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Emergent Prosocial Behavior During Dynamic Human Group Formation

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Data and Materials Availability: The full behavioral data and analysis codes are freely available at <https://osf.io/45r3x>. Additionally, a preprint of this work is available at <https://psyarxiv.com/s7z4j> under a CC-BY Attribution 4.0 International license. The corresponding author R.P.B. will promptly answer any further inquiries related to this study.

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Abstract

For scientists, policy makers, and the general population, there is increasing interest in how humans form cooperative groups. Probing the changes that emerge in cognition as group sizes increase is one important direction for understanding the evolution of large cooperative societies. However, capturing real-world dynamics of group size growth has been a historical challenge for laboratory studies. We hypothesize that humans will exhibit emergent prosocial behavior as their immediate group size increases. Using a new network-embedded-dyad prisoner dilemma task, with periodic opportunities to retain or remove group members, we find subjects consistently follow a well-performing reciprocal base policy (tit-for-tat-like) across the experimental session. However, subjects' strategies also became more forgiving and less exploitative as group size increased, with a default preference shift to cooperation. Thus, human cooperation may emerge from a desire to create and maintain larger and more cooperative groups, and multiscale strategies that consider both self-interest and group-interest.

Introduction

A longstanding unknown in evolution is why human cooperation emerges within groups while traditional economic theory predicts rational humans prioritize their own self-interest (Axelrod and Hamilton, 1981). Historically, much work has focused on individual-level computational questions related to whether such group cooperation emerges purely out of self-interest (i.e. humans are selfish agents), or whether humans inherently weigh both self-interest and group-interest during decision making (i.e. humans are “socially responsible” self-interested agents) (Axelrod and Hamilton, 1981; Hanaki et al., 2007; Jennings and Campos, 1997). However, increasing amounts of evidence suggests broader contexts such as social norms, risk factors and group size may be just as important as individual-scale, self-interested cognitive processes for understanding the social behaviors of groups and the individuals that comprise them (Yamagishi and Cook, 1993; Zitzler, 1999; Cacioppo and Patrick, 2008; Paluck, 2009; Rand et al., 2011; Pfeiffer et al., 2014; Henrich, 2015; Tomova et al., 2020; Badman et al., 2020; Szekely et al., 2021; Spektor et al., 2021; FeldmanHall and Nassar, 2021; Momennejad, 2022). Group

size effects on cooperation especially remain controversial and unclear (Hamburger et al., 1975; Rand et al., 2014; Yamagishi and Cook, 1993). Current studies however, typically monitor group cooperation across individuals *after* the size of the group is established by the experimenter (Hamburger et al., 1975; Rand et al., 2014; Yamagishi and Cook, 1993), rather than the emergence of new social tendencies within individuals as their group sizes changes in a subject-influenced manner (Cacioppo and Patrick, 2008; Yamagishi and Hayashi, 1996). From both ecological and laboratory results though, it is clear humans behave quite differently in solitary versus dyadic versus larger group contexts (Badman et al., 2020; Dunbar, 2014; Redcay and Schilbach, 2019; Tomova et al., 2020). For example, loneliness and social deprivation have been documented to cause altered behavioral and brain states even on hours-long time scales (Cacioppo and Patrick, 2008; Dewald-Kaufmann et al., 2021; Tomova et al., 2020). Thus, we posited that there are likely observable, emergent cooperative behavioral effects within humans as one's group size increases or decreases, even over typical one hour task session timelines. However, fully probing group size-mediated effects requires tuning group size dynamically across a given experimental paradigm with a within-subject design. Thus, we employ such a task design in this work using a new variant of network Prisoners' Dilemma (PD), as explained below.

Generally, PD has been one of the core experimental paradigms used to study human cooperation, as it quantitatively captures real world tensions involved in deciding whether to be selfish or cooperative in social situations (Axelrod and Hamilton, 1981). In a single round of traditional PD, two players simultaneously decide whether to “cooperate” or “defect” with each other, and in iterative designs play multiple sequential rounds together. In typical PD payoff matrices, mutual cooperation gives a modest reward to both players, but mutual defection brings no rewards to either player (or in some studies, brings only a very small reward to both players). However, if one player defects while the other cooperates, then the defecting player gets a larger reward than from mutual cooperation, while the cooperating player takes a significant loss (Nowak, 2006; Wedekind and Milinski, 1996). Group variations of PD include *n*-person PD (NPD) (subjects play with *n* partners simultaneously) (Rand et al., 2011, 2014; Hamburger et al., 1975) and network-embedded-dyad Prisoner's Dilemma (NEDPD) designs (subjects play with *n* partners consecutively, usually randomly, in dyads) (Yamagishi and Hayashi, 1996). Somewhat surprisingly, historically, most static network structures (fixed group size) for NPD empirically led to *decreases* in cooperation over time (Rand et al., 2011; Yamagishi and Cook, 1993), especially in larger groups (Rand et al., 2011, 2014; Hamburger et

al., 1975; Boyd and Richerson, 1988; Grujić et al., 2012). These collective uncooperative group results have been referred to as the “scalability problem”, as they disagree with our real world, daily life observations of human group cooperation (Hanaki et al., 2007). In contrast, more real world relevant (though less commonly empirically explored) dynamic network NPD structures and NEDPD designs appear to foster cooperation in larger groups in both theoretical contexts (Skyrms and Pemantle, 2000; Santos et al., 2006; Fu et al., 2008) and laboratory contexts (Rand et al., 2011; Yamagishi and Cook, 1993; Yamagishi and Hayashi, 1996) (Figure S1). However, the traditional simultaneous-play context of NPD confounds within-subject analysis and is highly susceptible to freeloaders (Hanaki et al., 2007; Rand et al., 2011, 2014), while NEDPD is a relatively unexplored design especially in varying group size contexts (Yamagishi and Hayashi, 1996). Furthermore, recent field work has found cultures with more voluntary and dynamic real-world social networks (i.e. higher “relational mobility”) display more prosocial and cooperative behaviors generally (Palla et al., 2007; Thomson et al., 2018; Yuki and Schug, 2020). These results suggest the presence of continual group formation and dissolution within networks may actually be vital for the emergence of real world group cooperation (Palla et al., 2007). Following this collective literature, we employ a novel and ecologically relevant (Peperkoorn et al., 2020) NEDPD task variant (Figure 1, Methods), with dynamic and behavior-influenced group size, to test the effects of group size changes on cooperative tendencies within individual subjects.

Results

In our NEDPD task, at the beginning of each trial, a “newcomer” automatically appears as a new group member ~10% of the time (Figure 1, A and B, Methods). Gaining a newcomer grows the group size by 1. Subjects (Japanese university students) then dyadically play PD with the newcomer. In non-newcomer trials, subjects play with a randomly chosen partner out of their current group (1-5 partners). In both types of trials, subjects see the PD outcome after the PD decision. Approximately 10% of the time a “stay/switch” decision occurs at the very end of the trial (Figure 1, A and B, Methods), where simultaneously the subject and current partner each independently decide whether to retain or permanently break their partnership. Breaking the partnership decreases the group size by 1. Subjects could see their own cumulative score, and avatars of each current partner within their group. While all subjects started the session in dyads (group size 1) (Figure S2), all group sizes were experienced fairly consistently across the experiment (Figure 1, C and D). Building larger group sizes does not provide an explicit reward

benefit however, and being in smaller groups does not have explicit reward-related downsides. Thus, our work investigates how changing group size mediates subjects' social economic behaviors when group size is not directly coupled to the extrinsic reward structure, unlike prior simultaneous-play NPD where group size is tightly coupled to the extrinsic reward structure (Rand et al., 2014). The task design for the investigation has ecologically-relevant social consequences present, as subjects may infer that group members could break ties with them more often if they play overly defective (subjects believed they were playing with real humans), but the task does not actively encourage cooperation through an extrinsic reward incentive structure.

Figure 1: Task description

(A) Steps of a single trial in the embedded-dyad network Prisoner's Dilemma (NEDPD) task, with (right insert) a screenshot of the PD choice task screen shown that contains current group members' avatars, the subject's avatar, and the cumulative score. (B) A cartoon schematic of task components described in (A), where "S" is the subject and "P" are partners. (C) Raw traces of the response time (moving average of 5 trials) (green), overlaid with unaveraged group size (blue). (D) Between-subject mean probability of each group size occurring in the first half (trial 1-

90) versus second half (trial 91-180) of the experimental session ($N=39$, for subjects with maximum group size of 5). Error bars are 95% CI.

In more detailed analysis, cooperation rate (CR) and response time (RT) were the first dependent variables studied, as modulated by group size across the NEDPD task. RT is defined as the time between the choice prompt's appearance and the subject making a choice through a button press. For these analyses, while all 75 subjects achieved at least a group size of 3, not all achieved a group size of 4 or 5 (Methods). Thus, we repeated this first analysis three times in different overlapping subsets based on the maximum group size that was reached in a session, to ensure robustness of results (Figure 2). The first subject set ($N = 75$, all subjects) included subjects whose maximum number of simultaneous partners (which we define as the group size) was 3 or higher, and only group sizes up to 3 were analyzed. Then the next subset analyzed was subjects with a maximum group size of at least 4 ($N = 57$), only analyzing up to group size 4. Then, the last subset was subjects with a maximum group size of 5 ($N = 39$) and all five group sizes were analyzed. We observed a group size-modulated prosocial behavioral change in the mean CR, with cooperative behavior modulated by the current group size (Figure 2A, Table S1, Figure S2 and S3). Next, we examined RTs for cooperate trials versus defect trials separately (Figure 2B) for each group size. We found that the RTs were similar for cooperate and defect choices with group size of 1, but then the RTs increased proportionally with group size for both cooperation and defection (Figure 1C, 2B). This baseline RT increase with group size (Figure 2B) possibly suggests tracking more social partners takes more mental effort, working memory resources, and/or deliberative thinking (Yamagishi et al., 2017). Interestingly, however, the RTs increased more for defection than cooperation with increasing group size (Figure 2C). Next, when plotting the difference between defect minus cooperate RTs per subject, there was a tendency of faster RT for cooperation than defection choices in larger groups (Figure 2D, Table S2). This prosocial behavior transition in RT was similar to the CR result (Figure 2, A and D). As in prior work (Rand et al., 2012; Yamagishi et al., 2017), we interpret the faster RTs for cooperation in larger group sizes to indicate a new default preference towards cooperation.

Figure 2: Modulation of subject behavior by group size

(A) Between-subject mean cooperation rate (CR) for all subject sampling subsets based on the maximum group size reached in each subject's session. (B) Plots of the mean response time (RT) per group size, of each subject who had a max group size of 5 ($N = 39$), as an example to show the underlying distribution of the RT data, with cooperate RTs (left) plotted separately from defect RTs (right). Box plots are 25%/75% box boundaries and 1 SD whisker. Slopes of these plots were calculated for each sampling subset, and plotted in (C) with the same color scheme for cooperation (green) and defect (pink) as (B). Error bars in (C) are 95% CI. (D) RT differences for defect minus cooperate, plotted against group size. In (A) and (D) error bars are 95% CI. Statistical significance was calculated through Holm-Bonferroni-corrected pairwise t -tests relative to the group size of 1, after one-way repeated measures ANOVA, with * being for $p < 0.05$ and ** for $p < 0.01$ (Table S1 and S2).

We next solidified that the enhanced CR emerged during strategic and engaged behavior, and then more closely examined subject strategies. Self-score (reward) was found unlikely to be the primary factor motivating prosocial behavior, as higher cumulative scores were significantly correlated with lower mean CR, yet most subjects play more cooperatively and less

optimally overall (Figure 3A). In contrast, more cooperative subjects were in a group size of three or larger more frequently (Figure 3B and S4), as a moderately cooperative strategy helped reduce the chance of partners leaving on average (Methods), similar to the real world. Thus, this task design allows us to infer that maintaining or growing group size is a driving motive behind increased prosocial behavior in groups. Furthermore, correlational analysis found that subjects responded more to partner behavior from the most recent previous trial with the current partner, rather than the immediately previous trial regardless of the current specific partner (Figure S5), which helped exclude the possibility that the prosocial shifts were just a general non-strategic prosocial bias. In finer-grain time-dependent analysis, average subject CR first matched average partner CR (~50% CR in both), with matching CR suggesting strict reciprocity (Figure S6). However, after a few tens of trials subject CR visibly increased towards ~60-65% while partner CR remained at ~50%, suggesting subjects became more prosocial than their partners on average (Figure S6 and S7). Additionally, when examining the traces of all trials played with each partner, subjects had a strong preference to cooperate on the first trial with a new partner (open with cooperate ~70% of the time), but then converged to an apparent behavioral equilibrium (“equilibrium” loosely defined): the final cooperation rate was stably higher for larger group sizes than for lower group sizes (Figure S8).

Figure 3: Subject behavioral strategy analysis

(A) Cumulative score versus mean cooperation rate for all subjects ($N=87$, Methods). (B) Plot showing how cooperation rate correlates with the frequency of being in a group size of three or

higher ($N=75$). Pearson correlation coefficients are presented in red text. (C) Plots for 30 trial intervals across the 180-trial session of (left-to-right, top-to-bottom): the mean fraction of trials that subjects' choices follow pure tit-for-tat (TFT), the mean probability of self-cooperation after a partner cooperation (p), the mean probability of self-cooperation after a partner defection (q), the mean self-cooperation rate, the mean reward rate for the subject (orange) versus partner (green), and the mean group size. Statistical significance was calculated through Holm-Bonferroni-corrected pairwise t-tests relative to first 30 sessions, after ANOVA ($N=75$) (Table S3). Error bars are 95% CI. (D) Scatterplot of mean q versus p per subject ($N=75$) for initial trials 1-60 (black) and trials of maximum p - q change 90-150 (red), with mean value per color marked with the straight lines. Typical game theory policies are labeled on the plot for reference: TFT, always cooperate (ALL-C), always defect (ALL-D), generous TFT (GTFT), and our addition, devious TFT (dTFT). * is for $p < 0.05$ and ** for $p < 0.01$.

Altogether, the behaviors seen in this descriptive analysis of subject strategy are consistent with variants of the highly reciprocal tit-for-tat (TFT) decision policy. Humans are known to gravitate towards TFT-variants in economic games (Wedekind and Milinski, 1996), and TFT-variants are generally well-performing strategies both at the individual and group scale (Wedekind and Milinski, 1996; Nowak and Sigmund, 1992; Nowak, 2006). In pure TFT, subjects open with cooperation for each new partner and then deterministically respond to partner cooperation (defection) with self-cooperation (defection) on the next trial with the same partner (Nowak, 2006). In a more forgiving variant, "generous" TFT (GTFT), subjects stochastically respond to partner defection with self-cooperate with a probability q (Nowak, 2006; Nowak and Sigmund, 1992). GTFT is broadly an optimal policy for individual payoff because the tit-for-tat component can defeat a large range of partner strategies, and the stochastic forgiveness aspect both helps prevent endless defection cycles and reduces predictableness so the partner(s) cannot predict all one's future choices (Nowak, 2006; Rapoport and Budescu, 1992).

Descriptively, subjects consistently engaged in behavior that exactly matched TFT on ~70% of all trials across the session (Figure 3C). This result suggests subjects were staying comparably engaged in the task throughout the session, while also prioritizing reciprocity and social norm enforcement. However, TFT is a deterministic model. Thus, considering the consistent partner behavior across the session (Figure S6 and S7), TFT alone cannot explain

the subjects' prosocial behavioral change. The emergent prosocial behavior must be characterized by the trials where subjects do *not* perform TFT. Indeed, we found over our session as group size increased, the forgiveness probability q increased in GTFT behavior, while the “deviousness” probability of defecting after prior partner cooperation, $1-p$, decreased (p is the probability of self-cooperation after partner cooperation), in what we call devious TFT (dTFT) behavior (Figure 3, C and D, Table S3). Increased p and q correlated with higher group size across the session (Figure 3, C and D). Furthermore, in addition to promoting larger group sizes, the higher mean p and q values of subjects in larger groups did not significantly increase or decrease subject reward rate, but did increase their partner reward rate (Figure 3C and S9, Table S3). This increased partner reward rate may suggest subjects prioritize group utility during group formation (Jennings and Campos, 1997), or may just be a secondary consequence of trying to maintain larger group sizes through cooperation (Figure 3C and S9). However, even with increased p and q , subjects maintained a baseline positive reward rate, implying humans can effectively balance both self-interest and group-oriented goals in social contexts (Figure 3C and S9).

For a final exploratory analysis: while up to this point we have detailed clear *effects* of group size on subject behavior within a dynamic social network, the logical follow-up analysis is to identify *mechanisms* underlying the observed effects. To provide preliminary mechanistic insight to guide future work, we examine subjects' cooperative behavior within windows around group size change events (Figure S10). On these short timescales, subject behavior was found to be especially responsive to group size change events, with both newcomers and social rejections immediately enhancing prosocial behavior in the consequent trial, but group size changes possibly causing longer lasting prosocial effects in bigger group sizes than dyads (Figure S10). However, future tasks will need to explore more controlled group size changes, perhaps with different task contexts (Figure S1) (FeldmanHall and Nassar, 2021; Fitouchi and Singh, 2021; Spektor et al., 2021; Szekely et al., 2021), to more comprehensively pin down the causal effects of group attributes and trial-level task events on emergent social behaviors across a range of ecologically relevant contexts.

Discussion

In summary, we have provided compelling evidence that prosocial group behavior in humans emerges out of a combination of seeking and maintaining larger group sizes, while possibly balancing self-interest and group-interest. These results qualitatively agree with recent

neuroscience evidence which suggests that having multiple motives (especially social-related) increases prosocial behavior over having a single motive or goal (Saulin et al., 2021). Specifically, both the RT and choice analyses show complementary group size-modulated effects, providing converging evidence that group-oriented prosocial behavior emerges as subjects transition from dyads to larger groups (Figure 2 and 3). Additionally, our results are consistent with the concept that humans place intrinsic value on social interactions (Cacioppo and Patrick, 2008; Pfeiffer et al., 2014; Tomova et al., 2020), such as cultivating group size and avoiding social rejection as in our task. Finally, in a departure from the rare prior network design variants where cooperation can at best be *sustained* in larger group sizes (Figure S1) (Hamburger et al., 1975; Rand et al., 2014, 2011; Yamagishi and Cook, 1993; Yamagishi and Hayashi, 1996), we showed subject cooperation is not only sustained but actually *enhanced* by our embedded-dyad dynamic network structure with continually ongoing group formation. The enhancement of cooperative tendencies in groups happens despite defective behavior being more optimal in our task (Figure 3A), and despite the ephemeral, anonymous nature of the social interactions. Thus, our work may also provide game theory insights towards a more fundamental understanding of the real world prosocial benefits observed when cultures have more dynamic social networks (Palla et al., 2007), including higher relational mobility for example (Thomson et al., 2018; Yuki and Schug, 2020). Overall, we hope these results broadly help inform a deeper understanding of intelligent social decision making and the evolution of groups, which better accounts for humans balancing goals and drives across multiple social scales from the individual, to close social circles, up to the larger society.

Limitations of the Study

Several limitations of this study are useful to note for guiding future work. The most obvious technical limitation is that our new variant of network PD with embedded-dyad sequential interactions is a quite different experience for subjects than the traditional simultaneous-play NPD designs which dominate historical literature in this research area (Nowak, 2006; Rand et al., 2014). Much work has been done exploring how differences in PD payoff matrix (i.e. score) values and network link update frequencies modulate subject behavior in simultaneous-play NPD designs (Rand et al., 2011, 2014), but not in embedded-dyad designs. Thus, more parameter exploration needs to be done in future experiments using variations of the new design presented here to see how different payoff values and different link update frequencies modulate the results observed in the current work. Then, the next major limitation of note is at the level of causal interpretation. Providing unambiguous, task event-locked causality for

behavior outcomes is difficult in our dynamic task, with its frequent newcomers and social rejections, and multiple interaction partners, all influencing subject behavior on multiple timescales. This limitation may hinder behavioral modeling of trial-level decision making for example, which is a reoccurring general problem in social neuroeconomic studies (FeldmanHall and Nassar, 2021). Thus, future work should consider studying more simple versions of our task without the full social dynamics included, though such reductionism may risk erasing emergent prosocial effects that only appear when all task components are present. Last, our task used a Japanese subject pool, but it is now established that subjects from different cultures sometimes behave differently from each other (on average) in many standard economic games, especially when prosocial behavior and social norms are involved as in our work (Henrich et al., 2005; Henrich, 2015). Exploring the universality of the behavioral trends observed here, across global cultures, thus also is an important additional future direction to pursue.

Materials and Methods

Task Design

Overview

Our network-embedded-dyad prisoner's dilemma (NEDPD) task uses a dynamic social network, with semi-frequent opportunities to break social links (at the end of ~10% of the trials), while a newcomer to the network is gained at the start of ~10% of the trials automatically (Figure 1, Figure S4). Subjects play dyadically with either the new group member on a newcomer trial, or with a randomly chosen group member on a non-newcomer trial. The number of the in-person subjects per session group varied from 3 to 5. Subjects were told they played the PD game with the other subjects in their session group, whose true identity was concealed with avatar faces (Figure 1). For group size 5 in the data (e.g. Figure 2, Figure 3), one subject with up to five group members in their network, the subjects were told the sixth person was playing in another room. Faces are taken from the neutral category of Paul Ekman's "Picture of Facial Affect". Unbeknownst to subjects, for detailed control of the experimental conditions, they were actually engaged in the game with prescheduled computer programs (see the *Algorithm of Social Partner* section below).

Subjects, Payment, Exclusion Criteria

A total of 87 healthy volunteers were recruited in the behavioral experiments. All subjects had normal or corrected-to-normal vision and were screened for the presence of psychiatric or

neurological disorders. Among them, 26 subjects participated in the behavioral task while simultaneously undergoing functional magnetic resonance imaging (fMRI), while the other 61 subjects participated in the behavioral experiment only outside of the fMRI. The fMRI imaging analysis is ongoing and not included in this work, only the pooled behavioral data for the fMRI and non-fMRI subjects was analyzed in this report.

Ten subjects were eliminated from the original 87 subjects due to either having less than five trials at a group size of one ($N = 1$), only pressing defect in each trial ($N = 2$), or not reaching a maximum group size of three in a preliminary test day with less subjects ($N = 7$). Additionally, two more subjects were excluded for missing too many trials: one subject was excluded from this analysis for not playing for the first ~45 trials, and another excluded for ending their session end at trial 146 after defecting for a long period of time. These twelve excluded subjects were only included in Figure 3A for score context. The remaining 75 subjects only (33 women, 42 men) were included in all other analyses. For 13/75 subjects, their age was not recorded though all subjects were visibly young adult students (~20-30 years old). The mean age of the 62 subjects with recorded age information was 22.0 ± 1.8 (SD). All subjects gave informed consent in accordance with the CiNet Research Ethics Committees. Subjects were paid 3000 yen (approximately \$30 US dollars) for their participation in the behavioral experiments and 5000 yen (approximately \$50 US dollars) for the participation in fMRI experiments.

Session start conditions

Before each session, the subjects received the task instructions and watched a randomly chosen subject (in the current session) play approximately the first ten trials (up to the first stay/switch decision) as an experimenter-guided demo of the task. Subjects were told that their social partners could break network links with them, but subjects specifically were *not* instructed that maintaining network links was important to score or task performance. The timing of the start of the game play was synchronized so that each session groups' subjects could feel that they were playing the game together. The session for the task began with the selection of a face of one's own avatar. There were four faces at the upper left corner of the screen. The subject pressed one of the four buttons corresponding to the four faces. After the selection of the face and the button press, one face remained on the screen as the self-avatar and other three faces disappeared from the screen. Then, the main set of trials began (Figure 1). In the pause before the first trial, there was no one in the social network. The first newcomer appeared in the very

first trial of the task and the subjects played the PD task with this partner. Subjects were not told how many exactly trials they would play.

Prisoner's dilemma choice details

The subjects won 30 points when both they cooperated and the partner cooperated. The payoff was 60 when the subjects defected and the partner cooperated. On the other hand, when the subjects cooperated and the opponent defected, the subjects lost 30 points. When both parties defected, the subjects earned nothing. The points were accumulated across trials and the cumulative score was shown on the task screen (Figure 1). The subjects were told that the participation rewards were adjusted based on this total value. But the actual participation rewards were the same across the subjects.

Network link dynamics

At the start of some trials (~10% of the trials) (Figure S4), subjects encountered a newcomer who automatically joins the network and becomes the current partner for that trial (Figure 1). The subjects then play the PD game with the newcomer in these trials, otherwise for trials without newcomers the current partner is randomly chosen from the existing network. At the end of some trials (~10% of the trials) after performing the PD game, subjects decided whether to continue to play the game with the current partner in that trial or not (the stay/switch decision). The partner was given the same stay/switch decision, and was more likely to switch if the subject was more defective recently. The social link was maintained if both chose to stay, while the link was broken if either partner or subject decided to break it. If the link broke, to “reset” future interactions with their session group, that partner’s avatar was never used again (instead a new avatar face is assigned to subsequent newcomers). In addition to sequential newcomer events being forbidden, the probability of a newcomer event is reduced by half if the subject defects sequentially on the two immediately preceding trials (while the probability of partner switching stays the same). This rule is to prevent extreme defective behavior by making highly defective subjects slowly trend towards having no partners over tens of trials, as reaching zero partners results in a short time-out period of a blank screen for several seconds before another newcomer is assigned. In terms of the bigger behavioral picture, when links are maintained, the interactions with specific social partners have to be memorized according to avatar faces in order to make adaptive decisions in the next encounter with the same social partner. No historical task summary for any partner is provided to the subjects during the session.

Session end conditions

At the end of the session, we debriefed the subjects about their general experience and to ensure they thought they were playing with the other human subjects in the experimental room. The feeling of deep engagement of subjects during the task was visibly noticeable. Some subjects squeezed their chairs, scratched their head aggressively, or cried out with frustration at times in response to events during their session. The subjects overall seemed exhausted but appeared to enjoy the experience in the task by the end. During the post-experiment interview, no subjects had explicitly reported they were aware of playing the game against computer opponents.

Algorithm of Social Partner: One reason why the social relationship in the task was dynamic is that we programmed the “attitude” of the computer agent to change dynamically. This dynamic nature came from two sources in the agents’ algorithm: one from the learning process provided by a reinforcement learning-like choice algorithm and another from cyclical alternations between the cooperative and non-cooperative strategies. The first mechanism was fairly predictable for the subjects. If the subject chose cooperation more frequently, then usually the partners would be more cooperative for a time. But if the subject defected often, the partner would generally eventually tend to reciprocate either through defection or link breaking. On the other hand, partner dynamics were often unpredictable, due to a sinusoidal “mood” variable that was sampled semi-randomly (more technically, the mood variable was sampled by the absolute trial number from a sine wave with a period of ~22 trials for each partner, each partner had a different wave phase, and newcomer partners were randomly chosen out of a pool of 30 possible pre-initialized partners throughout the session). Thus, even if the subject kept a cooperative attitude toward the computer agents, a computer partner could suddenly exhibit a non-cooperative attitude (or vice versa). See Supplementary Data for the task script containing the partner algorithm.

Partners had a weak starting preference for defection to ensure cooperation was not artificially promoted (partners empirically *defected* on 58.2% of all newcomer trials, while human subjects *cooperated* on 64.6% of all newcomer trials).

Statistical Tests

Overall, the basic goal of our statistical tests was to compare subject behavior in each larger group size to the behavior in group size of one in Figure 2, and then to compare subject behavior in later trials to the behavior in the first 30 trials in Figure 3C. Details of the standard

statistical tests done in Figure 2 and Figure 3 are provided in Tables S1, S2 and S3 (multiple comparisons ANOVA followed by pairwise comparisons). The Origin files that performed the statistical tests are provided in the Supplementary Data. Due to the repeated measures conditions in our work, all *p*-values in this work are adjusted using a Holm-Bonferroni correction, which is a standard correction in pairwise comparisons. Specifically, this correction controls the family-wise error rate while being more powerful than the Bonferroni correction. Figure 2D is missing 2/75, 4/57, and 4/39 subjects for max group sizes 3, 4 and 5 respectively in the statistical tests because these subjects did not have both cooperate and defect choices at one or more group sizes, and thus they were excluded from that sub-analysis.

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SUPPLEMENTARY INFORMATION

Supplementary Figures

Figure S1: Motivation for iterative embedded-dyad network prisoner's dilemma design

[related to literature discussion in the Introduction]

(A) Sketch conceptually summarizing prior results suggesting dynamic link variants of network prisoner's dilemma (PD) foster cooperation in iterative tasks above static link variants, as long as the link update frequency is not too frequent (Rand et al., 2011). We chose a moderate update frequency for both newcomer and link break options (Methods). (B) Sketch conceptually summarizing prior results finding for larger group sizes and fixed payoff matrix, that embedded dyadic PD interactions foster cooperation above simultaneous play interactions with many neighbors at once (Grujić et al., 2012; Hamburger et al., 1975; Yamagishi and Cook, 1993; Yamagishi and Hayashi, 1996). (C) In typical PD notation, our task payoff matrix has $T=60$, $R=30$, $P=0$, and $S=-30$ (Methods). Rand et al. found the condition for cooperation to succeed in typical static network PD designs is $Q^* > k$, for group size k , and $Q^* = (P+S-R-T)/(R+S-P-T)$, which we have plotted (Rand et al., 2014). For our task $Q^* = (0-30-30-60)/(30-30-0-60) = 2$. Our task is not static, so this plot should be interpreted as an approximate guideline. However, we have chosen payoff matrix values on the boundary of this plot to avoid biasing prosocial tendencies with unbalanced payoffs.

Behavioral Task Supplementary Flow Chart

Figure S2: Additional experimental task flow information and initial cooperation rate results [related to Figure 1]

Stage 1: For approximately the first ten trials, subjects start in the typical dyad (one partner) prisoner dilemma context. The mean group size is one social partner, and mean cooperation is slightly under 50% for the first ten trials ($N=75$). *Stage 2:* Over approximately the next few tens of trials, subjects generally experience larger group sizes of 2-5 social partners, with a mean group size of two social partners and mean cooperation rate of slightly over 50% now for trials 11-40 ($N=75$). *Stage 3:* Throughout the rest of the experiment, subjects display more of a “group maintenance mindset” as they dynamically move through the full range of group sizes. The mean group size is near three social partners, and the mean cooperation approaches 60% ($N=75$). All error bars are SD. The red dotted line on the cooperation rate plots marks 50%.

Figure S3: Supplementary mean cooperation rate versus group size [related to Figure 2A]
Plot of the mean CR of each subject who had a max group size of 5 ($N = 39$) to show the underlying distribution of the data in Figure 2A. Box plots are 25%/75% box boundaries and 1 SD whisker.

Figure S4: Frequency of group size change events versus mean cooperation rate [related to Figure 3A and 3B]

Plots of how (A) the self-switch (self-driven link breaking at the end of a trial) frequency correlates with the mean cooperation rate, (B) the other-switch (partner-driven link breaking at the end of a trial) frequency correlates with the mean cooperation rate and (C) the newcomer (automatic addition of a group member at the beginning of a trial) frequency correlates with the mean cooperation rate, across all trials for each subject ($N=75$). See Methods for related task information. Assignment of axes is not intended to suggest direct causality. Pearson correlation coefficients are listed above the plots, with * being for $p < 0.05$ and ** for $p < 0.01$.

Figure S5: Correlation matrix of experimental factors [related to Figure 3C]

Correlation matrix (averaged across all subjects' individual correlation matrices) of experimental variables and parameters, variable names provided on the left.

Figure S6: 95% Confidence Intervals for Self-Cooperation Rate, Other-Cooperation Rate, and Group Size Traces Across Subjects [related to Figure 3C]

Moving mean (5 trials) of (A) between-subject-averaged cooperation rate ($N=75$) of the subject (red) and partner(s) (gray) and (B) group size. Error bars are 95% CI.

Figure S7: Exploration of self versus partner cooperation rate across group sizes [related to Figure 3C]

Mean cooperation rate of the subject versus all their partners pooled for each group size, for the tier of subjects that had a maximum group size of 5 ($N = 39$) as an example. Statistical significance was calculated through pairwise comparison the partner and subject mean cooperation rate per group size, with * being for $p < 0.05$ and ** for $p < 0.01$ after two way repeated measures ANOVA with Holm-Bonferroni-correction (left-to-right p values are 0.093, 0.008, 0.008, 0.002, and 0.004). Error bars are 95% CI.

Figure S8: Description of time-dependent behavior [related to Figure 3C]

(A) The cooperation rate across subsequent relative trials played with the same partner, averaged across subjects ($N=75$). Trials played with the same partner were not necessarily immediately sequential in absolute trial number. Error bars are 95% CI. (B) Histogram of the number of trials played with each unique partner avatar. There were up to 30 possible unique partner avatars in the total pool) for all subjects ($N=75$).

Figure S9: Influence of cooperation rate on both self and partner reward rate [related to Figure 3C]

Using the same 30 interval bins as Figure 3C, the reward rate for self and partners per bin was plotted against cooperation rate. Each colored plot has 75 subjects multiplied by 6 bins, giving a total of 450 points per plot. Pearson correlation coefficients are listed above the plots, with ** for $p < 0.01$, and colors matching the plot legend.

Figure S10: Exploratory analysis of subject cooperation rate at link change events [related to Figure 3C]

Link breaking and newcomer (link formation) event-locked (vertical green dotted line) cooperation rate (unsmoothed) for 10 trials before and after events ($N=66$). Traces were grouped into dyad-to-triplet-group changes (black) and within-larger-group changes (red). For example, “2-4→3-5” means a transition from 2→3 or 3→4 or 4→5, since only 1 group size unit change per trial is allowed in the task. On these axes, link breaking events occur at the end of relative trial number “-1” after the PD decision on that trial, while newcomers appear at the start of trial “0” before the PD decision on that trial. Only group size change events where a newcomer event did not immediately follow a link breaking event were analyzed. Additionally, only 20 trial sequences where no missed button presses occurred were examined. Thus 9 out of 75 subjects did not meet these criteria in these plots. Additionally, in our highly dynamic network task, occasionally secondary group size change events could have occurred in the broad ± 10 trial window plotted here, thus this should be treated as an exploratory analysis. Error bars are SEM.

Table S1: Figure 2A Statistics

Pairwise Comparison (repeated measures, Holm-Bonferroni)	$Prob> t $ (Max Group Size of 3)	$Prob> t $ (Max Group Size of 4)	$Prob> t $ (Max Group Size of 5)
Group size 1 and 2	0.040	0.033	0.057
Group size 1 and 3	0.080	0.100	0.154
Group size 1 and 4	-----	<0.001	0.047
Group size 1 and 5	-----	-----	0.005

ANOVA results listed in order of max group size of 3, 4, 5 respectively:

Mauchly's Test of Sphericity, $Prob>ChiSq$: <0.001, 0.004, 0.006

Mauchly's Test of Sphericity (Greenhouse-Geisser Epsilon): 0.849, 0.820, 0.768

Mauchly's Test of Sphericity (Huynh-Feldt Epsilon): 0.867, 0.860, 0.843

Repeated measures ANOVA within-subject, $Prob>F$ (Sphericity-Assumed): 0.086, 0.009, 0.072

Repeated measures ANOVA within-subject, $Prob>F$ (Greenhouse-Geisser): 0.095, 0.015, 0.091

Repeated measures ANOVA within-subject, $Prob>F$ (Huynh-Feldt): 0.094, 0.013, 0.084

Table S2: Figure 2D Statistics

Pairwise Comparison (repeated measures, Holm-Bonferroni)	<i>Prob> t </i> (Max Group Size of 3)	<i>Prob> t </i> (Max Group Size of 4)	<i>Prob> t </i> (Max Group Size of 5)
Group size 1 and 2	0.148	0.018	0.028
Group size 1 and 3	0.054	0.056	0.149
Group size 1 and 4	-----	0.002	0.005
Group size 1 and 5	-----	-----	0.016

ANOVA results listed in order of max group size of 3, 4, 5 respectively:

Mauchly's Test of Sphericity, Prob>ChiSq: 0.989, 0.740, 0.739

Mauchly's Test of Sphericity (Greenhouse-Geisser Epsilon): 1.000, 0.968, 0.920

Mauchly's Test of Sphericity (Huynh-Feldt Epsilon): 1.000, 1.000, 1.000

Repeated measures ANOVA within-subject, Prob>F (Sphericity-Assumed): 0.134, 0.014, 0.045

Repeated measures ANOVA within-subject, Prob>F (Greenhouse-Geisser): 0.134, 0.015, 0.050

Repeated measures ANOVA within-subject, Prob>F (Huynh-Feldt): 0.134, 0.014, 0.045

Table S3: Figure 3C Statistics

Pairwise Comparison (repeated measures, Holm-Bonferroni)	Fraction of Trials Following TFT, <i>Prob> t </i>	"p", <i>Prob> t </i>	"q", <i>Prob> t </i>	Cooperation Rate, <i>Prob> t </i>	Self Reward, <i>Prob> t </i>	Partner Reward, <i>Prob> t </i>	Group Size, <i>Prob> t </i>
Interval 1 and 2	0.993	0.181	0.401	0.349	0.390	0.223	<0.001
Interval 1 and 3	0.622	0.055	0.123	0.123	0.219	0.370	<0.001
Interval 1 and 4	0.729	<0.001	0.004	0.003	0.974	0.006	<0.001
Interval 1 and 5	0.649	0.004	0.002	0.002	0.158	0.025	<0.001
Interval 1 and 6	0.941	0.048	0.068	0.064	0.371	0.186	<0.001

ANOVA results listed in order of columns (TFT, *p*, *q*, Cooperation Rate, Reward (self), Reward (partner), Group Size):

Mauchly's Test of Sphericity, Prob>ChiSq: 0.620, <0.001, <0.001, 0.009, 0.948, 0.006, <0.001

Mauchly's Test of Sphericity (Greenhouse-Geisser Epsilon): 0.943, 0.804, 0.815, 0.845, 0.964, 0.836, 0.725

Mauchly's Test of Sphericity (Huynh-Feldt Epsilon): 1.000, 0.856, 0.868, 0.908, 1.000, 0.892, 0.767

Repeated measures ANOVA within-subject, Prob>F (Sphericity-Assumed): 0.957, 0.018, 0.015, 0.014, 0.178, 0.089, <0.001

Repeated measures ANOVA within-subject, Prob>F (Greenhouse-Geisser): 0.951, 0.027, 0.023, 0.020, 0.181, 0.102, <0.001

Repeated measures ANOVA within-subject, Prob>F (Huynh-Feldt): 0.957, 0.024, 0.020, 0.017, 0.178, 0.098, <0.001

Supplementary References

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