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The Prosocial Phenotype and Cooperative Health Protective Behaviors: Insights from COVID-19

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66 <https://osf.io/xmzf3/> (Mills, 2025).

Abstract

Objectives: Identifying factors associated with cooperative health-protective behaviors (e.g., vaccination, social distancing) is critical during crises requiring collective action. This research examines two hypotheses in the context of the COVID-19 pandemic: (i) the *situational-strength hypothesis*, which predicts that the impact of prosocial preferences on repeated low-cost cooperative actions (e.g., adherence to government guidelines) is moderated by situational ambiguity (e.g., clarity of guidelines); and (ii) the *vaccination-altruism hypothesis*, predicting prosocial individuals are more likely to undertake high-cost cooperative actions (e.g., initial COVID-19 vaccination) due to other-regarding motives. *Methods:* Study 1 (N=2,861) assessed four prosocial behaviors (blood donation, organ donor registration, monetary donation, volunteering) and three classic cooperative games (dictator, trust, public goods) to validate a *prosocial-phenotype* (PP) measure. Study 2 (N=3,077) utilized an eight-wave UK panel survey (March 2020–July 2021) to test the situational strength and vaccine altruism hypotheses. *Results:* Study 1 found that past prosocial behavior was significantly correlated with behavior in cooperative games, supporting construction of the PP measure. In Study 2, higher PP, in line with the situational-strength hypothesis, was associated with greater adherence to guidelines, but only when rules were ambiguous. Higher PP was also associated with greater stated willingness and uptake of vaccination. Although self-protection was the most common motive to vaccinate, high-PP individuals were more likely to cite protecting others and achieving herd immunity. *Conclusions:* Prosociality plays a dynamic role in influencing both low- and high-cost cooperative health protective behaviors, offering insights for public health strategies in future crises.

Significance Statement

Understanding human cooperation is essential for solving public health challenges. This research demonstrates that individuals with stronger prosocial tendencies were more responsive during periods of ambiguous COVID-19 guidelines and more motivated by concern for others when choosing to vaccinate. These insights can inform targeted interventions to improve cooperation in future global health threats.

Keywords: Prosociality, Prosocial Phenotype, Cooperation Games, Cooperative Behaviors, COVID-19, Situational Strength, Vaccination-Altruism

The Prosocial Phenotype and Cooperative Health Protective Behaviors: Insights from COVID-19

Cooperation is a key part of public health (e.g., vaccination) and can be shaped by preexisting tendencies towards prosociality (Campos-Mercade et al., 2021; Cato et al., 2020; Fang et al., 2022; Müller & Rau, 2021) as well as the immediate normative constraints of a particular environment (Fehr & Gächter, 2000; Pfattheicher, Nielsen, & Thielmann, 2022). Indeed, general prosocial preferences are known to influence a wide array of cooperative behaviors, including pro-environmental action (Andre et al., 2021; Fuhrmann-Riebel et al., 2021; Lades et al., 2021), labor market participation (Dohmen et al., 2009; Kosse & Tincani, 2020), and redistributive voting (Epper et al., 2020), among others (Fang et al. (2022) for an overview).

However, little is known about the temporal dynamic of this influence in real-world cooperative settings, particularly in the domain of health protective behavior. Specifically, how prosocial preferences influence health-based cooperation across changing contexts that demand either repeated low-cost actions or a single high-cost action has not been explored in a single field-based study.

To address this gap, we test two related hypotheses. The first explores whether a changing cooperative context affects the extent to which past prosocial behavior is associated with future adherence to repeated, low-cost actions—in this case, ongoing compliance with government safety guidelines during the COVID-19 pandemic. The second examines whether past prosocial behavior is also associated with willingness to engage in a single high-cost cooperative act (COVID-19 vaccination) and the underlying motivations for this decision.

While there are many definitions of prosociality (see Pfattheicher, Nielsen, and Thielmann (2022)), we define it as encompassing “...the broad range of actions intended to benefit one or more people other than oneself” (Learning, 2003, p.463). Cooperation is operationalized within the framework of a public goods social dilemma, where overall benefits are maximized when the majority contribute (e.g. follow guidelines, vaccinate), despite the individual incentive to defect (Chaudhuri, 2018; Fehr & Gächter, 2000, 2002).

Regarding the first hypothesis, while the influence of prosocial preferences on cooperation has been established (Campos-Mercade et al., 2021; Cato et al., 2020; Fang et al., 2022; Müller & Rau, 2021), much less is known about the temporal dynamics of this relationship with respect to repeated acts of low-cost cooperation (e.g., social distancing). We add to the literature by drawing on the ‘situational strength

hypotheses’ (Cooper & Withey, 2009; Li et al., 2024; Meyer et al., 2010, 2017) to explore how the influence of previous prosocial behavior on cooperation is a function of the cooperative context. Specifically, this hypothesis posits that the influence of stable domain-general traits (e.g., a propensity toward prosociality) should be less pronounced in ‘strong’ situations where social norms/sanctions are clear and enforceable, and more pronounced in ‘weak’ ambiguous situations (Cooper & Withey, 2009; Meyer et al., 2010, 2017).

The second hypothesis explores the ‘vaccination-altruism hypothesis’, which proposes other-regarding preferences (i.e., consideration of others) as a key motivational factor driving vaccination decisions (Betsch et al., 2017; Böhm & Betsch, 2022; Brockmann, 2017; Cucciniello et al., 2022; Pfattheicher, Petersen, & Böhm, 2022). However, we extend this prediction by exploring how motivations for vaccination vary across the high-cost context of the COVID-19 pandemic in terms of the strength of a person’s prosocial preferences. Isler et al. (2020) indicate that, in high-cost contexts, the strongest vaccination motivation is self-protection, not the protection of others. However, we argue that those with strong preexisting prosocial preferences are more likely to vaccinate as they will also be motivated to protect others and attain herd immunity. It is this combination of self- and other-regarding motivations that drive higher vaccination uptake in those with strong prosocial preferences.

As the COVID-19 pandemic required sustained mass cooperation to reduce the spread of infection, we explore these hypotheses using a unique longitudinal panel data set over eight waves (from March 2020 to July 2021 in the UK: Study 2), capturing periods of varying clarity, consistency and enforcement of UK government guidelines. Through the use of Google trends data as well as our own panel data, we show strong evidence that the later periods of COVID-19 in the UK were perceived as situationally ‘weaker’ than the initial period (i.e., the first lockdown). Thus, we test how an existing propensity for prosociality influences repeat cooperation over time across contexts that change in their situational-strength (Pfattheicher, Nielsen, & Thielmann, 2022). Vaccination behavior and motivations to vaccinate were assessed across the last two waves. This work also adds a longitudinal analysis to the existing literature on prosocial preferences during the COVID-19 pandemic, which has mainly been cross-sectional (Campos-Mercade et al., 2021; Cato et al., 2020; Fang et al., 2022; Müller & Rau, 2021). Unlike prior cross-sectional studies, our eight-wave panel allows us to examine how associations between prosocial traits and behavior change as external constraints evolve.

A propensity towards prosociality can be understood within the context of the ‘cooperative

phenotype' (CP) (Peysakhovich et al., 2014). The CP describes a broad underlying psychological preference for cooperation that is domain-general (i.e., a preference for cooperation across a wide variety of contexts) and temporally stable (i.e., past cooperative behavior predicts future cooperative behavior) (Claessens et al., 2022; Reigstad et al., 2017). While initially defined in terms of positive co-occurrence of cooperative economic preference (Peysakhovich et al., 2014), we examine the existence of a 'prosocial phenotype' (PP) based on the occurrence of previous real-world prosocial behaviors (Bekkers, 2006; Studte et al., 2019).

We define the PP as a tendency to have incurred personal costs across heterogeneous domains (blood donation, organ donor registration, monetary donations and volunteering time) for the benefit of others. While conceptually related to the CP, the PP differs in both scope and operationalization: it reflects concrete, voluntary helping behavior observed in everyday life, rather than decisions made in stylized experimental contexts. Thus, the two constructs share a prosocial core but differ in behavioral breadth, measurement and focus. In Study 1, we test the association between PP and CP, which serves a methodological purpose: to test whether these two measures covary, and in so doing, validating the PP as a compact, field-based index of prosociality.

Establishing that link is important, because Study 2 examines the PP to ask under what conditions it is associated with cooperative health behaviours during COVID-19. Building on the 'situational strength' theory, we predict the PP will influence cooperative behaviors differently across various stages of COVID-19 in the UK, being more strongly associated with cooperative behavior when situational strength is weak. According to Meyer et al. (2010, 2017), situational strength consists of four key facets: clarity, consistency, constraints, and consequences. Strong situations, characterized by high clarity and consistency, enforceable constraints, and significant consequences, minimize individual differences in behavior by providing clear cues on how to act. Conversely, weak situations allow greater behavioral variability, increasing the role of personality traits.

In the early stages of the pandemic within the UK, the first lockdown was the most stringent, with legally enforceable explicit mandates to "stay at home" except for very limited purposes, with enforcement powers granted to the police (from March 2020). This created a high-clarity, high-consistency environment with strong consequences for non-compliance (Institute for Government, 2021). These clear sanctions also resonate with the wider literature on altruistic punishment, whereby higher levels of cooperation are sustained over time when non-cooperation is punishable (Fehr & Gächter, 2000, 2002). These sanctions are

also effective when centrally enforced (Baldassarri & Grossman, 2011). Accordingly, the situational strength hypothesis predicts a convergence of behaviors and less divergence across prosocial types (the PP). As the first lockdown eased (May 2020), restrictions relaxed, and the government encouraged the public to resume their regular activities. Clarity and consistency in this period remained high, maintaining high situational strength. However, this relaxation had lasting effects, as reinstating stringent restrictions after they had been relaxed proved substantially more challenging.

This was exemplified in the latter periods of COVID-19 in the UK, characterized by regional differences and two further lockdown periods (from October 2020). During this time, the UK's approach changed significantly, featuring regional tiered restrictions, inconsistent messaging, and lower enforcement, creating ambiguity in behavioral expectations (Department of Health and Social Care, 2021). Increased public fatigue and confusion during this period further contributed to the weakening situational strength (Michie et al., 2020; Williams et al., 2021). This shift is fully outlined in the supplementary information (Table S32 in SI), where we document evolving clarity, consistency, and consequences across COVID-19 periods. Consequently, we expect that the PP will be more strongly associated with adherence to cooperative health protective behavior during the latter period of COVID-19 in the UK, characterized by more situational ambiguity.

Hypothesis 1a: Individuals higher in the PP will report greater adherence to repeated low-cost COVID-19 compliance behavior across the study period.

Hypothesis 1b: The influence of the PP on compliance behaviors during COVID-19 will be moderated by situational strength, with stronger effects observed in weaker contexts where government rules are less clear or enforceable.

With respect to vaccination behavior, the vaccination altruism hypothesis predicts that people are more likely to vaccinate if (i) attaining herd-immunity ("resistance to the spread of a contagious disease within a population" (OED) and (ii) protecting others is made salient. While there is a large evidence base to support this (Betsch et al., 2017; Böhm & Betsch, 2022; Brockmann, 2017; Cucciniello et al., 2022; Pfattheicher, Petersen, & Böhm, 2022), there are also a number of studies that find prosocial messages have not outperformed other messages (Isler et al., 2020; Milkman et al., 2021; Rabb et al., 2022). The COVID-19 pandemic represented a high-risk environment with significant uncertainty for the individual. In

such high-risk contexts, it has been proposed that vaccinating to ‘protect oneself’ is the primary motivation (Isler et al., 2020). However, because people higher in the PP are likely to have stronger other-regarding preferences; they should not only be more likely to vaccinate but will also be more likely to express motivation to help others and attain herd immunity. Thus, we predict that the single strongest motivation to vaccinate will be to protect oneself, but higher PP individuals will be differentiated from others by their desire to help others and attain herd immunity.

Hypothesis 2a: Individuals with higher PP will be more likely to undertake high-cost cooperative actions, such as vaccination (both stated willingness and actual uptake).

Hypothesis 2b: Among those who choose to vaccinate, (i) self-regarding motives (e.g., “to protect myself”) are expected to remain the most frequently endorsed, though (ii) individuals with higher PP will be more likely to endorse other-regarding motives (e.g., “to protect others” and “to achieve herd immunity”), compared to those with lower PP.

Study 1: A ‘Prosocial Phenotype’ Index

Introduction

Before testing our main hypotheses (Study 2), we first establish some initial measurement properties of the PP index based on self-reported history of real-world helping behaviors: donating blood, registering as an organ donor, giving to charity, and volunteering time.

To validate the PP, we compared it to the CP, a construct based on behavior in a set of well-established economic games: the Dictator Game, Trust Game (Investor and Trustee roles), and Public Goods Game (Peysakhovich et al., 2014). While individual game decisions can be context-sensitive, aggregate behavior across multiple games has been shown to reflect reliable differences in prosocial orientation (Galizzi & Navarro-Martinez, 2019; Haesevoets et al., 2022; McAuliffe et al., 2019; Thielmann et al., 2020). A positive association between the PP and CP would thus provide some evidence that PP captures meaningful individual variation in prosociality, justifying its use in our main analyses on situational strength and vaccine-altruism.

Method

Sample and Design

Participants ($N = 2,861$) were recruited via Prolific (8th to 13th May 2024). While the survey focused on plasma donation (OSF preregistration, see Desai (2024)), participants completed background information on four real-world prosocial behaviors and the three economic games used to define CP. Participants were compensated roughly £9 p/h in accordance with standard policy on Prolific.

Measures

Real-World Prosociality: Participants were asked four ‘Yes/No’ questions about their past prosocial behavior: blood donation (“Have you ever donated blood?”); organ registration (“When the opt-in system operated, did you carry a donor card or sign up to the organ donor register in your lifetime?”); money donation (“Have you ever donated money to charity?”); and volunteering (“Have you ever given time to volunteer for charity work?”). 39% of the sample had donated blood before, 48% had signed on the organ donor registry, 97% had donated money to charity, and 53% had volunteered their time for charity (see SI Section S1.1).

Economic Games: Participants completed three hypothetical unincentivized economic games: (i) Dictator Game (DG) – Participants could allocate any degree of an endowment (£10) between themselves and an anonymous recipient (ii); Trust Game Investor (TG-I) – Participants could decide how much of a £30 endowment to invest to another person (person B), and this amount is tripled for Person B, (iii) Trust Game Trustee (TG-T) – Participants decide how much of a £90 that they are the trustee for (this represents a tripled £30 investment) to return to the investor, and (iv) Public Goods Game (PGG) – Participants contribute to a shared pool with three other people, the total amount in the collective pool is divided equally across all four people (SI S1.2 for full instructions). Following Peysakhovich et al. (2014), all game allocations were normalized to range from 0 to 1, ensuring comparability across tasks (Figure S3 in SI).

Analytic Strategy

We initially examined the latent structure of PP and CP, with a series of Confirmatory Factor Analyses (CFAs) in MPlus 8.4. A diagonally weighted least squares estimator was used to account for the mix of dichotomous (PP) and continuous (CP) variables. Following Hu and Bentler (1999), we adopted an index combination rule to judge fit: (i) root-mean-square error of approximation (RMSEA: acceptable fit

$\leq .10$; good fit $\leq .06$; and a p-value showing that the RMSEA is not significantly different to .05), comparative fit index (CFI: acceptable fit $\geq .90$; excellent fit $\geq .95$) and a standardized root-mean-square-residual (SRMR $\leq .10$). We tested six models: (i) a single factor (four PP items and four CP games load on a single factor), (ii) two orthogonal factors (four PP items and four CP games load on separate uncorrelated factors), (iii) two correlated factors (four PP items and four CP games load on separate correlated factors), (iv) a hierarchical factor model (four PP items and four CP games load on separate factors that load on a higher order factor: iii and iv are equivalent), (v) an orthogonal G-2S bi-factor model (there is a general factor derived from PP items and CP games with two specific orthogonal factors that are uncorrelated with the general factor) and (vi) a correlated S factors G-2S bi-factor model (Southward et al., 2023). We then used OLS regression to explore the association between PP and CP. The bifactor models have been suggested as a good representation of cooperative behavior (McAuliffe et al., 2019).

Results and Discussion

The results of the CFA models are shown in SI (Tables S6-S9). The correlated S factors G-2S bi-factor model showed the best fit (CFI = .95, RMSEA = .038, associated $p = 0.98$, and RMSR = .038), with the PP and CP items loading significantly on the correlated S factors and the G factor loading losing some significance. The correlated factors and hierarchical models also demonstrated acceptable fit (both CFI = .90, RMSEA = .04, $p = 0.81$, RMSR = .06), supporting the distinction between PP and CP as related but separable constructs. A composite PP index (sum of these four dichotomous indicators) was created, ranging from 0 (no prosocial acts) to 4 (engaged in all four). For visualization purposes, this was further categorized into three groups: Low-donors (0-1 acts), Mid-donors (2 acts), and high donors (3-4 acts).

OLS models showed that relative to low-PP, Mid-PP exhibited a statistically significant increase of 0.131 SD units in the CP ($p < .01$) and High-PP exhibited a stronger association of 0.214 SD units ($p < .01$), suggesting a monotonic association between PP and CP. To visualize these results, we estimated predicted values of cooperative game behavior (z-scored) at the mean of covariates for each donor group (see Figure 1).

[Figure 1 about here]

Sensitivity analysis: To account for the limited variability in the charity money item (97% endorsed “Yes”), we conducted a series of sensitivity analyses using extended-response formats collected

for each PP item (see SI Section S1). Specifically, participants also reported the frequency of their blood and monetary donations, as well as the number of hours volunteered in the past year. These responses allowed us to construct more extended, ordinal versions of each item. We re-ran the CFAs using these extended measures in place of the dichotomous items. The results indicated comparable model fit to those reported above (see SI Section S1).

Taken together, the observed association between PP and CP supports the interpretation of the PP as a meaningful index of prosociality. The two-factor structure observed in our best-fitting model — with PP and CP loading on correlated but distinct latent factors — mirrors prior work suggesting that lab-based and real-world prosociality reflect overlapping but non-identical constructs (McAuliffe et al., 2019). Given this convergence, we treat the PP as a suitable, field-derived index. While we do not claim to comprehensively validate the PP here, this evidence justifies its use in subsequent tests of our central hypotheses in Study 2: namely, whether personality traits (indexed by PP) matter more in weak social situations, and whether they interact with perceptions of altruistic versus self-interested vaccination.

Study 2: Prosocial Phenotype and Cooperation during COVID-19

Study design, setting and participant recruitment

The data analyzed in Study 2 are drawn from the UK COVID Mental Health and Wellbeing (UK COVID-MH) study, a longitudinal panel study recruiting a quota-sample of the UK population (quotas based on age, gender, socio-economic grouping, and geographic region) via online surveys (Panelbase.net) conducted across eight waves from March 2020 to July 2021 (O'Connor et al., 2021). The initial wave (N=3,077) occurred from 31 March to 9 April 2020, coinciding with the first UK lockdown, followed by seven subsequent waves until July 2021, with N=1,994 participants in wave 8. Participants in the study received compensation of roughly £1.50 for each survey they completed, and they were also included in prize draws. All information on the study, recruitment methods, and sample retention across waves are detailed in the SI (see section S2 in SI). Fig. 2 depicts the timelines of the study and shows varying degrees of lockdown restrictions accompanied by rates of new daily COVID-19 cases (from gov.uk (link)). As outlined previously, we categorize waves 2 to 5 with ‘strong’ situational strength and waves 6 to 8 with ‘weak’ situational strength.

[Figure 2 about here]

Measures:

Real-World Prosociality In wave 1, participants were asked the same four ‘Yes/No’ questions about their past prosocial behavior as in Study 1 for blood donation, organ donor registration, money donation, and volunteering. These measures were asked at later waves, but due to little variation across time points (Table S20 in SI), these were treated as fixed (only information from wave 1 used). In wave 1, 31% of the sample had donated blood before, 43% had signed on to the organ donor registry, 90% had donated money to charity, and 50% had volunteered their time for charity work. Pairwise correlations showed that all measures were correlated (Table S21 in SI). As before, to measure PP, we constructed a composite index of the four prosocial behaviors that ranged from 0 to 4: Low-PP (0-1 prosocial acts), Mid-PP (2 acts), and High-PP (3-4 acts). This split results in a relatively even spread of participants across the PP, with 28% Low-PP, 35% Mid-PP, and 37% High-PP types (Fig. S7 in SI). Lastly, we test consistency in attrition rates for waves 1 and 8, finding no difference in the distribution of PP types ($\chi^2_4 = 3.48, p = 0.481$).

Cooperative Health Protective Behavior - COVID-19 Compliance: Cooperative behavior reported during the COVID-19 pandemic is measured through the following: (i) following government guidelines, and (ii) vaccine willingness. Following government guidelines is made up of several variables that change over time due to fluctuating government guidelines and circumstances. They involve participants being presented with statements surrounding adherence to government guidelines and asked to select from a Likert-type scale how often they performed the behavior (1-always, 2-often, 3-sometimes, 4-rarely, 5-never; reversed scored so that a higher score equates to greater adherence). Statements cover a range of adherence behaviors: leaving the house (“In the past two weeks, I only went outside for food, health reasons or essential work.”); social distancing (“In the past two weeks, if I went out, I always stayed 2 meters (6 feet) away from other people at all times.”); hand hygiene (“In the past two weeks, I always washed my hands as soon as I got home.”); meeting people externally (“In the past two weeks, I stuck to guidelines about not meeting more than 6 people from 2 households while outside.”); face covering in stores and shops (“In the past two weeks, I have worn a face covering when inside a store or shop.”); and face covering in public transport: (“In the past two weeks, I have worn a face covering when on public transport”). In waves 7 and 8, a general question on adherence to COVID-19 restrictions was asked (“Can you tell us how often you have followed the Governments COVID-19 guidelines in the last 2 weeks?”).

These measures of cooperative behavior with regard government guidelines were positively

correlated with one another within and between waves (Fig. S8 in SI). Exploratory Factor Analysis (EFA) was conducted on these measures for each wave from 2 to 6, with parallel analysis showing that the measures load onto a single factor (Tables S22-S31 for EFA results, and Figs. S9 and S10 for Screeplots and histograms in SI). We summed the items within each wave (2-6) to produce a composite score, which is normalized between 1 and 5, thus ensuring consistent scales across waves 2 to 8. The composite measure was reliable in each wave (Cronbach's alphas = 0.76, 0.75, 0.74, 0.78, 0.75, 0.79, and 0.79, respectively). As the measures at waves 7 and 8 are single items we show that they are correlated with (i) the composite scores within each wave (r 's range from 0.23 to 0.33, $p < .01$), (ii) with each other ($r = 0.38$, $p < .01$) and (iii) the aggregate on the composite measures ($r_{wave-7} = 0.36$, $p < .01$; $r_{wave-8} = 0.42$, $p < .01$). These results support the reliability of the adherence measures across waves 2-8.

Lastly, to verify that participants perceived the situation to be weaker during the later periods of COVID-19 in the UK, we use a combination of data from the panel survey and information collected from Google Trends. In the survey, participants were asked: "In the past two weeks, I have found the government guidance on COVID-19 restrictions easy to understand" (Strongly disagree, Disagree, Agree, Strongly agree —recoded from Strong agree to Strong disagree). This question was asked in Waves 5 and 6, an important period in the UK as it transitioned from minimal restrictions (out-of-lockdown) to the second lockdown (which began with a tier-based system introducing varying rules across England). Though valuable data, it only covers part of the study period. To complement this, we also use Google Trends data to examine how frequently the terms "Rules, Restrictions, Guidelines, Requirements, Measures" were searched across the world (for the top 50 countries in each) from waves 1 to 5 in our data between 31 March and 17th August (strong situational strength), and (b) waves 6 to 8 in our data between 1 October 2020 to 9 July 2021 (weak situational strength).

Both of these approaches allow us to explore public uncertainty about COVID-19 rules over the course of the pandemic, with the expectation that as restrictions became more ambiguous and complex, survey respondents would report greater difficulty understanding the guidance, and search activity for rule-related terms would increase, reflecting heightened public confusion (Kelly et al., 2024; Michie et al., 2020; Williams et al., 2021).

Cooperative Health Protective Behavior - Vaccination: An index of vaccine willingness was constructed through two questions: (i) "Have you been offered a COVID-19 vaccine yet?" ('Yes- offered

and awaiting first dose'; 'Yes- offered and have had at least one dose'; 'Yes – I do not plan to accept a vaccine'; 'No, I have not been offered a vaccine yet'); (ii) "If you have not yet had a COVID-19 vaccine, how likely will you be to take the vaccine?" ('Very likely'; 'Likely'; 'Unlikely'; 'Very unlikely'). Participants who did not answer 'Yes- offered and have had at least one dose' to the first question, were asked the second question. A binary variable for vaccine willingness was constructed for those who had at least one dose, or those who were likely or very likely to take the vaccine, else zero (zero includes people who stated 'Unlikely' and 'Very unlikely' to likelihood of accepting vaccine after not selecting 'Yes- offered and have had at least one dose'). A binary variable for vaccination behavior was constructed for those who had at least one dose, else zero (zero includes all respondents who did not respond 'Yes- offered and have had at least one dose'). These questions were asked in waves 7 and 8 when the vaccine became available. Overall, vaccine willingness was high, with 1,833 of 2,224 (84.67%) participants being willing in wave 7 and 1,795 of 1,994 (90.02%) in wave 8. Rates of vaccination (i.e., those who had at least one dose of the vaccine) were low in wave 7 (15.96%) and higher in wave 8 (77.28%).

Statistical Analysis:

All analyses in this study were conducted using Stata 18. Generalized Estimating Equation (GEE) models (Gardiner et al., 2009), were employed, using a linear Gaussian identity for continuous outcomes and binomial logit models for binary outcomes. All specifications are adjusted for potential confounders (i.e., age, gender, ethnicity, education level, relationship status, employment status, socio-economic grouping, tenure, region of the UK, keyworker status, and pre COVID-19 finances). A rationale for these additional controls is provided in the SI (see Section S2.8.1).

Missing data due to attrition was accounted for as follows. Once people who dropped out at each wave (attrition) were removed, there was no missing data at an item-level. Therefore, we conducted OLS within waves with no need to conduct item-level imputation. However, there is a 35% attrition rate (wave 1 to wave 8). We adopted two sensitivity checks to account for any bias due to attrition: (i) restricting the sample to those who completed Waves 1 and 8 (see Section S2.9.3 in SI) and (ii) Propensity Score Matching (PSM) within wave (see Section S2.9.4 in SI). The rationale for the sample restriction is that Low-PP types are not more likely to show attrition than High-PP types. Thus, the main predictor is not subject to attrition bias. GEE was applied to these data. PSM was used to deal with attrition by balancing the sample within waves on demographics that are associated with attrition. PSM is a technique that has

been used in the literature on prosociality to reduce potential selection effects (Studte et al., 2019). The robustness of PSM was ensured by (i) comparing pre- and post-mean differences in the matching variables, (ii) comparing mean bias before and after matching, and (iii) employing a common support condition that ensures only participants whose propensity scores overlap to a ‘certain’ extent are compared (i.e., kernel matching algorithm: Epanechnikov kernel function and a bandwidth parameter of 0.06) (Caliendo & Kopeinig, 2008). Consistency in data patterns across the OLS and PSM within wave and with the GEE across waves indicates that the results are not attributable to attrition-based sample-bias.

Results

The following results show how PP is associated with cooperative health protective behavior across the waves.

Prosocial Phenotype and COVID-19 Compliance Behavior: Testing the Situational Strength Hypothesis

With respect to perceptions of clarity surrounding government guidance during COVID-19, our survey data shows a statistically significant decrease between waves 5 and 6, with participants stating that government guidelines were less clear ($b = 0.212, SE = 0.02, p < .01$, Table S36 in SI). Additionally, the data from Google Trends shows a clear difference in the volume of searches surrounding the term “Rules, Restrictions, Guidelines, Requirements, and Measures” (Fig. 3), with the UK ranked 16th (Index: 52) in the world during waves 1 to 5 (strong situational strength) and 2nd in the world (Index: 100) across waves 6 to 8 (weak situational strength). These results provide compelling evidence that the situation was perceived as weaker during the latter period of COVID-19 in the UK than the first.

[Figure 3 about here]

Turning to stated COVID-19 compliance behavior, consistent with the wider literature those with high-PP reported higher levels of following guidelines than Low-PP (High-PP vs Low-PP $b = 0.064, SE = 0.03, p < .05$), while Mid-PP did not (Mid-PP vs. Low-PP $b = 0.002, SE = 0.03, p > 0.1$) (Fig. 4 (a), Table S34 for GEE models and Table S36 for OLS models in SI). Consistent with the situational strength hypothesis for PP and cooperative health behavior, we observe an interaction between PP and lockdowns. There was no evidence to suggest High-PP were more likely to report higher levels of cooperation during waves 2 to 5 (relative to Low-PP) but were associated with higher levels between waves 6 to 8 (Weak situation x High-PP $b = 0.109, SE = 0.04, p < .01$). Fig. 4 (b) plots the

interaction of PP with situational strength, showing a clear divergence in PP between the strong vs. weak situational periods in our data.

[Figure 4 about here]

Thus, these results support both H1a and H1b, showing for the first time in the field that the way in which existing prosocial preferences influence cooperation depends on the cooperative context and, in particular, the degree of ambiguity about what to do.

Prosocial Phenotype and Vaccination Behavior: Testing the Vaccination-Altruism Hypothesis

High-PP and Mid-PP participants were more willing to vaccinate and be vaccinated (High-PP vs Low-PP $b = 0.076$, $SE = 0.02$, $p < .01$; Mid-PP vs Low-PP $b = 0.101$, $SE = 0.02$, $p < .01$), with the expected relationship of High-PP being greater than Mid-PP (High-PP vs Mid-PP $b = 0.044$, $SE = 0.01$, $p < .01$) (Fig. 5 (a), Table S37 in SI). The exact same pattern was observed for those who stated they received a vaccine (i.e., who had at least one dose) (Fig. 3, Table S38 in SI). There is also an interaction between PP and with waves 7 and 8, where high-PP is associated with higher levels of vaccination (High-PP vs Low-PP $inter.b = 0.091$, $SE = 0.03$, $p < .01$). These results are in line with H2a.

Fig. 5 (b) shows that across the board, protecting oneself was cited as the most frequent reason for vaccination (76%), followed by protecting others (48%), social life (42%) and herd-immunity (41%). Relative to Low-PP, Mid-PP or High-PP were more likely to mention protecting others (Mid-PP vs Low-PP $b = 0.265$, $SE = 0.10$, $p < .01$; High-PP vs Low-PP $b = 0.484$, $SE = 0.10$, $p < .01$) and herd immunity (Mid-PP vs Low-PP $b = 0.414$, $SE = 0.10$, $p < .01$; High-PP vs Low-PP $b = 0.537$, $SE = 0.10$, $p < .01$) (Fig. 5 (b), Table S39 in SI). These results indicate that there was greater consideration of others and the overall public good among those with higher levels of the PP. However, despite this, the most frequently cited reason to vaccinate was self-protection, in line with H2b.

[Figure 5 about here]

Robustness Checks

Time correlated with situational strength: It might be argued that changes in compliance behavior between the first period (waves 2 to 5) and second period (waves 6 to 8) were driven not by a weakening of situational strength but by compliance fatigue, disproportionately affecting Low-PP compared

to High-PP. This suggests that a temporal approach to examining situational strength risks conflating time with context. While time is an inherent part of context, context also encompasses factors beyond temporal changes. If the situational strength hypothesis holds, we should be able to demonstrate its effects independently of time, using a cross-sectional approach.

England's tier-based system (14 October – 5 November 2020) provides a valuable opportunity to address this concern. Applying a simplified classification system (Section S9.1), we categorized regions based on their highest tier during this period: Tier 1 (Medium), Tier 2 (High), and Tier 3 (Very High). This framework aligned almost perfectly with Wave 6 of our data collection (1 October – 8 November 2020), enabling us to exploit cross-regional variation in situational strength while holding time 'fixed.'

We conceptualize situational strength as weakest in Tier 1 (Medium), where restrictions and enforcement were minimal, increasing in Tier 2 (High), characterized by moderate restrictions and enforcement, and strongest in Tier 3 (Very High), with the most stringent restrictions, consistent enforcement, and clear consequences. The progression from Tier 1 to Tier 3 represents increasing situational strength, with greater clarity, consistency, and perceived consequences of government guidelines (see Section S2.9.1 in SI)

Consistent with the situational strength hypothesis, adherence to government guidelines was significantly higher in regions with stronger situational strength (i.e., Tier 2 and Tier 3) and diverged in regions with weaker situational strength (i.e., Tier 1). These findings reinforce the argument that situational strength, rather than time alone, shapes compliance behaviors, offering a robust cross-sectional validation of H1b.

Selection Bias: Individuals who have engaged in previous prosociality were more likely to be older, women, tertiary educated, and from a higher socio-economic grouping (Table S17 in SI). Also, attrition rates are correlated with demography (age, gender, education level: Table S18 in SI). As such, we conducted Propensity Score Matching independently for each of the waves, matching on age, gender, education, region, and socio-economic group. The results from this analysis confirmed that the findings using GEE and OLS are robust to any selection effect (Figs. S13-S15 and Tables S48-S55 in SI).

Discussion

Our results support the validity of the PP across domains: both in its association with behavior in cooperative games (Study 1) and in its relation to real-world health behaviors (Study 2). A key strength of

the study is its multi-wave design, which allowed us to examine how the influence of past prosocial behavior on cooperation changes over time as public health policies evolve. This quasi-natural experiment—spanning lockdowns, easing phases, and renewed restrictions—provided a rare opportunity to test the situational strength and vaccine-altruism hypotheses.

Consistent with the ‘situational strength’ hypothesis (Cooper & Withey, 2009; Li et al., 2024; Meyer et al., 2010, 2017), the influence of the PP was strongest during later periods of COVID-19 in the UK, when government directives were more ambiguous. During this time, those exhibiting higher levels of the PP, were more likely to comply with cooperative health protective behaviors, to support the public good. Conversely, during the pandemic’s initial phase, when government directives were clearer, behavioral variability diminished, resulting in more uniform adherence across all PP levels. These findings are in line with recent meta-analytic evidence demonstrating that strong situations reduce behavioral variance (Li et al., 2024). Moreover, they are also consistent with recent literature on strategic uncertainty. Dimant et al. (2024) highlight how individuals react differently to strategic environments that vary in the variance and shape of descriptive norms. Their findings experimentally show that in polarized environments, where behaviors are highly dispersed, personality traits and values play a more significant role in determining actions. We also observed that following guidelines to protect the public good declined over the course of the pandemic. Such a decline in cooperative behavior is observed in the lab in public goods games (Andreoni, 1995). Moreover, public goods games also often observe a jump in contributions as the game is restarted (Chaudhuri, 2018), and this is observed in the second lockdown with a sharp increase in adherence behavior.

The findings also add to our understanding of the motivations driving vaccination. While self-protection is important across all levels of the PP for vaccination; higher levels of the PP are associated with a greater emphasis on achieving immunity and protecting others. These findings provide ecological validity for the key central tenets of the ‘vaccination altruism’ hypotheses, that protecting others and herd immunity are key components of messages to encourage vaccination (Cucciniello et al., 2022). However, they qualify this by showing that protecting others and attaining herd immunity is more critical for those with a greater level of PP. For those with lower levels of PP, protecting others and herd immunity are less salient. Importantly, protecting self is the primary motivation across all people, which most likely reflects that this is a high-cost action (Isler et al., 2020). That is, having the first vaccines for COVID-19 in the UK,

which was the first country to vaccinate, is likely to have been high-cost as (i) there was uncertainty about the efficacy and possible side-effects, (ii) people had to come together *en masse* for the first time in nearly two years which was linked to perceptions of higher infection risk, and (iii) during this period of vaccination, infection rates were rising (see Fig. 2). This suggests important nuances within the ‘vaccination altruism’ hypothesis. While protecting others and achieving herd immunity play a crucial role, self-protection remains a dominant motivator, particularly in high-risk contexts.

Implications for public policy: Our findings offer insights from a policy perspective, emphasizing the critical role of prosociality in effectively managing global crises.

First, identifying individuals with a preexisting tendency toward cooperation (i.e., those already involved in charity work) could be a strategic starting point for any future global crisis that requires mass cooperation. In particular, engaging with these individuals as early adopters and role models may enhance adherence to various directives and accelerate the uptake of preventive measures via conditional cooperation (Fischbacher et al., 2001).

Second, our results suggest a more balanced public health messaging that emphasizes both individual and collective benefits of vaccination. Our findings clearly show that protecting oneself remains the dominant motivational factor behind vaccination, consistent with past literature (Böhm et al., 2017; Isler et al., 2020). However, the results also indicate that messages focusing on protecting others and promoting social solidarity (herd immunity) are likely to be effective, especially among those who already have a propensity towards prosociality (Betsch et al., 2017; Böhm & Betsch, 2022; Brockmann, 2017). This dual strategy is likely to be most effective when the cost to the individual is high (as in the pandemic), as under such circumstances, self-protection may be the most salient motivation (Isler et al., 2020).

Third, we observe reduced adherence to guidelines across the pandemic, particularly during the second lockdown when government directives were less clear. This decline indicates that situational ambiguity can undermine public compliance with health protective behaviors. Our findings suggest that clear, consistent and unambiguous rules are essential to maintain high levels of adherence, especially among low PP-types. Indeed, global evidence suggests that countries with clear and stringent government directives experienced better pandemic outcomes (Hale et al., 2021). Additionally, implementing strategies to support greater cooperation, including the potential for greater sanctions is one possibility (Fehr & Gächter, 2000, 2002; Ferguson et al., 2020). However, such sanctions should always be considered with the

possibility of “backfire effects”, whereby those with lower prosocial orientations comply only grudgingly or lash out in other ways (e.g., spreading misinformation or decrying government ‘paternalism’ online), ultimately undermining long-term trust and cooperation (Meyer et al., 2017).

Limitations and future research: While our two studies have numerous strengths, including the use of a variety of methods: (i) survey data, and (ii) a large-scale panel survey examining behaviors across different stages of a global crisis, there are limitations to consider. For Study 1, our cooperative game measures were not incentivized, although previous work has described this as less important in social preferences (Camerer & Hogarth, 1999). For Study 2, self-reported measures could be subject to bias (Hall, 2001). However, research indicates that self-reports of past-prosociality are accurate (Bekkers & Wiepking, 2011; Bertalli et al., 2011), and our adherence and vaccination results mirror UK ONS data (Office for National Statistics, 2023). Furthermore, there is good empirical evidence that reports of COVID-19 vaccination behavior are very accurate (Archambault et al., 2023). There is also evidence that self-reported compliance with COVID-19 is often higher than seen in observable and more objective data (Davies et al., 2022). Thus, there is some reporting bias. However, we are primarily interested in the way in which these cooperative behaviors vary by lockdown ambiguity as a function of PP. Thus, it is the pattern rather than the absolute value we are interested in.

Future research should explore the mechanisms that underpin the relationship between prosociality and cooperative behavior potentially informing the development of interventions aimed at fostering prosocial dispositions in the population. For instance, the role of trust across institutions (government, healthcare, and police) as well as individuals is likely an important motivator of cooperative behaviors. Prosociality might better sustain trust in institutions, which could result in greater cooperation during global health crises. Moreover, there may be substantial variation across different countries. The results of this study could be contrasted against other longitudinal studies that collected similar information during the pandemic.

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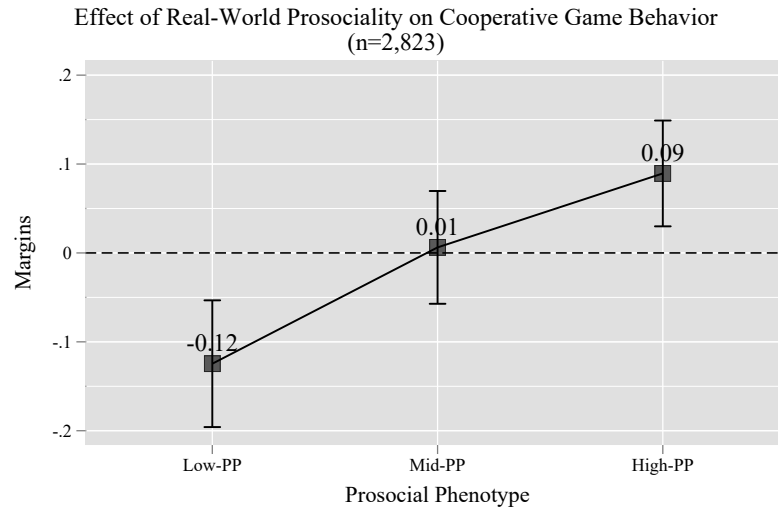
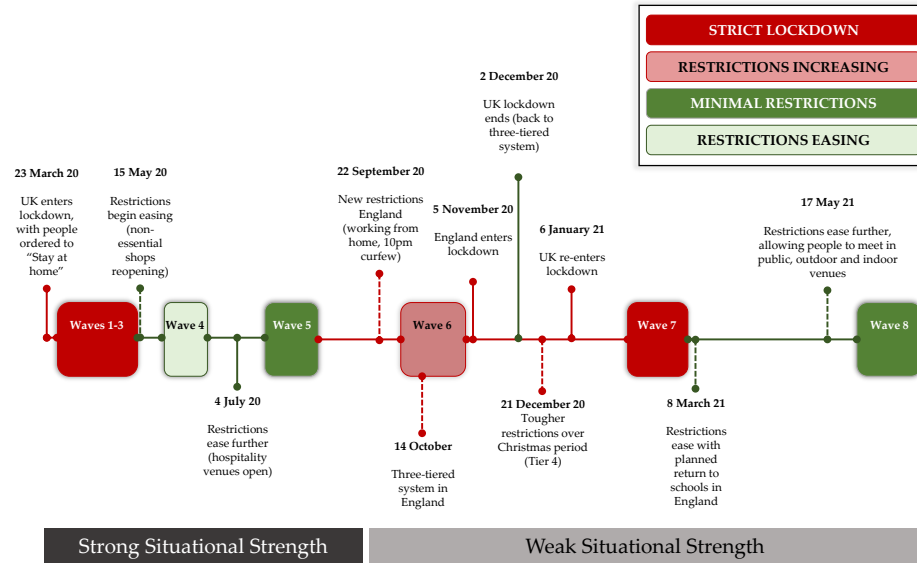
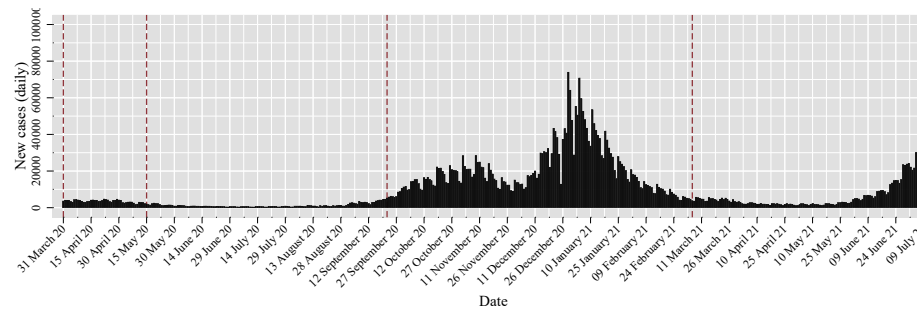


Figure 1

Notes: Predicted margins from an Ordinary Least Squares (OLS) regression. The dependent variable is the standardized Economic Games Factor ($\bar{x} = 0$, $SD = 1$), derived via exploratory factor analysis (EFA) from four behavioral measures: the Dictator Game, Trust Game (Player A and B decisions), and Public Goods Game. The key independent variable is Prosocial Phenotype (PP) group (Low, Medium, High). Models adjust for age, gender, ethnicity, and education. Full regression results are provided in the supplementary materials.



(a) Timelines and lockdown periods in the UK

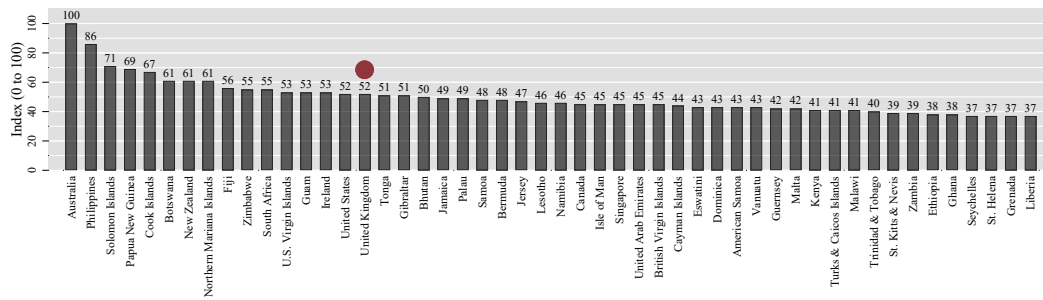


(b) Number of new daily cases in the UK

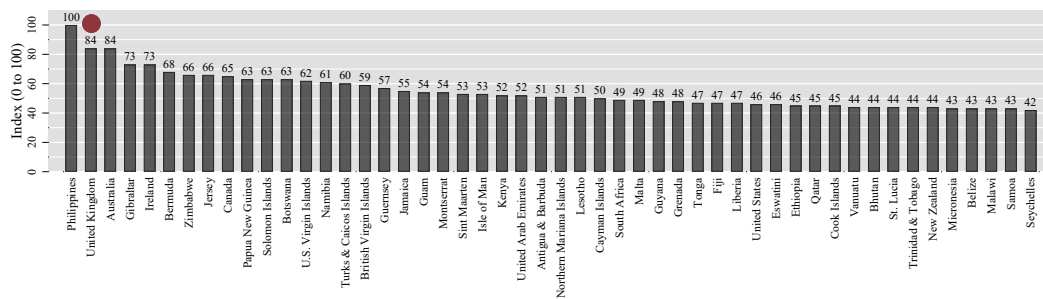
Figure 2

Timelines, lockdown periods, and new daily COVID-19 cases in the UK. (a) The timelines represent when each wave was conducted, with their associated dates. Key events are provided in this figure (for more information, see Institute of Government report (Institute for Government, 2021)). Dark red depicts 'Strict lockdown', with severe restrictions in place. All 'non-essential' high street businesses were closed, and people were ordered to "stay at home", permitted to leave for essential reasons only. Lockdown measures legally came into force on 26th March 2020 ((Crown Prosecution Service, Coronavirus, 2020)). The light-shaded green reflects 'Restrictions easing', with phased reopening of schools and some non-essential shops. Dark green depicts easing of lockdown restrictions characterized by 'Minimal restrictions'. This involved the reopening of non-essential shops (i.e., pubs, etc.). Moreover, schemes in the UK like Eat Out to Help Out (announced 3rd August) were introduced to incentivize economic activity ((HM Treasury, 2020)). The light-shaded red reflects 'Restrictions increasing', with a new three-tier system of COVID-19 restrictions starting in England only. Areas categorized as 'medium', 'high' or 'very high'. As COVID-19 cases rapidly increased during Christmas 2020, the UK entered its second national lockdown on 5th November, with a third on the 6th January 2021. By June 2021, schools in England were open again, and most legal limits on social contact were removed in England. Many of these restrictions remained in the other UK nations. (b) The data for the COVID-19 cases was downloaded from gov.uk (link). The maroon dashed vertical lines represent the 'first' lockdown (waves 1-3 in our dataset) between 31 March and 15 May 2020 and the broader 'second' lockdown (waves 6 and 7) between 12 September 2020 and 8 March 2021, as defined in our data. These periods are often referred to as the 'first' and 'second waves' of the COVID-19 pandemic (Office for National Statistics, 2021).

Google Trends across the world (Searches: ‘Rules, Restrictions, Guidelines, Requirements, Measures’)



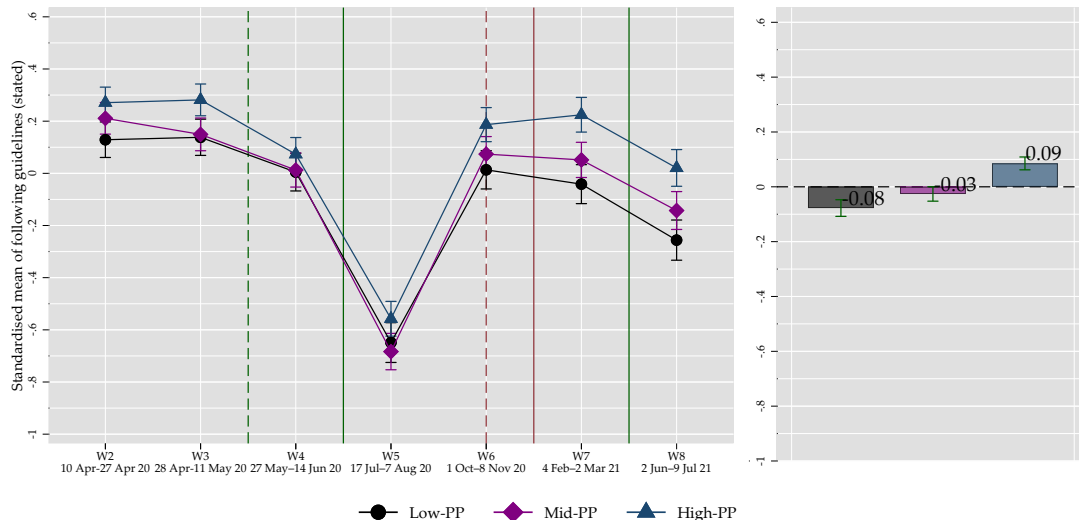
(a) Period from 31 March to 17 August 2020 (waves 1 to 5 of our study data)



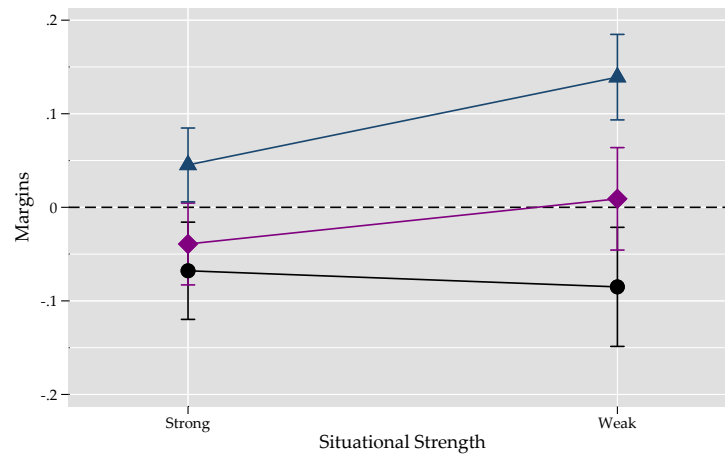
(b) Period from 1 October 2020 to 9 July 2021 (waves 6 to 8 of our study data)

Figure 3

Google Trends results for search terms related to “Rules, Restrictions, Guidelines, Requirements, and Measures” across the world (for the top 50 countries in each). The y-axis refers to Google’s ‘Interest’ index, described as: “Numbers represent search interest relative to the highest point on the chart for the given region and time. A value of 100 is the peak popularity for the term. A value of 50 means that the term is half as popular. A score of 0 means there was not enough data for this term.”. (a) covers the timeline from wave 1 to 5 in our data (strong situational strength with respect to government guidelines), and (b) waves 6 to 8 (1 October 2020 to 9 July 2021). The UK ranked 16th globally (Index: 52) during waves 1 to 5 and rose to 2nd (Index: 84) during waves 6 to 8. The data to produce these graphs can be accessed from Google Trends.



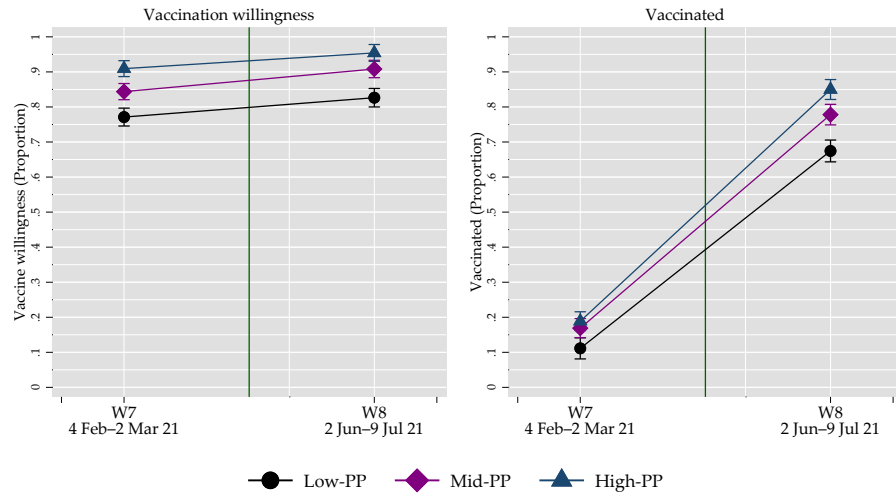
(a) Cooperative behaviors across PP, as well as the aggregate effect.



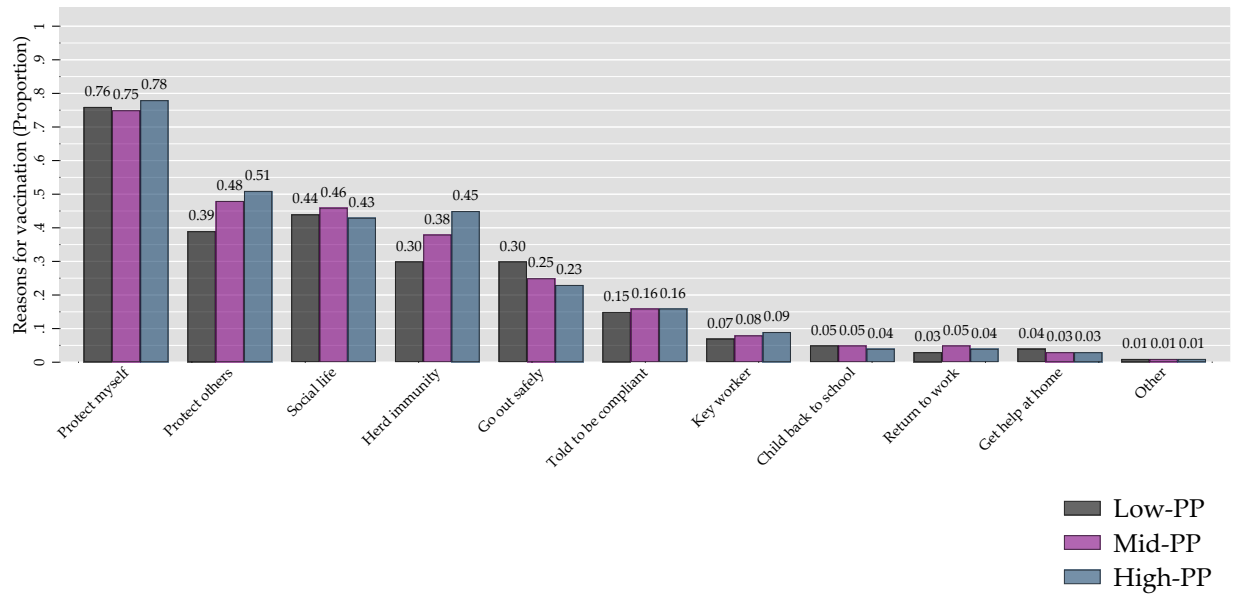
(b) Linear interactions across PP and situational strength

Figure 4

Notes: (a) shows cooperative behaviors across prosocial phenotype (PP) over the eight waves of the data (left-hand figure) as well as the aggregate effect (right-hand figure). Following guidelines is a composite measure comprising several behaviors during the pandemic: leaving the house, practicing social distancing, hand washing, meeting people externally, and face covering (in transport and stores) (standardized with $\bar{x} = 0$ and $sd = 1$). 'Low-PP' refers to individuals who indicated engaging in one or fewer prosocial activities from blood donation, organ donor registration, monetary donations, or volunteer work. 'Mid-PP' refers to those who had engaged in two prosocial activities, and 'High-PP' refers to those engaged in at least three of the four prosocial activities. The dashed green line signifies the end of the first lockdown in the UK, while the solid green line indicates a transition to minimal restrictions. The dashed red line represents the reimplementing of restrictions (i.e., the tier-based system introduced in the UK), and the solid red line represents a second lockdown period. The data is presented with 95% confidence intervals. (b) displays the linear interaction from a generalized estimating equation (GEE) regression between low, medium, and high PP and the strong and weak situations: strong situational strength (waves 2, 3, 4, and 5) and weak situational strength (waves 6, 7, and 8). The dependent variable is following government guidelines (standardized with $\bar{x} = 0$ and $sd = 1$). Additional controls, including age, gender, ethnicity, education level, relationship status, employment status, socio-economic grouping, tenure, region of the UK, keyworker status, and pre-COVID-19 finances, are included in supplementary materials.



(a) Vaccination willingness and rates



(b) Reasons for vaccination by donor type

Figure 5

Notes: (a) Vaccination willingness and rates across prosocial phenotypes (waves 7 and 8). Vaccination in the UK began 8th December 2020. By June 2021, all adults 18+ were able to get their first dose of the vaccine (see information). Vaccine willingness: a composite measure constructed through two questions. The data is presented with 95% confidence intervals. (b) Vaccination reasons by donor type. Each bar represents the proportion of respondents who selected a specific reason, ranging from personal protection against the coronavirus to compliance with vaccine recommendations. After stating their willingness to vaccinate, each participant was asked to select three reasons surrounding their willingness to vaccinate. Reasons include (1) personal health and safety, (2) resuming safe movement outside the home, (3) receiving necessary care at home, (4) being a key worker, (5) returning to the workplace, (6) allowing social and family life to return to normal, (7) minimizing educational disruption for children, (8) achieving herd immunity, (9) protecting others, (10) compliance with recommendations, and (11) other various reasons. These reasons are placed in descending order from most frequently cited to least.