize kin or kin-like groups over abstract ideals. Yet, one finding of our qualitative frontline interviews is that combatants make painful decisions when prioritizing value over group. We empirically tested how people reason over such tradeoffs and to what extent they predicted willingness to fight, in a sequence of studies beginning on the frontlines (study 1). We asked participants to choose between sacred values and fused groups. All combatants were devoted actors who regarded

relevant values as sacred and who were fused with at least one larger group: comrades, Muslim Ummah, kin-like group of friends (often comrades in arms), Iraqi people or their own groups (Peshmerga, Iraqi Army Kurds, Sunni Arab militia). Most were also fused with their families (>90% for all three groups). We pitted their two most important groups against their two most important sacred values whenever possible. Most combatants chose at least one value over a group (86%), with more than half of them choosing at least one value over their families (59%). Combatants scored more highly in the costly sacrifice scale if they chose the value over the group in general ($t_{49} = 2.24$, $P = 0.03$) and family in particular ($t_{49} = 3.35$, $P < 0.01$) (Fig. 1, study 1).

Study 1 suggests that a defining feature of willingness to fight for abstract causes is the relative priority given to a sacred value over important groups, such as family. We investigated this further in studies in Spain. In study 3 ($n = 545$), which focused on devoted actors, participants self-defined a group that they felt fused with and a value sacred to them. Participants were then introduced to a dynamic analysis for choosing between this value and group, and asked which they would choose if forced to do so. Most participants chose family as the group with which they were most fused (>70%). Unlike combatants, most Spanish participants chose family over sacred value (>77%). However, those who chose value over the group were more willing to make costly sacrifices for their value than those who chose the group ($F_{1,540} = 19.40$, $P < 0.001$, $\eta^2_p = 0.04$), especially when the group was family ($F_{1,540} = 19.77$, $P < .001$, $\eta^2_p = 0.04$), but also when applied to other groups ($F_{1,540} = 4.90$, $P = 0.027$, $\eta^2_p = 0.01$) (Fig. 1, study 3; see Supplementary Information for details).

Study 4 ($n = 280$) confirmed that devoted actors who chose value over family expressed greater willingness to make costly sacrifices than those who chose family over value (Supplementary Information). This choice was perceived as extremely difficult compared to those who chose family instead of the value ($F_{1,276} = 30.69$, $P < 0.001$, $\eta^2_p = 0.10$) and compared to those chose the value over other groups ($F_{1,276} = 13.10$, $P < 0.001$, $\eta^2_p = 0.05$) (Supplementary Information). Indeed, frontline fighters would be highly emotional when discussing making such tragic choices¹⁶.

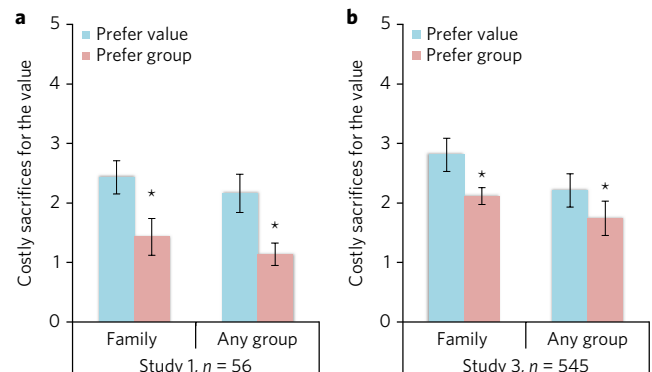


Fig. 1 | Willingness to make costly sacrifices for participants who forsake their fused groups for sacred values in frontline (study 1) and online (study 3) studies. a, b, Willingness to make costly sacrifices for the value from frontline fighters (a, study 1, $n = 56$) and non-fighters (b, study 3, $n = 545$) when they choose value over family or any other group.

Participants who chose value over group were more willing to make costly sacrifices for their value than those who chose family, $t_{49} = 3.35$, $P = 0.002$ (study 1), $F_{1,540} = 19.77$, $P < 0.001$, $\eta^2_p = 0.04$ (study 3); or other group, $t_{49} = 2.24$, $P = 0.029$ (study 1), $F_{1,540} = 4.90$, $P = 0.027$, $\eta^2_p = 0.01$ (study 3). Asterisks indicate significant differences by preference ($*P < 0.05$). Error bars represent 95% confidence intervals. The scale for study 1 was from 0 to 5; the scale for study 3 was from 0 to 6.

Table 1 | Peshmerga are more likely to express willingness to make costly sacrifices than Iraqi Army Kurds or Sunni Arab militiamen (see study 1)

| Group | n | Wounded | Sacrifices (mean \pm s.d.) |
|--------------------|----|----------|------------------------------|
| Peshmerga | 19 | 12 (63%) | 2.56 \pm 1.07 |
| Iraqi Army Kurds | 17 | 8 (47%) | 1.82 \pm 0.95 |
| Sunni Arab Militia | 20 | 9 (45%) | 1.70 \pm 1.13 |

To be sure, choosing value over group may be accompanied by changes in how the group is perceived and, although not the topic of interest here, it is an interesting topic for further inquiry.

Spiritual versus physical formidability. In the frontline and online studies, we find that relative spiritual formidability of groups, compared to relative physical formidability, is more related to willingness to sacrifice. Within a rational actor framework, perceived intergroup difference in material formidability would strongly relate to willingness to engage in costly sacrifices. By contrast, within a devoted actor framework, perceived spiritual formidability would be most relevant when sacred values are in play. Although the term ‘spiritual formidability’ may have religious connotations to some, it more properly refers to non-material strength.

Using techniques to judge physical formidability that assessed the perceived strength of various combatant groups in Iraq, we found that both avowedly religious ISIS fighters and avowedly secular PKK fighters (the only force that held fast against the ISIS onslaught in summer 2014) disregarded consideration of ingroup and outgroup physical formidability. They argued during our initial experiments in early 2015 that most important was spiritual formidability (*ruhi bi ghiyrat*, in both Arabic and Kurdish, ‘spirituality with bravery’ to defend what is most cherished, which they recurrently described in terms of ‘strength of belief in what we are fighting for’ and ‘what is in our heart’). Thus, we adapted dynamic analyses of physical formidability to spiritual formidability to compare the ingroup’s perceptions of their own physical versus spiritual formidability on willingness to fight, as well as the ingroup’s perceptions of the physical versus spiritual formidability on willingness to fight of various outgroups, whether friend or foe (Fig. 2).

Further frontline interviews and experiments in 2016, together with online studies, sought to determine the general validity and relevance of comparing physical to spiritual formidability with regards to willingness to make costly sacrifices, that is, whether physical and spiritual formidability are markedly different constructs for other frontline groups of combatants and non-combatants, how individuals perceive ingroup and outgroups on these dimensions, and whether spiritual formidability is more strongly associated with costly sacrifices for sacred values than is physical formidability.

Frontline participants interpreted physical formidability in terms of manpower and firepower, and spiritual formidability in terms of inner conviction (whether associated with religious or secular beliefs and values). In a pair of online studies (study 5, $n = 499$; study 6, $n = 447$; see Supplementary Information), we demonstrated the content validity of this analysis by asking participants to describe the meaning of their responses to the spiritual formidability measure. Participants tended to refer to spiritual formidability in terms of convictions (strength of values and beliefs, 59% of participants) and internal strength (‘heart’, ‘energy’ and ‘willpower in pursuit of

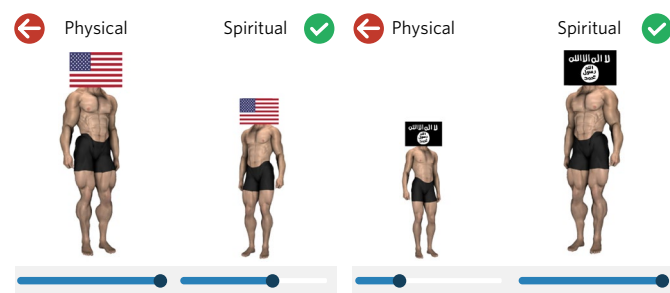


Fig. 2 | Sample judgment of spiritual formidability versus physical formidability of USA versus ISIS by a Kurdish fighter using touch-screen sliders on a tablet.

goals and facing adversities’, 58% of participants). These two dimensions of sentiment also characterize the way ISIS and PKK fighters interpreted spiritual formidability in our 2015 frontline interviews.

Studies 7–11, demonstrate the predictive validity of this analysis. In a series of three studies, online participants judged the spiritual and physical formidability of Spaniards, ISIS and the United States, and expressed the costly sacrifices that they (Spaniards) and the others (ISIS and the United States) would make for their respective sacred values and groups (Fig. 3). In study 7 ($n = 206$), participants rated the spiritual and physical formidability of Spain and ISIS, their identity fusion with Spain, the extent to which they regarded democracy to be a sacred value and their willingness to sacrifice for democracy and their country. Spiritual and physical formidability were distinct constructs ($r_{204} = 0.10$, $P = 0.140$). Participants perceived Spaniards as physically more formidable than members of the Islamic State ($t_{205} = 2.48$, $P = 0.014$), but weaker spiritually ($t_{205} = 21.43$, $P < 0.001$). Estimates of relative spiritual, but not physical, formidability predicted willingness to sacrifice for both country ($\beta = 0.21$, $t_{201} = 3.02$, $P < 0.01$) and value ($\beta = 0.18$, $t_{201} = 2.62$, $P < 0.01$) in regressions that controlled for fusion and SV measurements.

Study 8 ($n = 315$) replicated these findings, while revealing that Spanish participants believe that Islamic State members also consider themselves stronger spiritually than physically ($t_{314} = 6.31$, $P < 0.001$), and that only spiritual formidability predicts costly sacrifices for jihad ($\beta = 0.31$, $t_{312} = 5.56$, $P < 0.001$). People in this study, conducted just days after major terrorist attacks in Paris (November 2015), judged spiritual formidability more important than physical formidability in motivating attacks on behalf of the Islamic State ($t_{314} = 17.22$, $P < 0.001$), and also a reason to fear the Islamic State ($t_{314} = 10.04$, $P < 0.001$). In interviews with captured ISIS fighters and would-be recruits in Europe and North Africa, as well as with potential target populations, we find that suicide attacks, in particular, are perceived as being driven by convictions of spiritual strength¹⁷.

In study 9 ($n = 1,164$), participants perceived Americans as physically more formidable than the members of the Islamic State ($t_{1,163} = 20.70$, $P < 0.001$), but weaker spiritually ($t_{1,161} = 18.37$, $P < 0.001$). Perceived relative spiritual, but not physical, formidability predicted perceived willingness of Americans to fight for democracy ($\beta = -0.07$, $t_{1,159} = -2.45$, $P = 0.014$), and of ISIS to fight

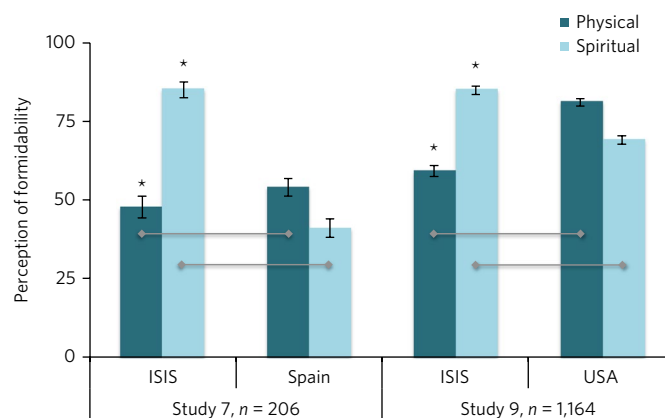


Fig. 3 | Perceived physical versus spiritual formidability for ISIS, Spain and USA. *t*-Tests revealed that the Islamic State was perceived physically less formidable than Spain (study 7; $t_{205} = 2.48$, $P = 0.014$) and USA (study 9; $t_{1,163} = 20.70$, $P < 0.001$); but stronger spiritually compared to Spain ($t_{205} = 21.43$, $P < 0.001$) and USA ($t_{1,161} = 18.37$, $P < .001$). Asterisks and horizontal bars indicate significant differences between groups (* $P < 0.05$). Error bars represent 95% confidence intervals.

for jihad ($\beta=0.11$, $t_{1,159}=3.77$, $P<0.001$). Although participants judged both spiritual and physical formidability important for winning a battle, spiritual formidability was the strongest factor ($\chi^2_{P(1)}=21.45$, $P<.001$).

A field experiment with combatants demonstrated the external validity of the spiritual formidability analysis (to illustrate how the analysis was used in the field, in this case by a Peshmerga fighter, see Supplementary Video 1; the viewer will see that the analysis was readily understood and easily manipulated). As in the online studies, the perception of frontline combatants of spiritual formidability positively correlated with willingness to make costly sacrifices ($r_{53}=0.32$, $P=0.02$). Combatants also judged the United States high in physical formidability, but low spiritually, while judging ISIS low physically, but high spiritually (Fig. 4). A fighter typically remarked: “They are weak now, because they have used up their resources but their fighters don’t retreat even if the battle is lost”.

Follow-up online studies 10 ($n=441$) and 11 ($n=523$) further explored possible effects of spiritual and physical formidability on willingness for costly sacrifices and armed intervention. Participants who perceived Islamic State as spiritually strong were least willing to sacrifice for democracy and support the country in an armed intervention (pairwise comparisons with Bonferroni Tests $P<0.001$ compared to remaining conditions; see Supplementary Information).

Study 12 ($n=470$) revealed that when participants were asked to estimate the spiritual formidability of Spain versus the Islamic State, they invoked negative emotions (fear, panic, defenselessness, anger) when perceiving the Islamic State as spiritually stronger than the ingroup ($r_{467}=0.35$, $P<0.001$). Together, the Spanish findings suggest that perception of an adversary’s great spiritual strength relative to one’s own may hamper and deter willingness to sacrifice in opposing the adversary.

Perhaps most important, we consistently find that the relative spiritual, but not physical, formidability of groups predicts willingness to engage in costly sacrifices. This was true for combatants and online non-combatants (Fig. 5). Study 13 (online, $n=311$) confirmed that the intergroup difference in spiritual formidability predicted costly sacrifices for democracy ($\beta=0.22$, $t_{308}=3.47$, $P=0.001$) and for country ($\beta=0.25$, $t_{308}=4.03$, $P<0.001$). These results paralleled frontline findings that intergroup spiritual formidability predicts costly sacrifices for sacred values ($\beta=0.40$,

$t_{51}=3.08$, $P=0.003$). Neither at the frontline nor online did differences in physical formidability reliably predict people’s willingness to make costly sacrifices.

Discussion

In frontline and online studies, we found that willingness to fight is associated with sacrifice of material concerns (fighters’ lives, well-being of kin) for the sake of sacred values, and with the weight people give to the relative spiritual (rather than physical) formidability of themselves and their adversaries. Together, these findings indicate the importance of apparently non-material concerns in motivating and sustaining violent conflict, however materially consequent belief in sacred values and perceived spiritual formidability may prove in the long run¹⁸.

Many published studies in military history, sociology and psychology, and related investigation in political science, considers group dynamics—often involving commitment to comrades/buddies/training or combat group—as key to ‘fighting spirit’. In one recent and particularly relevant study for our investigation, Whitehouse and colleagues show identity fusion with close comrades to be a principal determinant of will to fight among Libyan insurgents fighting against the Gaddafi regime¹⁹. However, as we noted in our published response to that study²⁰, although arguments for the role of fusion were compelling, there was no consideration of values at all, much less of the relative contribution of commitment to values versus commitment to fused group. There was also no examination of any other aspect of what we refer to as the spiritual dimension of human conflict (for example, judgments of spiritual versus physical formidability). Here, we provide an arguable advance over the most common single-factor explanation of will to fight in terms of social bonds (that is, adding value as a predictor of willingness to fight), in line with the dual framework of the devoted actor (that is, the interaction of sacred values and identity fusion).

In fact, apart from some suggestive studies^{21,22} and historical analyses^{23,24}, ‘ideology’, whether secular or religious, is viewed most often in terms of instrumental ‘opportunity structures’ to reduce ‘transaction costs’ in mobilizing violence for strategic advantage²⁵; as a conceptual ‘proxy’ for framing political and economic ‘asymmetries’ in readily understandable and actionable ways²⁶; or as a consequentialist means for emotionally regulating violence to appropriate levels of military effectiveness, including efforts to demoralize or to enlist sympathy among enemy civilian populations²⁷. Our investigation revealed that abstract commitments may have more than instrumental value in promoting actions that are dissociated from material interests and expectations, and can trump group loyalty in willingness to fight. An important issue for further investigation is why some groups are better able to inspire loyalty to an abstract cause than others²⁸.

Our findings are relevant to different contexts, including the frontlines of violent conflict. Although these studies do not directly focus on transnational terrorism, they were motivated in part by earlier and parallel ethnographic fieldwork, semi-structured interviews and pilot experiments with ISIS and PKK (both groups being on the official US list of terrorist organizations). This research with ISIS and PKK proved highly relevant to how those fighting ISIS perceive and act upon ISIS’s will to fight relative to their own. The unsolicited responses (controlling and monitoring for possibilities of deception, see Supplementary Information), of captured ISIS fighters and of PKK fighters holding the line against ISIS, regarding what is sacred and spiritual were spontaneously echoed by other frontline combatants. They argued that most important was their own, as well as the enemy’s, spiritual formidability rather than physical formidability.

Although the numbers of ISIS and PKK fighters interviewed were too few for statistical analyses, insights gained with them were directly responsible for the elaboration of analyses that we validated in a number of studies among a wider group of combatants and a

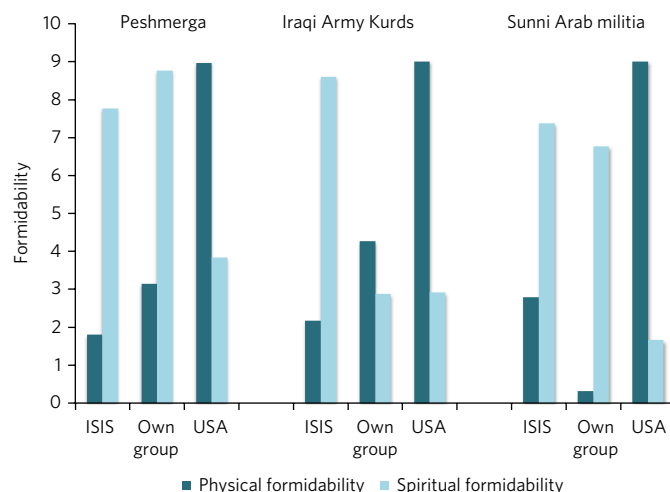


Fig. 4 | Average (descriptive) rank of physical and spiritual formidability in study 1 for Peshmerga ($n=19$), Iraqi Army Kurds ($n=17$) and Sunni Arab militia ($n=20$). Rank order of formidability is reversed for illustration: low numbers in task correspond to high numbers (high ranking) in the figure.

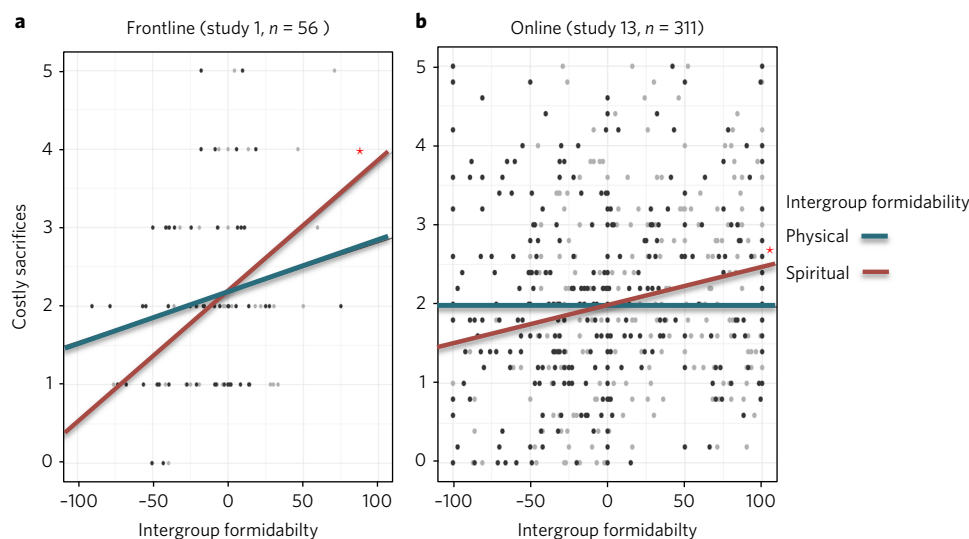


Fig. 5 | Slopes of multiple regression analysis of costly sacrifices on intergroup differences in physical and spiritual formidability (own group versus ISIS). Only spiritual differences predict sacrifices. **a**, Study 1 ($n = 56$, $F_{2,51} = 6.06$, $P = 0.004$, $R^2 = 0.19$), intergroup formidability slopes for physical ($t_{51} = 1.36$, $P = 0.180$) and spiritual ($t_{51} = 3.08$, $P < 0.001$) formidability are shown. **b**, Study 13 ($n = 311$, $F_{2,308} = 17.63$, $P < 0.001$, $R^2 = 0.04$), intergroup formidability slopes for physical ($t_{311} = -0.04$, $P = 0.971$) and spiritual ($t_{311} = 3.47$, $P < 0.001$) formidability are shown. Asterisks indicate significant effects ($*P < 0.05$). The scale for study 1 was from 0 to 5; the scale for study 13 was from 0 to 6.

much larger group of non-combatants from an entirely different cultural context. The fact that these hypotheses-driven measures reliably elicited statistically significant responses in the direction intimated by the ISIS and PKK interviews suggests that the information from ISIS and PKK fighters was both genuine and generalizable. More broadly, our findings suggest that insights gained from studies on the ISIS frontline are theoretically and methodologically robust among large samples of non-combatants in an entirely different cultural context.

On a more general plane, the findings of apparent preference for value over kin by devoted actors provides empirical support for the idea that humans may form their strongest (and potentially most expansive) political and religious ties by subordinating devotion to kin to a more abstract ideal. Indeed, a founding parable of monotheistic religions involves Abraham's willingness to sacrifice beloved progeny to signal devotion to a sacred value (absolute commitment to God). The very term Islam, or 'submission', refers to sublimation of tribal and all other prior group affinities to God's message. Historically, willingness to sacrifice family and tribe was arguably critical to construction of larger groups founded on political principles²⁹.

Finally, we have also attempted to address a problem in social science: equating expressed willingness to act with behaviour. By measuring behaviour more directly on the frontline of combat, we provide a critical check on claims that combatant's choices are driven by cost-benefit calculations, and this may help to inform policy decisions for the common defense.

In conclusion, the studies reported here support theory development on 'will to fight' in three ways. First, although devoted actors are defined both by experiencing identity fusion with relevant groups and by construing issues under dispute as sacred, we show that those willing to carry out the most extreme behaviours are characterized by a willingness to prioritize sacred values over groups, including kin. Second, on the basis of interviews with frontline combatants, and particularly those belonging to groups on the official US list of terrorist organizations (that is, ISIS, PKK), we found and tested the effects of an undervalued factor, perceived spiritual formidability, which may help us to understand how devoted actors perceive and act upon their own and others' willingness to make

costly sacrifices. Third, the back and forth between online and field studies has allowed us to explore, replicate and extend our findings with actual combatants, and to thus provide a conceptual and empirical advance in addressing claims that combatants are driven by cost-benefit calculations³⁰.

Previous work has shown that commitments to non-material or abstract ideals, in the form of sacred values, leads to duty-bound (deontological) decision making and choices that cannot be accounted for simply in terms of material utility. However, this previous work has been done by investigating popular support for violence or with potentially violent populations. We replicate and complement these findings with theoretical constructs and analyses among actual combatants that can be extended to non-combatants in entirely different cultural contexts. The studies are not only intended to furnish empirical support for theory development on will to fight, but also to offer policymakers evidence to help to make informed decisions for the common defense. Although we believe that the testing of hypotheses and the evaluation of evidence must be wholly independent of policy priorities and concerns, we also hold that policies affecting the security of the lives of our citizenry and others are better informed than not by scientific evidence of the sort we have provided, with due consideration for the tentative nature of our findings subject to further replication³¹.

Understanding the will to fight in the face of lethal danger may remain imponderable—and attendant security challenges seemingly intractable—as long as we view such actions through a narrow lens of instrumental rationality³². This optic tends to disregard the immediate and remote consequences of actions motivated by spiritual and moral virtues that, as Darwin noted, "come to be highly esteemed or even held sacred"³³; for, such virtues "will certainly give an immense advantage" to one group over another when possessed by devoted actors who would "by their example excite...in a high degree the spirit" in others to sacrifice self for the cause of comrades³⁴.

Methods

Participants. For the frontline field studies, work with PKK fighters and captured ISIS fighters was given IRB approval and participant anonymity was assured along with explicit assurance that interviews or experiments involving verbal answers to questionnaires could be terminated at will. The IRB decision

acknowledged the special circumstances of persons on the USG list of terrorist organizations pertaining to constraints imposed by the US Supreme Court in *Holder v. Humanitarian Law Project*, which prohibits by law formal consultation with, or advice to, members of terrorist organizations with regard to meeting the requirements of any humanitarian endeavour (including those of an IRB)³¹. For all other participants, whether on the frontline or online, consent and anonymity were required in accordance with standard IRB protocols. Participants agreed on a voluntary basis to participate in interviews and experiments involving answers to questionnaires. They were reminded that they could abandon the investigation at any time if they felt uncomfortable. Participants were thanked and debriefed at the end of the interview and questionnaire. They received the contact information of the investigators in case they were interested in receiving further information.

Study 1 (frontline) consisted of in-depth interviews and psychological experiments conducted in February–March 2016 with 19 Peshmerga, 17 Iraqi army regulars and 20 Arab Sunni militiamen from the Kudilah battle. Both the Peshmerga and Iraqi regulars were Kurds and all groups identified as Sunni Muslims. We intended to interview 20 combatants from each group, but difficulties in getting to the front, the wounding or death of planned interviewees and changes in military scheduling prevented achieving total parity between the groups before the second battle of Kudilah began in late March 2016. Each interview, with accompanying quantitative analyses, took one to two hours; traveling to the front took several hours daily.

In parallel, we conducted 14 online experiments with non-combatants in Spain ($n = 6,649$) drawn from all regions, including the Spanish enclaves of Ceuta and Melilla in North Africa. Here we describe analyses used throughout different studies.

Analyses. Sacred values. Whether religious or secular, sacred values are ideas, preferences or beliefs that people refuse to measure along material scales, typically evidenced by a refusal to trade off for economic (for example, money), social (for example, status) or other material benefits. To measure sacredness, we investigated willingness to trade-off values in exchange for material benefits, whether for individual or collective gain. Absolute refusal to contemplate such trade-offs was taken as an indicator of a sacred value^{10,35}.

Identity fusion. This refers to a visceral feeling of connectedness between self and group that has been assessed by pictorial¹⁶, verbal¹³ and dynamic³⁷ methods (see Supplementary Information). Here we investigated identity fusion as follows: participants viewed a pictorial array with pairs of circles with different degrees of overlap. One circle represented the participant (me) and a larger circle represented ‘the group’ that was tagged with a flag or other identifying icon (see Supplementary Fig. 1; see also sample video with ISIS fighter—Supplementary Video 2). Participants who choose the ‘F’ option as best reflecting their relationship with the group, think and behave in ways different from those who choose any other option: they wed their personal identity (who I am) to a unique collective identity (who we are), perceiving the personal and social identities as a single identity. Such total fusion demonstrably leads to a sense of group invulnerability and willingness of each individual in the group to sacrifice for every other¹³. The pictorial index of identity fusion we used is a variation of an analysis that has been validated in multiple studies in large- and small-scale societies, and has been shown to predict judgments and decisions relating to extreme behaviours^{38,39} (see Supplementary Information).

Costly sacrifices. Participants in study 1 (frontline) and studies 2–4, 7–11, 13 were asked about willingness to make costly sacrifices for the given sacred value. In study 1, these costly sacrifices to defend the value were dying, letting their family suffer, killing civilians, undertaking a suicide attack and torturing women and children (see Supplementary Information). For each of their sacred values, participants were asked if they would take each of the actions to defend or achieve their sacred values. We counted how many of these actions they were willing to take for any of their sacred values resulting in a score of 0 (none of the actions we investigated) to 5 (all actions). For the online studies, we investigated less extreme, but more contextually relevant actions using a Likert scale. Participants responded to a five-item scale about their willingness to engage in actions to defend the value used in previous studies¹⁴. They indicated to what extent they agree with the following 5 statements: “If necessary, I would be willing to lose my job or source of income/go to jail/use violence/let my children suffer physical punishment/die to defend my value” on a 7-point Likert scale from 0 (strongly disagree) to 6 (strongly agree). Quest for variance in responses motivated use of different sets of costly sacrifices for frontline combatants and European non-combatants (in pilot work, elements of the non-combatant set produced ceiling effects on the frontline, whereas elements of the combatant set produced floor effects online). See Supplementary Information for details.

Values versus group. Previous studies of combat soldiers stress devotion to comrades over cause^{19,40,41} as do online studies of western Europeans⁴². However, this may be otherwise when combatants consider the cause sacred. In in-depth interviews with (captured) ISIS and PKK (Kurdish Marxist) combatants in Iraq in 2015, some told us of how they had to give up their families to fight for their cause

(Islamic Caliphate, Kurdish homeland)⁴³; and in fact, ISIS has divulged children’s public executions for parents who opposed the Caliphate and its leader^{44,45}.

Accordingly, in both online and frontline studies we systematically examined readiness to forsake fused group for sacred values. Participants were presented with a dynamic analysis involving a series of two large circles representing their fused group and their sacred value, and a small circle representing themselves (Supplementary Fig. 3a). A screen then showed the three circles overlapping simultaneously—one’s group, sacred value and personal identity—conforming to a representation of what a devoted actor is (Supplementary Fig. 3b). Participants were asked whether or not their relation with the group and value might be represented in this way. After learning that in some circumstances the interest or goals of the group were incompatible with the values, the group and value circles moved, respectively, to the left and to the right of the ‘self’ circle, which remained in the middle (Supplementary Fig. 3c). Then participants were asked to choose or prioritize group or value by dragging the small circle representing personal identity to one or the other (Supplementary Fig. 3d and Supplementary Video 3). As validation of this analysis, results from study 14 ($n = 375$), study 3 ($n = 545$), and study 4 ($n = 280$) confirmed that most devoted actors considered the analysis to be a good representation of how they feel about the group and value as compared to non-devoted actors, 97.9% versus 65.9%, $\chi^2 = 65.76$, $P < 0.001$, 98.3% versus 65.1%, $\chi^2 = 219.44$, $P < 0.001$, and 97.1% versus 61.4%, $\chi^2 = 122.22$, $P < 0.001$ (see Supplementary Information).

Spiritual formidability versus physical formidability. Perception of physical size and strength are vital to outcomes of hand-to-hand combat, and humans rely on representations of relative physical strength, including assessments of manpower and weapons, when deciding whether to fight⁴⁶. When people perceive their own group members as physically formidable, and outgroups as not so formidable, then ingroup members perceive outgroups as vanquishable through force, which favours aggressive solutions to intergroup conflict⁴⁷. Using techniques to judge physical formidability that assessed the perceived strength of various combatant groups in Iraq, we found that both ISIS and PKK fighters disregarded consideration of ingroup and outgroup physical formidability. They argued that most important was spiritual formidability (*ruhi bi ghyrat*). Yet, there is little scientific understanding of the motivating effect of the spiritual, expressly non-utilitarian dimension in human conflict generally^{48–50} (however implicitly utilitarian⁵¹ or not⁵² and only intermittent awareness in the psychological and sociological military literature^{53–55}).

Thus, we adapted analyses of physical formidability to spiritual formidability, comparing the relative impact of physical and spiritual formidability in willingness to fight. Although the term spiritual formidability may have religious connotations to some, it more properly refers to non-material strength (see Supplementary Information).

Earlier studies into physical formidability used a combination of static analyses of size and of muscularity⁴⁶. We developed an overall body size/muscularity analysis using a dynamic slider interface to measure both physical and spiritual formidability. Two male bodies (of medium size and muscularity) were presented on the screen, and participants informed that each body represents a different group. Flags covering each head were used to represent each specific group. Participants were instructed to modify the figures to show how they see such groups, by horizontally dragging the slider to the left or to the right, reducing or increasing both the size and strength of each body (Fig. 2). Across studies, participants readily distinguished between physical and spiritual formidability.

Data availability. The data that support the findings of all studies are available from the corresponding authors upon request.

Received: 7 December 2016; Accepted: 31 July 2017;
Published online: 4 September 2017

References

1. Payne, S. Obama: US misjudged the rise of the Islamic State. *Washington Post* (2014).
2. *Quadrennial Defense Review Report* (US Department of Defense, 2006).
3. *Quadrennial Defense Review 2014* (US Department of Defense, 2014).
4. Arreguin-Toft, I. How the weak win wars: a theory of asymmetric conflict. *Int. Secur.* **26**, 93–128 (2001).
5. Atran, S. & Ginges, J. Religious and sacred imperatives in human conflict. *Science* **336**, 855–857 (2012).
6. Atran, S., Axelrod, R. & Davis, R. Sacred barriers to conflict resolution. *Science* **317**, 1039–1040 (2007).
7. Swann, W. B. Jr., Jetten, J., Gómez, Á., Whitehouse, H. & Bastian, B. When group membership gets personal: a theory of identity fusion. *Psychol. Rev.* **119**, 441–456 (2012).
8. ARTIS Research. *Theoretical frames on pathways to violent radicalization*. http://www.artisresearch.com/articles/ARTIS_Theoretical_Frames_August_2009.pdf (Office of Naval Research, 2009).
9. Davis, R. *Hamas, Popular Support and War in the Middle East* (Routledge, Oxford, 2016).

10. Tetlock, P. Thinking the unthinkable: sacred values and taboo cognitions. *Trends Cogn. Sci.* 7, 320–324 (2003).
11. Ginges, J., Atran, S., Medin, D. & Shikaki, K. Sacred bounds on rational resolution of violent political conflict. *Proc. Natl Acad. Sci. USA* **104**, 7357–7360 (2007).
12. Dehghani, M. et al. Sacred values and conflict over Iran's nuclear program. *Judgm. Decis. Mak.* 5, 540–546 (2010).
13. Gómez, A. et al. On the nature of identity fusion: insights into the construct and a new measure. *J. Pers. Soc. Psychol.* **100**, 918–933 (2011).
14. Sheikh, H., Gómez, Á. & Atran, S. Empirical evidence for the devoted actor model. *Curr. Anthropol.* **57**, S204–S209 (2016).
15. Ginges, J., Atran, S., Sachdeva, S. & Medin, D. Psychology out of the laboratory: the challenge of violent extremism. *Am. Psychol.* **66**, 507–519 (2011).
16. Atran, S. The devoted actor: unconditional commitment and intractable conflict across cultures. *Curr. Anthropol.* **57**, S192–S203 (2016).
17. Atran, S. & Hamid, N. Paris: the war ISIS wants. *NYP Daily* (2015).
18. Gavrillets, S. & Richerson, P. Collective action and the evolution of social norm internalization. *Proc. Natl Acad. Sci. USA* **114**, 6068–6073 (2017).
19. Whitehouse, H., McQuinn, B., Buhmester, M. & Swann, W. B. Jr. Brothers in arms: Libyan revolutionaries bond like family. *Proc. Natl Acad. Sci. USA* **111**, 17783–17785 (2014).
20. Atran, S., Sheikh, H. & Gómez, Á. Devoted actors sacrifice for close comrades and sacred cause. *Proc. Natl Acad. Sci. USA* **111**, 17702–17703 (2014).
21. Sanín, F. G. & Wood, E. J. Ideology in civil war. *J. Peace Res.* **51**, 213–226 (2014).
22. Jurgensmeyer, M. *Terror in the Mind of God: The Global Rise of Religious Violence* (California Univ. Press, Berkeley, 2003).
23. McPherson, J. *For Cause and Comrades: Why Men Fought in the Civil War* (Oxford Univ. Press, Oxford, 1997).
24. Fritz, S. *Frontsoldaten: The German Soldier in World War II* (Univ. Kentucky Press, Lexington, 1995).
25. Varshney, A. Nationalism, ethnic conflict, and rationality. *Perspect. Politic.* **1**, 85–99 (2003).
26. Collier, P. & Hoeffler, A. Greed and grievance in civil war. *Oxf. Econ. Pap.* **56**, 563–595 (2004).
27. Hoover Green, A. *Repertoires of Violence Against Noncombatants: The Role of Armed Groups and Ideologies*. PhD thesis, Yale Univ. (2011).
28. Atran, S. in *Beyond Convergence: World Without Order* (eds. Matfees, H. & Miklaucic, M.) 61–88 (National Defense Univ., 2016).
29. Fukuyama, F. *The Origins of Political Order* (Farrar, Straus and Giroux, New York, 2012).
30. Humphreys, M. & Weinstein, J. M. Who fights? The determinants of participation in civil war. *Am. J. Polit. Sci.* **52**, 436–455 (2008).
31. Atran, S., Axelrod, R., Davis, R. & Fischhoff, B. Challenges in researching terrorism from the field. *Science* **355**, 352–354 (2017).
32. Toynbee, A. *A Study of History* (Oxford Univ. Press, Oxford, 1934).
33. Darwin, C. *Descent of Man and Selection in Relation to Sex* (D. Appleton, New York, 1872).
34. Buckley, C. & Xiaobo, L. Chinese dissent who won Nobel while jailed, dies at 61. *New York Times* (2017).
35. Baron, J. & Spranca, M. Protected values. *Organ. Behav. Hum. Decis. Process* **70**, 1–16 (1997).
36. Swann, W. B. Jr., Seyle, C., Gómez, Á., Morales, J. F. & Huici, C. Identity fusion: the interplay of personal and social identities in extreme group behavior. *J. Pers. Soc. Psychol.* **96**, 995–1011 (2009).
37. Jiménez, J. et al. The dynamic identity fusion index: a new continuous measure of identity fusion for web-based questionnaires. *Soc. Sci. Comput. Rev.* **34**, 215–228 (2016).
38. Swann, W. B. Jr. et al. Contemplating the ultimate sacrifice: identity fusion channels pro-group affect, cognition, and moral decision-making. *J. Pers. Soc. Psychol.* **106**, 713–727 (2014).
39. Gómez, Á. & Vázquez, A. The power of 'feeling one' with a group: identity fusion and extreme pro-group behaviours. *Int. J. Soc. Psychol.* **30**, 481–511 (2015).
40. Stouffer, S. et al. *Studies in Social Psychology in World War II* (Princeton Univ. Press, Princeton, 1949).
41. Smith, R. B. Why soldiers fight. Part I. Leadership, cohesion and fighter spirit. *Qual. Quant.* **18**, 1–32 (1983).
42. Gómez, Á., López-Rodríguez, L., Vázquez, A., Paredes, B. & Martínez, M. Morir y matar por un grupo o unos valores. Estrategias para evitar, reducir y/o erradicar el comportamiento grupal extremista. *Anu. Psicol. Juríd.* **6**, 122–129 (2016).
43. Ócalan, A. *Prison Writings: The PKK and the Kurdish Question in the 21st Century* (Pluto Press, London, 2011).
44. Taylor, H. & Moyer, J. Islamic state fighter publicly executes own mother; Syrian activists say. *Washington Post* (2016).
45. Ahlul Bayt News Agency. ISIS militant executes own father in Mosul for insulting Abu Bakr al-Baghdadi. <http://en.abna24.com/service/middle-east-west-asia/archive/2016/10/13/785201/story.html> (2016).
46. Fessler, D., Holbrook, C. & Snyder, J. K. Weapons make the man (larger): formidability is represented as size and strength in humans. *PLoS ONE* **7**, e32751 (2012).
47. Holbrook, C., López-Rodríguez, L., Fessler, D., Vázquez, A. & Gómez, Á. Gulliver's politics: conservatives envision potential enemies as readily vanquished and physically small. *Soc. Psychol. Pers. Sci.* doi:10.1177/1948550616679238 (2016).
48. Bowles, S. & Polanía-Reyes, S. Economic incentives and social preferences: substitutes or complements? *J. Econ. Lit.* **50**, 368–425 (2012).
49. Graham, J. & Haidt, J. in *The Social Psychology of Morality: Exploring the Causes of Good and Evil* (eds. Mikulincer, M. & Shaver, P.) 11–31 (American Psychological Association, 2012).
50. Ginges, J. & Atran, S. War as a moral imperative (not just practical politics by other means). *Proc. R. Soc. B* **278**, 2930–2938 (2011).
51. Fiske, A. & Rai, T. S. *Virtuous Violence: Hurting and Killing to Create, Sustain, End and Honor Social Relationships* (Cambridge Univ. Press, Cambridge, 2015).
52. Kahane, G., Everett, J., Earp, B., Farias, M. & Savulescu, J. 'Utilitarian' judgments in sacrificial moral dilemmas do not reflect impartial concern for the greater good. *Cognition* **134**, 193–209 (2015).
53. Dollard, J. *Fear in Battle* (Institute of Human Relations, Yale Univ., 1943).
54. Watson, S. J. Religion and combat motivation in the Confederate armies. *J. Mil. Hist.* **58**, 29–55 (1994).
55. Fearon, J. D. Rationalist explanations for war. *Int. Org.* **49**, 379–414 (1995).

Acknowledgements

We thank everyone who participated in the studies, especially those on the frontline in Iraq. We acknowledge partial funding support from the Minerva Program of the US Department of Defense (ONR N000141310054 and AFOSR FA9550-14-1-0030 DEF), as well as the Office of Naval Research (N00014-16-C-3032), US National Science Foundation (SES 1559387) and Spanish Government (PSI2015-67754-P). Funders had no role in the conceptualization, design, data collection, analysis, decision to publish, or preparation of the manuscript. We thank R. Axelrod, B. Fischhoff, X. Lois, J. Smith and D. Stone for assistance in developing and informally reviewing this research.

Author contributions

S.A. conceived and directed frontline investigations and was overall project director. Á.G. conceived and directed online studies. S.A. and Á.G. managed project communication. Á.G. and L.L.-R. prepared online protocols and collected online data. S.A. and H.S. prepared frontline protocols. S.A., L.W. and H.W. collected frontline data. S.A., H.S., J.G. and A.V. participated in refining and developing online protocols and experimental design. Á.G., J.G., L.W., H.W. and R.D. participated in developing frontline protocols and experimental design. Á.G., H.S. and L.L.-R. initiated data analysis. S.A., Á.G. and J.G. initiated manuscript preparation. All authors reviewed and approved the final version of the manuscript for submission.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at doi:10.1038/s41562-017-0193-3.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to S.A. and Á.G.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Life Sciences Reporting Summary

Nature Research wishes to improve the reproducibility of the work we publish. This form is published with all life science papers and is intended to promote consistency and transparency in reporting. All life sciences submissions use this form; while some list items might not apply to an individual manuscript, all fields must be completed for clarity.

For further information on the points included in this form, see [Reporting Life Sciences Research](#). For further information on Nature Research policies, including our [data availability policy](#), see [Authors & Referees](#) and the [Editorial Policy Checklist](#).

▶ Experimental design

1. Sample size

Describe how sample size was determined.

For frontline studies we anticipated, based on pilot findings, that 1. only combatants who participated in the Battle of Kudilah would be tested, and 2. that approximately 20 subjects per combatant group would be needed to show statistical reliability even for robust trends. The limit of 20 subjects per combatant group was also dictated by time constraints on access to the front. No statistical model, however, was used to determine sample sizes. For the 15 online studies, no specific statistical method was used to predetermine sample size. Generally, we established a period of 5 days for data collection based on the average n usually collected in previous research for the same period as attested to in a number of previously published papers. Variations depended on the period of the year (e.g., vacations, weekends).

2. Data exclusions

Describe any data exclusions.

Exclusion criteria were pre-established. Data were pre-screened for completeness and repeat participation. Those participants that showed duplicated answers were identified (if they reported the same personal ID or code together with the same sex and age). In such cases, the duplicate case(s) was/were deleted. The primary case was left. Those participants that left in blank most important variables were also excluded. In some studies (e.g., Study 3 and 4) other criteria were additionally applied and they described in the Supplementary Information (e.g., not reporting a valid group/value).

3. Replication

Describe whether the experimental findings were reliably reproduced.

The findings presented in the manuscript have been replicated in the same report. Field and lab studies also yielded common findings .

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

Samples were randomly allocated into experimental conditions as described in Supplementary Information.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

Investigators were unaware of the sample group allocation during experiments as the studies were run with Qualtrics, with an automatic randomization. For the analyses, investigators were initially unaware of which alternative hypotheses were expected to be validated for the for the frontline studies (value or group, spiritual formidability or physical formidability), but in the subsequent online studies they were not blinded.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or the Methods section if additional space is needed).

n/a Confirmed

- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
- A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly.
- A statement indicating how many times each experiment was replicated
- The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
- A description of any assumptions or corrections, such as an adjustment for multiple comparisons
- The test results (e.g. p values) given as exact values whenever possible and with confidence intervals noted
- A summary of the descriptive statistics, including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
- Clearly defined error bars

See the web collection on [statistics for biologists](#) for further resources and guidance.

► Software

Policy information about [availability of computer code](#)

7. Software

Describe the software used to analyze the data in this study.

SPSS and R

For all studies, we encourage code deposition in a community repository (e.g. GitHub). Authors must make computer code available to editors and reviewers upon request. The *Nature Methods* [guidance for providing algorithms and software for publication](#) may be useful for any submission.

► Materials and reagents

Policy information about [availability of materials](#)

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

There are no restrictions on availability upon request of materials for bona fide researchers, scholars and lay persons expressing legitimate interest in the studies.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

n/a

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

n/a

b. Describe the method of cell line authentication used.

n/a

c. Report whether the cell lines were tested for mycoplasma contamination.

n/a

d. If any of the cell lines used in the paper are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

n/a

► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

Animals were not used in these studies.

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

This information can be found in the Supplementary Information for each study in the Participants section