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LEADERS-CHEATERS IN MALE GROUP COOPERATION: DIFFERENCES IN NONVERBAL COMMUNICATION AND GENETIC FACTORS

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Лидеры-обманщики в контексте кооперации в мужских коллективах: особенности невербальной коммуникации и генетические факторы

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Abstract

Here we report on the results of an experimental study investigating "who?" emerges as a leader in the context of male group cooperation and "how?" they do that. The study was designed based on the iterated Public Goods Game, played

Аннотация

В настоящей работе представлены результаты экспериментального исследования индивидуальных лидерских качеств в контексте кооперативных взаимодействий в мужских коллективах. Эксперимент проводился на основе экономической игры «Общественное благо», в

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face-to-face in groups composed of four male strangers. The game involved interactions both with and without communication to allow the assessment of individual cooperative strategies, leadership potential, and individual features of positive nonverbal expressiveness during interactions. Along with the individual behavioural characteristics we have addressed personality traits (the Big Five) and an oxytocin receptor gene polymorphism (OXTR: SNP rs53576; A/G) as putative markers of individual sociability. Our results revealed that emergent leaders most often employed the strategy of unconditional cooperation ("altruism") and were characterized by enhanced positive facial expressiveness and extraversion compared to nonleaders. However, a fraction of emergent leaders (25%) turned out to be occasional free-riders ("cheaters"). Their distinctive features were the highest scores on extraversion, exaggerated activity in negotiations, and over-expression of positive nonverbal elements. Given the high efficiency of leaders-cheaters' behaviour, we consider this result as the evidence for supernormal stimuli functioning in humans. Moreover, leaders-cheaters were characterized by a specific allelic frequency of OXTR rs53576 (heterozygosity: AG). The homozygous GG variant of this SNP is argued to be associated with prosociality, and the AA, on the contrary, with poor sociability. The heterozygous variant (AG) probably is a compromise that enables its carriers to successfully combine high social skills with antisocial behavior (free-riding). This finding supports existing evidence on the role of OXTR rs53576 in human social behaviour.

условиях взаимодействий «лицом к лицу», в группах, состоявших из четырех незнакомых друг с другом молодых мужчин. Экспериментальная игра включала взаимодействия как без коммуникации между участниками, так и при прямом вербальном общении, что позволило оценить индивидуальные кооперативные стратегии, лидерский потенциал и особенности невербальной коммуникации во время кооперативных взаимодействий. Помимо индивидуальных поведенческих характеристик, в исследовании также рассматривались психологические особенности участников и полиморфизм гена рецептора окситоцина (OXTR rs53576) в качестве потенциального маркера индивидуальной социабельности. Результаты исследования показали, что лидеры (в отличие от не-лидеров) в игре чаще всего прибегали к стратегии безусловной кооперации (альтруизму), также им были свойственны повышенная позитивная мимическая экспрессивность и более высокие баллы по шкале экстраверсии (опросник самооценки NEO-FFI). Однако часть лидеров (25%) оказались обманщиками (применяли стратегию обмана в кооперативных взаимодействиях). Их отличительными чертами были: самые высокие баллы по шкале экстраверсии, чрезмерная активность в переговорах во время игры, чрезмерная позитивная невербальная экспрессивность. Поскольку поведение лидеров-обманщиков было высокоэффективным, мы склонны интерпретировать его как свидетельство использования невербальных позитивных сверхстимулов в поведении человека. Также лидеры-обманщики характеризовались специфическим OXTR rs53576 генотипом (преимущественно гетерозиготы AG). Гомозиготный GG вариант этого локуса считается ассоциированным с просоциальностью, а AA, напротив, — со скудными социальными способностями. Гетерозиготный вариант AG, возможно, позволяет его носителям сочетать такие поведенческие качества, как повышенная коммуникабельность и асоциальное поведение (обман). Наш результат согласуется с существующими в литературе сведениями о роли OXTR rs53576 в социальном поведении человека, однако его следует рассматривать как предварительный ввиду относительно маленького размера выборки для исследования генетики поведения.

Keywords: leadership, cooperation, Big Five, OXTR rs53576, Oxytocin, nonverbal communication, Public Goods Game, Buryats, altruism, free-riding, cheater, supernormal stimuli.

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Here we report on the results of a multifaceted study investigating a leadership potential in young men in the context of male group cooperation, and its possible association with a number of individual features. Mechanisms of cooperation, as one of the key features of progressive evolution and sociality, have been investigated already for more than a century (Fehr & Fischbacher, 2003; Nowak, 2006). Based on empirical and theoretical studies, it is suggested that humans employ a number of complex cooperative strategies, including different styles of cooperation. On the one hand, such strategies include conditional cooperation (based on reciprocity), or unconditional cooperation (altruism); and on the other hand, selfish behaviour, free-riding (or cheating) (Kurzban & Houser, 2005; Kocher et al., 2008; Fischbacher et al., 2012; Nielsen et al., 2014). Cooperative and altruistic strategies are basically aimed at achieving the common good, which is beneficial both at individual and group levels. In turn, selfish and cheating strategies are aimed at maximizing individual benefits by free-riding on the costly efforts of others. A number of

recent studies have demonstrated that individuals differ consistently in their propensity for prosocial behaviour meaning that individual predispositions to apply certain cooperative (or free-riding) strategies are considerably stable in time and across contexts (Volk et al., 2012; van den Berg & Weissing, 2015; Yamagishi et al., 2013; Peysakhovich et al., 2014). It is widely accepted that all these strategies coexist in populations at some kind of dynamic equilibrium sustained by frequency-dependent selection (Heino et al., 1998; Nowak, 2006; Wolf & Weissing, 2010; van den Berg & Weissing, 2015). Free-riders can prosper only when surrounded by cooperators and altruists. The latter implies unceasing "arms race" between prosocial and asocial strategies, which is basically manifested in the development and constant improvements of abilities for a successful imitation of prosocial intentions (by cheaters) and a successful recognition of free-riders (by cooperators).

Cooperation and leadership are closely related in nature (King et al., 2009). In leaderless groups (or dyads) a leader-follower structure emerges automatically (Bass, 1949; van Vugt, 2006; Harcourt et al., 2009; Guastello, 2010; Weissing, 2011), based on common needs and individual qualities (Mann, 1959; Zaccaro et al., 2018). It is usually assumed that a leader should act in the interests of a group and coordinate members of a group to achieve common goals (van Vugt, 2006). However, little has been done so far to examine to what extent emergent leaders actually behave prosocially. To address this question, we have set up an experiment based on the iterated Public Goods Game (iPGG) played face-to-face in groups of four young males. The iPGG (Ledyard, 1994; Chaudhuri, 2011) allows estimating individual predispositions for cooperation, altruism, and free-riding (or cheating). At the same time, provided there is some verbal communication between participants, this game also allows assessing leadership potential of each group member. In the current experiment we have employed two types of the iPGG played by the same subjects: first, under the condition of no verbal communication (assessing basic individual predispositions for cooperation), and, second, involving negotiations (assessing the participants' leadership potential).

Our choice to conduct the study specifically among men was explained by the growing evidence that suggests that the propensity for group cooperation is more characteristic of men than of women (David-Barrett et al., 2015; Rostovtseva et al., 2020). The theoretical explanation of such a phenomenon can be rooted in certain evolutionary processes. One of the theories predicting gender differences in group cooperation is the Male Warrior Hypothesis (MWH) of van Vugt and colleagues (van Vugt et al., 2007; McDonald et al., 2012). The MWH is based on the observation that inter-group conflicts are common in all kinds of human societies and that most warfare, both at present and in the past, is predominantly or exclusively a male activity (Bowles, 2009; McDonald et al., 2012; Micheletti et al., 2018; van Vugt, 2009). In warfare, leadership, coalition formation, coordination of actions, and other forms of cooperation are crucial for success. Therefore, the Male Warrior Hypothesis predicts that a higher tendency to cooperate in same-gender interactions has evolved in men rather than in women (Balliet et al., 2011). Along with the MWH, a special role of group cooperation in male-specific activities is predicted by

the general gender division of labor practiced during a long period of human history (e.g., male big-game hunting) (Bird, 1999; Murdock & Provost, 1973; Panter Brick, 2002), as well as by the theory of kin selection (Hamilton, 1964) based on a widely spread tradition of patrilocality (Fox, 1967; Manson et al., 1991; Murdock & Provost, 1973; Murdock, 1981) (although see Quinones et al., 2016 for an alternative view). Taking into consideration these notions, research involving cooperation in all-male groups was of particular interest.

Along with investigating the actual cooperativeness of emergent leaders, we have also addressed possible distinctive features of their communicative behaviour. Numerous studies on direct communicative behavioural characteristics associate leadership potential with talkativeness and initiative during interactions (Bass, 1949, 1954; van Vugt, 2006; King et al., 2009; Derue et al., 2011). As has been previously shown, communication and communicative traits, both verbal and nonverbal, play a special role in human cooperation and leadership (Limon & La France, 2005; Gerpott et al., 2018, 2019). Numerous concepts explain the functional relevance of nonverbal expressions from communicative and affect-inducing perspectives, prescribing a great social value to positive facial displays (Ramachandran, 1998; Owren & Bachorowski, 2003; Rychlowska et al., 2017). Starting from the expectation of emergent leaders to perform highly communicative traits and sociability, we hypothesize that they also demonstrate enhanced levels of positive facial expressiveness. In the present study we focus on individual nonverbal profiles including such elements as smiles and laughter (Lockard et al., 1977; Provine, 2000; Ross et al., 2009; Rychlowska et al., 2017). Given the context of cooperative interactions, we consider these emotion-conveying facial expressions as positive stimuli (Otta et al., 1996; Dunbar & Mehu, 2008; Dunbar et al., 2011) essential for gaining trust and emotional support in becoming a leader.

Despite the fact that the present work is mainly focused on the analysis of associations between experimentally measured behavioural traits (leadership potential, cooperativeness, and nonverbal expressivity), we have also complemented our investigation with the assessment of possible associations between actual leadership skills and a set of basic personality traits measured via a self-report psychological inventory. A number of studies have revealed emergent leaders to carry certain personality traits, including extraversion, advanced verbal skills and high cognitive capacities (Mann, 1959; Stogdill, 1948; Judge & Bono, 2000; Judge et al., 2002, 2009; Derue et al., 2011; Zaccaro et al., 2018). We hypothesize that along with these features emergent leaders should score high on the reliability (or trustworthiness) trait and low on neuroticism. Both of these psychological features, along with extraverted personality, are expected to contribute to a successful realization of the leadership potential. In order to test this assumption we have used the Five-Factor Inventory (NEO FFI) (Costa & McCrae, 1989) that measures five basic personality traits (neuroticism, extraversion, agreeableness, openness to new experience and conscientiousness). This inventory includes a comprehensive set of traits that we found of interest.

Since most of behavioural traits exhibit a high degree of individual stability (Wolf & Weissing, 2010; Peysakhovich et al., 2014; Anusic & Schimmack, 2016), a

large body of research has been conducted on heritability of leadership traits. It was demonstrated that genetic factors significantly contribute to leadership potential (for review see: Zaccaro et al., 2018), however, almost all evidence is derived from twin-studies, and the data on the specific contributions of genes is extremely scarce (de Neve et al., 2013; Li W. et al., 2015). Based on the expectation that emergent leaders carry highly extraverted and communicative traits, we hypothesize that they may also demonstrate enhanced levels of sociability that was previously shown to be associated with certain physiological and genetic markers. Oxytocin (OXT) is a well-known candidate for the association with sociability in humans. OXT is a very abundant neuropeptide involved in regulation of numerous physiological and behavioural reactions in the human organism. The OXT system plays a crucial role in sexual, reproductive, and maternal physiology, and is also involved in the central behavioural regulation associated with social bonding and numerous aspects of prosocial behaviour (for review see: Richard et al., 1991; Gimpl & Fahrenholz, 2001; Lee et al., 2009). In humans OXT produces its effects through the OXT receptors (OXTR) (Kimura et al., 1992), and since the discovery of the *OXTR* gene structure (Inoue et al., 1994) numerous studies have been focused on the association between the *OXTR* gene polymorphisms and different aspects of human physiology and behaviour. Variation in this gene is assessed through single nucleotide polymorphisms (SNPs) (Syvänen, 2001). Studies matching SNPs in the *OXTR* gene with various aspects of social behaviour show that the most frequent associations occur with SNP rs53576 (G/A). Several studies demonstrate that rs53576 A-allele carriers (especially AA-homozygotes) have a weaker functional connectivity of the hypothalamus and an increased right amygdala activation (Tost et al., 2010; Wang et al., 2013); this most likely affects prosocial behaviour and perception. On the other hand, a large number of studies show that G-allele presence is associated with advanced empathic abilities (with GG-homozygous individuals demonstrating higher levels of empathy) (for review see: Gong et al., 2017), higher general prosociality, including helping and sharing behaviour (Wu & Su, 2015), social sensory processing (Tops et al., 2011), emotional support seeking (Kim et al., 2010), and other (for review see: Li J. et al., 2015). Although the listed effects are observed more or less universally, large-scale studies demonstrate that rs53576 allelic frequencies differ among populations (e.g., A-allele carriers being prevalent in Asian populations and G-allele in Caucasian populations) (Luo & Han, 2014; Butovskaya et al., 2016). Furthermore, the impact of rs53576 SNP on behaviour and psychology may be differently modulated by Eastern and Western cultural backgrounds (Kim et al., 2010, 2011; Sasaki et al., 2011), which certainly should be taken into consideration.

In the present study we also focus on the *OXTR* rs53576 as a potential correlate with leader behaviour. However, this part of our work faces considerable limitations imposed by a relatively small sample size (which in turn is caused by the experimental nature of the study). Therefore, our results related to the part with the genetic analysis should be considered as preliminary.

To sum up, the final goal of our study was to test weather potential leaders carry specific individual features in four independent dimensions: (1) prosocial behaviour

in cooperative group interactions; (2) positive nonverbal expressiveness (such as expression of smiles and laughter); (3) Big Five personality traits (Costa & McCrae, 1989); and (4) genetic polymorphism of the *OXTR* gene (SNP rs53576). To our knowledge, this is the first study to consider the role of the oxytocinergic system in the complex phenomenon of human leadership.

Methods

Participants

Participants of the study were 104 young men (17—28 years, mean age 20 ± 2 years) of the Mongolian origin, Buryats of Southern Siberia. All of them were students of different disciplines (natural and social sciences, economics, and arts) and based in the capital of Buryatia (Ulan-Ude). All participants were native Russian speakers. Six participants (three pairs) were excluded from the analysis, since they turned out to be acquaintances. Accordingly, our final sample consisted of 98 male individuals. Within the given age range, statistical analysis did not reveal any age effects on the experimental parameters.

Experimental Procedure

The whole study was conducted in Russian. For testing cooperativeness and individual leadership potential, all subjects participated in the real-time face-to-face iterated Public Goods Game (Ledyard, 1994; Chaudhuri, 2011). The participants were randomly sorted into groups of four individuals who were strangers to each other. The subjects were informed that during interactions they would earn tokens to be converted into real money at the end of the experiment. The conversion rate was not announced; however, the participants were informed that the average overall pay-off would equal approximately 20 USD, but it would widely vary based on individual performance. The rules were explained in detail to the participants. Participants of each group were seated at a table facing each other. Each group was placed in a separate room equipped with two cameras (Web-camera Logitech Pro C920, HD 1080p). The cameras were placed to provide the necessary viewing angle for a detailed post-hoc behavioural analysis.

The iPGG implies several repeated interactions between participants, each conducted in the same way. The general scheme of the iPGG was as follows. During each interaction subjects were suggested to invest funds (real monetary equivalents at their disposal) into a “common pool”. In each interaction, each participant was given 20 initial tokens and had to individually decide how many tokens (from 0 to 20) to invest in the “common pool”. Each participant wrote the amount he was willing to invest on a personal sheet of paper that could be seen only by him and by the experimenter. All participants were informed and reassured that the amounts of their individual investments would be kept confidential during the entire experiment. Tokens not invested were kept by the participants. When all group members had made their investment decisions, the amount of tokens in the “common pool”

was doubled and distributed equally between all four group members. The amounts of the returned tokens were publicly announced, but no information was provided concerning individual contributions, since the amounts of returned tokens per each group member were always equal. However, based on the returned amounts, the participants could judge the overall level of cooperativeness in the group. After the result had been announced, the next interaction proceeded in the same way. The iPGG in our experiment consisted of two parts each involving three repeated interactions: (1) during the first part no intentional communication (negotiations, gestures or intentional facial expressions) was allowed; (2) during the second part participants could negotiate prior to each investment decision to arrive at some consensus concerning the amount of subsequent investments. During the part with negotiations participants could try to convince each other, offer solutions, promise to invest certain amounts, or discuss anything, except for their individual investments in the previous rounds. The privacy of the decisions was maintained in this part of the game as well, so that after negotiations, information on exact individual investments was not available to other members of the group; the decisions were written down on personal sheets, and verbal agreements could be privily violated. The experimenter was present in the room during the entire experiment to ensure that the experimental rules were followed properly.

Measurement of a Leadership Potential

A leadership potential of the participants was assessed based on the analysis of verbal communication during negotiations in the second part of the iPGG. The general classification of leaders/non-leaders was carried out according to their activity and initiative during negotiations (Bass, 1949, 1954; Derue et al., 2011). The main criteria of leadership were: initiation of discussion, propositions of particular solutions, and general activity during negotiations. Participants who met all these criteria were classified as leaders. In particular, the classification was carried out according to the following scheme: (1) a leader: a participant who initiated negotiations by proposing solutions, reasoned, actively participated in discussions, summarized agreements before the decision-making; (2) not a leader: did not suggest anything, could participate in negotiations, but in a passive manner (agreed with solutions proposed by a leader or expressed distrust without making any own propositions), or kept silent. During the analysis it turned out that leaders could be classified into two different types based on the content of their verbal behaviour: (1.1) creative leaders: did not insist on their suggestions; were ready to adjust the proposed solutions if other group members expressed distrust or criticized it; reasoned without excessive eagerness; (1.2) leaders-stimulators: actively impelled to follow their strategy (always to make a maximum investment); did not compromise with other group members; insisted on proposed solutions by resorting to a variety of arguments. Since these two types of leaders (creative leaders and leaders-stimulators) were clearly different, we have kept all three types in our classification, namely "not a leader" (60% of participants), "creative leader" (30% of participants), and "leader-stimulator" (10% of participants). This classification is relative,

as it estimates individual leadership potential in a certain social environment (group). The classification was blind to the investment decisions of the participants.

To verify the validity of the method we have invited one more rater who used the same method to independently assess the behaviour of 40 participants randomly chosen from the general subject pool. Both raters were experts in anthropology and human ethology. Cohen's Kappa (κ) test was run to determine if there was an agreement between the raters' judgments on the leadership potential of the participants. According to the literature (Landis & Koch, 1977; Sim & Wright, 2005) there was a substantial agreement between the two raters ($\kappa = .751$, $p < .001$; for reference: the "almost perfect" agreement starts from $\kappa = .81$). The inter-rater agreement on the classification of "leaders-stimulators" was 100%. Thus, the inter-rater reliability of coding was good enough to apply analysis based on the coding of the major rater.

Communicative Behaviour Analysis

Individual nonverbal behaviour was assessed through the analysis of videos recorded during the experimental interactions. Nonverbal behaviour involved major patterns of positive facial expressiveness: (1) a modest smile — a not intense smile with no canine teeth visible; (2) a broad smile — a wide opened smile with premolars exposed; (3) unvoiced laughter; (4) voiced laughter with an opened mouth (Lockard et al., 1977; Bachorowski & Owren, 2001; Dunbar & Mehu, 2008). All these patterns could be well detected from the video records. The coding was carried out by estimation of the relative duration of each pattern according to the following formula:

$$\frac{\sum Duration\ of\ \ pattern}{Total\ time\ of\ \ observation} \times 100\%,$$

where the duration of each pattern was assessed by the rater (accurate to a second) and was separately coded for each part of the game. The rater was blind to the participants' investment decisions in the game. As mentioned above, both raters were experts in anthropology and human ethology. To verify the validity of the method we have engaged one more rater who independently coded nonverbal behaviour of 20 participants according to the given method. To test the between-rater reliability we have applied the Intraclass Correlation Coefficients (ICC) (Koo & Li, 2016). The inter-rater reliability of coding was good enough (ICC = .86, $p < .001$) to apply analysis based on the coding of the major rater.

Unfortunately, not all video records could be properly analyzed due to technical issues. Therefore, in all parts of the analysis involving nonverbal behaviour only 70 cases were considered, whereas the leader potential was assessed for 72 individuals.

Personality Test

To get an insight into the personalities of our subjects we have applied self-report Five-Factor Inventory (NEO FFI) (Costa & McCrae, 1989) that measures

five basic personality traits (neuroticism, extraversion, agreeableness, openness to new experience and conscientiousness) on a five-point scale; higher average scores reflect a more reported expressivity of the measured trait. Since all our participants were native Russian speakers, we have used one of the official Russian adaptations of the inventory (adapted by V. E. Orel, A. A. Rukavishnikov, I. G. Senin, T. A. Martin, 2010). Prior to major analysis each personality trait was checked for reliability by calculating Cronbach's Alpha on each set of questions constituting a trait. Reliability of two traits (openness to new experience and agreeableness) was very poor ($\alpha < .35$), thus these traits were excluded from the analysis. Neuroticism, extraversion, and conscientiousness were reliable enough ($\alpha > .75$).

Genetic Analysis

Genotyping of the study sample has been done through Taqman (Real time qPCR). After the DNA purification we have measured concentrations with Nanodrop-1000 spectrophotometer. Two samples were of inadequate quality and were excluded from the analysis. Then we diluted in 96-well plates the DNA samples with H_2O to obtain 5 ng/μL of DNA concentration in 15 (μL) of volume. The aliquoted DNA samples were stored at −20°C. To do the genotyping we prepared a MIX solution (for a sample) composed by 2.5 (μL) of masterMIX reagent, 1.45 (μL) of distilled water and 0.05 (μL) of specific probe. Then we blended the MIX solution and put 4 (μL) for a well. Finally, we also put 1 (μL) of DNA 5 ng/μL concentration in each well. The *OXTR* gene (SNP rs53576) was genotyped using the TaqMan 5'-exonuclease allelic discrimination assay (Applied Biosystems) with the custom assay C__3290335_10.

Statistical Analysis

Statistical analysis was conducted in SPSS v.23 (SPSS Inc, Chicago, IL). As distributions of all continuously-scaled variables were not normal (highly skewed), for testing differences we have applied nonparametric test, a Kruskal-Wallis test for independent samples. Comparison of distributions was conducted through a chi-squared goodness-of-fit test. The Fisher's exact test of independence was used to assess relationship between categorical variables in cases when the sample sizes were small. In other cases a chi-squared test of independence was used.

To test reliability of the obtained scores using the Five-Factor Personality Test (NEO FFI), Cronbach's Alpha on each set of questions constituting a trait was calculated.

Results

Individual Cooperativeness

Analysis of individual investments in the first part of the iPGG (without negotiations) allowed distinguishing four basic strategies of behaviour: (1) self-oriented — always unconditionally invested < 50% of own funds into the "common pool";

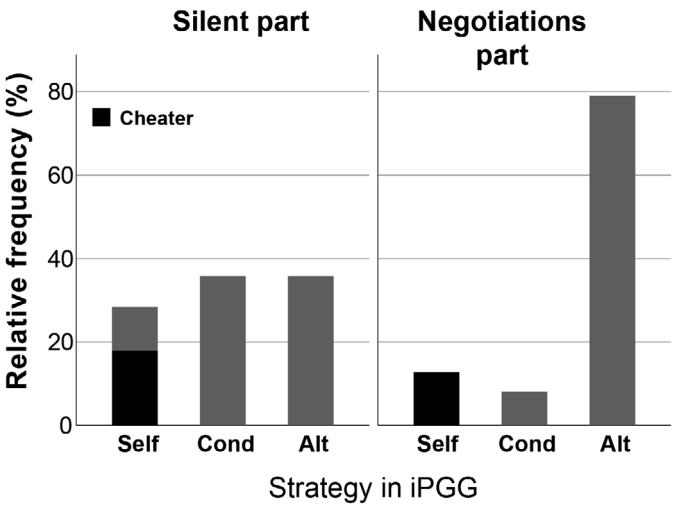
(2) an unconditional cooperator — always invested ≥ 75% of own funds, even if the cooperation failed in a previous round; (3) a conditional cooperator — varied investments depending on the outcomes of the previous rounds (either started with high investments and then declined in the course of the game due to non-cooperative environment, or started with low investments and raised subsequently due to favorable contributions of others); (4) an occasional free-rider — suddenly crucially decreased investments or invested zero amid high investments of other group members. This classification was justified in detail in our recent publication (Rostovtseva et al., 2020), therefore we will not dwell on this issue here. Three subjects, whose decisions' sequence did not fit the scheme explained above (namely, always invested 50–75% of own funds) were excluded from the analysis.

Strategies in the second part of the iPGG (with negotiations) were assessed considering both amounts of investments and agreements during negotiations, such as promises and personal agreements with the group consensus (if such was achieved). Achieving group consensus implies that all or the majority of the group members agreed on the exact amount of individual investments that they were going to make in an upcoming round. A personal agreement with the group consensus means that the subject has confirmed (verbally or by nonverbal means) that he will invest in the upcoming round with accordance to the agreement. Agreements during negotiations were revealed by the post-hoc analysis of the videos recorded during the experiment. Despite the fact that it was beneficial to agree on the maximum contributions, the negotiations did not always end up with such a consensus, and sometimes the subjects agreed on investing approximately half of the individual funds (primarily this happened due to mutual mistrust of some members of a group). Finally three strategies were identified for the part with negotiations: (1) an unconditional cooperator — always followed group consensus or invested ≥ 75% of own funds, even if the cooperation failed in a previous round; (2) a conditional cooperator — followed/avoided group consensus depending on the outcomes of the previous rounds (either started with following agreements and then broke due to non-cooperative environment, or refrained from high investments at the beginning and raised subsequently in the course of the game due to favorable contributions of others); (3) a cheater — practiced "cheap talk" (promised to invest, but did not keep the promises), or did not protest against group consensus but invested zero amid high investments of other group members. In the part of the iPGG with negotiations the "self-oriented" strategy (always to unconditionally make low investments) was not detected.

Figure 1 displays distributions of strategies across first (silent) (N = 95) and second (negotiations) (N = 86) parts of the iPGG. Apparently, verbal communication crucially improved prosocial behaviour. Comparison of the distributions of strategies in the first and the second parts of the iPGG clearly demonstrates the shift of behaviour towards unconditional cooperation (applying the altruistic strategy) in the second part of the iPGG (the chi-squared test of independence: N = 181, $\chi^2 = 40.051(4)$, $p < .001$). This finding is not a discovery, but rather a reproduction of a well-established positive effect of face-to-face negotiations on human cooperativeness (Balliet, 2010; Ghate et al., 2013; Quinones et al., 2016).

Figure 1

Distribution of Strategies in the First (Silent) and Second (Negotiations) Parts of the Iterated Public Goods Game



Note. Strategies: Self — selfish strategies, combining both the "selfish" strategy per se and the "occasional free-rider" strategy (cheating), Cond — conditional cooperator, Alt — altruist (unconditional cooperator). The chi-squared test of independence: N = 181, $\chi^2 = 40.051(4)$, $p < 0.001$.

Cooperation and Individual Leadership Potential

The leadership potential of participants was assessed based on verbal communication and contents of negotiations in the second part of the iPGG (see Methods for details).

Solutions proposed by the leaders in all cases contained exact amounts of tokens suggested to invest. Therefore, it was possible to estimate willingness of other group members to follow propositions of each leader. Likelihood of being followed (for each leader) was calculated as a percentage of investment decisions of other group members, which supported the amount of tokens initially proposed by a leader (over all interactions in the second part of the iPGG). We have not observed any statistically significant differences in the willingness to follow "creative leaders" or "leaders-stimulators", thus both of these types of leaders were equally followed by other participants (with median at 88% for both types).

Figure 2 displays correspondence of leadership qualities to cooperative strategies. We have observed a clear-cut split of the distribution of the strategies according to the leadership skills in the first part of the iPGG (the Fisher's exact test of independence: N = 69, $p = .014$) (Figure 2a). To assess the statistical significance of the correspondence of certain strategies to a particular leadership style we have combined "selfish" and "occasional free-riding" (or "cheating") strategies into one "self-oriented" strategy, and have run pairwise the Fisher's exact test of independence, setting

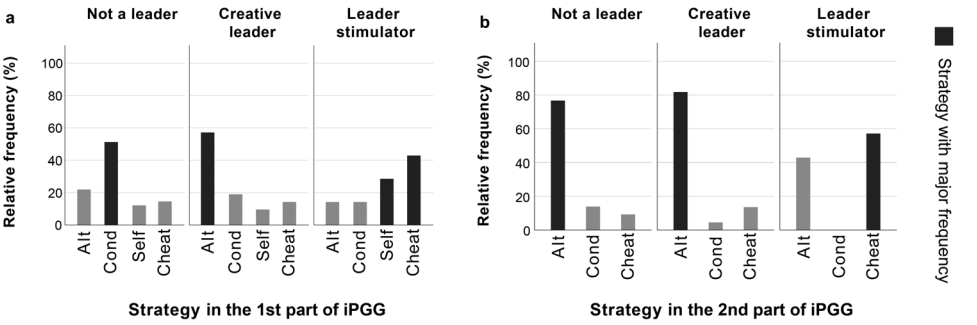
each of the three strategies ("self-oriented", "altruistic", and "conditional cooperation") against each of the three leadership styles. The Bonferroni correction, therefore, was applied for nine tests. In the first part of the iPGG non-leaders most often applied the strategy of conditional cooperation ($p = .0057$; $p_{(\text{Bonferroni corrected})} = .05$); creative leaders in majority were "altruists" (unconditional cooperators) and applied this strategy more often than others ($p = .0047$; $p_{(\text{Bonferroni corrected})} = .04$); leaders-stimulators applied the "self-oriented strategy" ("selfish" and "cheating" strategies) more often than others ($p = .024$, did not survive Bonferroni corrections presumably due to the small amount of "leaders-stimulators" in the general sample). In the second part of the iPGG (with negotiations) most of participants switched to "altruistic" behaviour (the strategy of unconditional cooperation) (Figure 2b). However, "leaders-stimulators" have most often applied the "cheating" strategy, and more often than others (pairwise Fisher's exact test of independence with Bonferroni correction for three tests: T = 72, $p = .009$; $p_{(\text{Bonferroni corrected})} = .027$). These results apparently demonstrate that emergent leadership is not always associated with prosociality. A small fraction of leaders were characterized by an exaggeratedly active style of negotiations and selfishness (even cheating), with both qualities measured independently.

Leadership Potential and Personality Traits

From five personality dimensions measured via the Five-Factor Inventory (NEO FFI) only three (neuroticism, extraversion, and conscientiousness) were reliable according to Cronbach's Alpha estimates (see Methods). Individuals with different leadership styles differed significantly only in one of these traits (extraversion) (Independent-Samples Kruskal-Wallis Test: N = 72, H = 6.697(2), $p = .035$) (Figure 3). Leaders in general scored higher on the extraversion trait, with "leaders-stimulators" having the highest scores. This result fully supports the literature

Figure 2

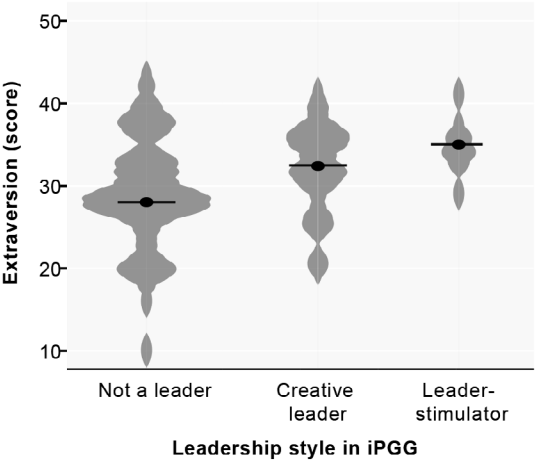
Correspondence of Leadership Qualities to Cooperative Strategies in the Iterated Public Goods Game



Note. Strategies: Alt – "altruist" (unconditional cooperator); Cond – conditional; Self – selfish; Cheat – cheater (or occasional free-rider for first part of the iPGG).

Figure 3

Variation in Self-Reported Extraversion with Regard to Leadership Skills in the iPGG



Note. Extraversion is measured via NEO-FFI, medians are displayed (black horizontal lines). Kruskal-Wallis test for independent samples: N = 72, H = 6.697(2), p = .035.

that states extraversion to be one of the most important personality traits for leadership (Zaccaro et al., 2018); however, the significance levels did not survive Bonferroni correction for three tests.

Leadership Potential and Nonverbal Expressiveness

Analysis of nonverbal expressiveness with regard to the styles of leadership also revealed considerable differences. The analysis of videos allowed distinguishing four major elements of facial positive expressiveness: a modest smile (S1); a broad smile (S2); unvoiced laughter (L1); voiced laughter (L2). Individual expressiveness on the listed elements was estimated as percentage of time spent performing the element during experimental interactions (see Methods for more details). In general, leaders were characterized by increased positive expressiveness, with "leaders-stimulators" over-expressing both smiles and laughter (Table 1). A distinctive feature of "leaders-stimulators" was over-expression of voiced laughter that is argued to be especially efficient in eliciting positive affect in perceivers (Provine, 2000; Bachorowski & Owren, 2001; Sander & Scheich, 2001; Owren et al., 2013).

Individual Leadership Potential and Variation in OXTR rs53576

The complementary part of our analysis was the analysis of genetic variation in *OXTR* gene SNP rs53576 between participants with regard to their individual leadership skills.

Table 1

Variation in Positive Nonverbal Expressiveness between Individuals with Different Leadership Skills

Part of the iPGG	Communicative element	Mean Rank			H	*p*
		Not a leader	Creative leader	Leader-stimulator		
Part 1	Modest smile	29.42	41.21	54.86	12.137	.002*
	Broad smile	32.80	35.83	50.71	5.465	.065
	Unvoiced laughter	30.36	40.52	51.29	14.440	.001*
	Voiced laughter	34.50	34.50	44.50	18.265	<.001**
Part 2	Modest smile	32.83	38.74	41.79	1.921	.383
	Broad smile	34.71	36.62	36.86	0.158	.924
	Unvoiced laughter	32.44	40.21	39.71	2.425	.297
	Voiced laughter	31.92	37.57	50.79	10.110	.006*

Note. Part 1 of the iPGG — no intentional communication allowed; Part 2 — with negotiations. Mean ranks are displayed for relative time spent on each communicative element. Results of Kruskal-Wallis test for independent samples (test statistics: H), N = 70.

* $p < .01$; ** $p < .001$ (all survived Bonferroni correction).

The Buryat sample studied was in Hardy—Weinberg equilibrium ($\chi^2 = 0.439$, d.f. = 1, $p = .507$). The allele frequencies were: A = 0.60, G = 0.40, and the genotype frequencies were as follows: AA = 0.36, AG = 0.48, GG = 0.16. The differences between the expected and observed heterozygosity were almost absent (Hobs = 0.448, Hexp = 0.480). The frequency of the A-allele, which is known to be the minor allele for European populations (Butovskaya et al., 2016), was higher than the G-allele frequency. This fits the literature data known for Yakuts (Alfred database: A = 0.74, G = 0.25). The obtained distribution is also consistent with the existing information that A-carriers are very common in Asian populations (Luo & Han, 2014; Butovskaya et al., 2016). Our goal in the current study was to assess a possible association of the genetic polymorphism in rs53576 with three types of individuals distinguished by leadership skills.

Variation in given SNP across different leadership styles is presented in Table 2. According to the chi-squared goodness-of-fit test, distributions of the *OXTR* gene SNP rs53576 genotypes within non-leaders and creative leaders did not differ significantly from the overall distribution of these genotypes. However, AA-homozygotes were completely absent among "leaders-stimulators", although this genotype was very common in our sample. At the same time heterozygotes (AG) made up the main fraction of the leaders-stimulators. The observed shift in distribution of rs53576 genotypes within leaders-stimulators is statistically significant (the Fisher's exact test of independence comparing leaders-stimulators and the rest of the sample: N = 70, $p = .038$).

Table 2

Association between Leadership Styles in the Iterated Public Goods Game and OXTR Gene SNP (rs53576) Genotypes

Leadership style	N	OXTR rs53576 genotypes			
		GG	AG	AA	
Not a leader	42	7	18	17	N
		16.7%	42.9%	40.5%	Relat. freq.
Creative leader	21	2	8	11	N
		9.5%	38.1%	52.4%	Relat. freq.
Leader-stimulator	7	1	6	0	N
		14.3%	85.7%	0%	Relat. freq.

Note. The Fisher's exact test of independence for the distribution of genotypes (AA and the other) between leaders-stimulators and the rest of the sample: N = 70, p = .038.

Discussion

Our study has demonstrated that in small leaderless groups involved in a cooperation task, leaders emerge automatically based on the individual traits of group members.

The majority (~ 60%) of participants from our sample were identified as non-leaders (predominantly followers with a small fraction of nonconformists). They were basically characterized by conditional cooperation and poor nonverbal expressiveness, which fully complies with expectations (Stogdill, 1948; Bass, 1949; Mann, 1959; Judge & Bono, 2000; Beauchamp, 2000; Judge et al., 2002; van Vugt, 2006; King et al., 2009; Judge et al., 2009; Derue et al., 2011; Edelson et al., 2018; Zaccaro et al., 2018).

The remaining ~ 40% of the participants were identified as individuals with leadership potential. Approximately 75% of them were classified as "creative leaders" who initiated negotiations and proposed good solutions to a social dilemma. The majority of this type of leaders were strongly prosocially oriented (applied the "altruistic" (unconditionally cooperative) strategy, showed moderate to high positive nonverbal expressiveness). Apparently, individuals of this type could potentially succeed as effective leaders in a long-term perspective due to guiding the group to the common good, reinforcing in-group cooperation by their own example, and positively affecting emotional and affiliative components of social interactions.

The remaining 25% of individuals with leadership potential (that constituted 10% of the general sample) were identified as "leaders-stimulators" based on their excessive verbal activity during negotiations (intensive prompting to invest maximum). Distinctive features of "leaders-stimulators" were exaggerated positive expressiveness, excessive voiced laughter and proneness to free-ride. The experi-

mental conditions provided full privacy of decisions, so that group members could only guess who may have cheated, when free-riding occurred. The fact that "leaders-stimulators" were followed by other group members as frequently as "creative-leaders", indicates that the participants did not recognize free-riders in "leaders-stimulators". Apparently, if their cheating had been revealed, the potential of such leaders would have inevitably collapsed. Therefore, perhaps, it would be more accurate to say that "leaders-stimulators" were actually cheaters who successfully imitated leader qualities.

The ability for active cheating obviously requires advanced social skills and intelligence. Some previous studies suggest that predisposition to deceive is associated with extraversion and intelligence (Sarzyńska et al., 2017), whereas probability of not being detected grows with an increase in social involvement and positive expressiveness while cheating (Burgoon et al., 1995; Stouten & de Cremer, 2010; Schwardmann & van der Weele, 2019). A recent work has already demonstrated that cheaters can disguise their genuine emotions by more intense positive nonverbal expressiveness that is perceived by others as a sign of trustworthiness (Okubo et al., 2012). The attractiveness of exaggerated key stimuli (extreme or even "supernormal stimuli") is a well-known phenomenon in ethology (Tinbergen, 1948, 1951; Tinbergen & Perdeck, 1950). A supernormal stimulus, despite its possible artificial nature, is capable of inducing a positive response in perceivers, as empirically demonstrated in a wide variety of species (Staddon, 1975; Bielert & Anderson, 1985; Barrett, 2007; Jaffe et al., 2007; Moreno et al., 2008; Tanaka et al., 2011; Kral, 2016), and humans are no exception (Costa & Corazza, 2006; Barrett, 2007, 2010; Morris et al., 2013; Pazhoohi et al., 2020). This ethological mechanism may underlie the reaction to intensified positive expressiveness in the direction of enhancing a prosocial response in perceivers, and contribute to successful cheating by those who use it. Importantly, "leaders-stimulators" were followed by other group members even after the failure of cooperation in a previous round (occurrence of cheating in the group was obvious to the group members). Hence, the behavioural strategy of leaders-cheaters (the exaggeration of positive nonverbal expressiveness and verbal activity) was very efficient. Our data provides the empirical confirmation of a "natural" implementation of supernormal nonverbal stimuli in human social interactions.

The increase in positive nonverbal expressiveness characteristic to "leaders-stimulators" in our study was basically manifested via an increase in modest smiles and voiced laughter, whereas broad smiles did not show any significant differences across leadership styles (Table 1). Previous studies suggest that smiles with different intensities are perceived differently. Apart from just positive emotional messaging, modest (not intense) smiles are perceived as a sign of competence, whereas broad (intense) smiles, despite being warmer, were reported to indicate subordinance (Lockard et al., 1977; Kraus & Chen, 2013; Wang et al., 2016). The same can be denoted concerning laughter. Generally, more intense, not inhibited laughter conveys information about a dominant status, whereas suppression of laughter may be perceived as indication of shyness and submissiveness (Szameitat et al., 2011; Oveis et al., 2016), which are well-known opposites of leader qualities (Bass, 1949,

1954; van Vugt, 2006; King et al., 2009; Harcourt et al., 2009; Kurvers et al., 2009; Derue et al., 2011; Bevan et al., 2018; Sasaki et al., 2018). Thus, by exaggerating the expression of modest smiles and laughter, leaders-cheaters could enhance an impression of social dominance thereby stimulating followership.

Finally, we have detected the prevalence of a specific allelic variant of *OXTR* gene SNP rs53576 among leaders-stimulators: there were no AA-allele carriers within the fraction of this type of "leaders", and the majority of them were AG-heterozygotes. According to statistical analysis the possibility of occurring of such an allelic distribution just by chance is less than 3.8%. The obtained result is fully in line with literature on the *OXTR* gene polymorphism in the given SNP and its functionality within Asian populations. It has been recently revealed on a Chinese sample that AA-carriers have weaker functional connectivity of the hypothalamus and increased right amygdala activation (Wang et al., 2013), which presumably affects social skills, prosocial behaviour and perception. The A-allele presence (especially in the AA variant) has been shown to be associated with autism within Chinese Han population (Wu et al., 2005). There are also a number of studies in the field that demonstrate that A-allele carriers have weaker empathic abilities, which is true both for Asians and Caucasian populations (for review see: Gong et al., 2017). At the same time, GG-carriers are characterized by the most developed empathic abilities (Ibid.), high general prosociality, including helping and sharing behaviour (Wu & Su, 2015), and other (for review see: Li J. et al., 2015). All this evidence makes up a fine argument in the explanation of the *OXTR* gene (rs53576) allele distribution within "leaders-stimulators". As has been demonstrated in our study, "leaders-stimulators" were very sociable individuals, with advanced verbal skills, intensified positive nonverbal expressiveness, and extraverted personality. In accordance with the literature, such traits are unlikely to be characteristic of AA-carriers, and we actually do observe this in our study. On the other hand, GG-carriers are expected to demonstrate higher levels of prosociality (empathy, sharing, helping), which also does not fit the anti-social behaviour (cheating) of "leaders-stimulators" in the iPGG. The AG genotype appeared to be the most adequate combination that enabled its carriers to succeed in performing leader qualities matched with their active cheating abilities.

Generally, our finding supports existing evidence that OXT is involved in regulation of social behaviour (for reviews see: Richard et al., 1991; Gimpl & Fahrenholz, 2001; Lee et al., 2009), with the *OXTR* gene (SNP rs53576) being a fine predictor of prosocial skills in males. However, our results related to genetic analysis should be taken with caution due to the relatively small sample size of our study, primarily limited by its experimental nature. More research is required for reproducing the results obtained. Considering truly outstanding social qualities of "leaders-stimulators" that allowed them to successfully apply active cheating in face-to-face interactions, the fact that they constituted only a small fraction of the general sample is not surprising. Increased sample sizes or a few repeated studies using the same methodology would help clarify the consistency of our findings.

Taken together, our results suggest that male cooperation in small leaderless groups is a sufficient condition for emergence of leadership. Each type of individu-

als distinguished on the basis of leadership skills was characterized by a certain set of independently measured traits, namely, cooperative strategy, nonverbal features and personality. Among individuals with leadership potential there was a small fraction of cheaters, who were distinguished by very active behaviour during negotiations, excessive positive nonverbal expressiveness and laughter, and increased extraversion. Other group members did not distinguish between prosocial leaders (creative leaders) and leaders-cheaters (leaders-stimulators), since the willingness to follow these two types of leaders in the iPGG did not differ significantly. Our results also suggest that behavioural features characteristic of the leaders-cheaters may be associated with a specific polymorphic variation in the *OXTR* gene (SNP rs53576), but this conclusion should be carefully tested in the future.

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