

Sleep Deprivation Impairs Cooperative Behavior Selectively: Evidence from Prisoner's and Chicken Dilemmas

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Objective: The aim of our study was to investigate the influences of acute sleep deprivation on cooperation with two classical social dilemmas, the Prisoner's dilemma (PD) and the chicken dilemma (CD).

Methods: All participants (N=24) were required to come for the experiments twice; one time for normal sleep condition, the other time for sleep deprivation condition, with a counter-balanced sequence. In the following afternoon, participants completed the psychomotor vigilance task (PVT) and two social dilemmas tasks, as well as the Karolinska Sleepiness Scale (KSS), the Risk Orientation Questionnaire (ROQ) and the Positive and Negative Affect Schedule (PANAS).

Results: Our results demonstrated that sleep deprivation significantly impaired cooperative behaviors in the CD but not in the PD. In addition, this detrimental effect was not related with the alteration in the risk-seeking, objective alertness, subjective sleepiness, and mood.

Conclusion: The current findings revealed that sleep deprivation impairs cooperative behaviors under social dilemmas selectively. However, the underlying mechanism remains to further explore with neuroimaging studies and better ecological approach.

Keywords: sleep deprivation, cooperation, risk-seeking

Introduction

"No man is an island entire of itself; every man is a piece of the continent, a part of the main." Just as the poet John Donne said, cooperation, simply defined as two or more people working together toward a corporate aim, is inevitable owing to its fundamental role of social interaction. Doubtlessly, cooperation, a prerequisite of group, organization, and society, is essential not only for human evolution, but also for individual development, organizational management, and social progress.¹

The social dilemma is one of the common approaches for investigating human cooperative behavior, mainly including two dilemma prototypes: the prisoner's dilemma (PD) and the chicken dilemma (CD, also known as the hawk-and-dove game).^{2,3} In both scenarios, two players choose to cooperate or defect, and each of them is paid according to mutual choice made by these two players. Considering individual player's payoffs, unilateral defection in the PD game benefits the most, followed by mutual cooperation, then mutual defection, and finally unilateral cooperation. In the CD game, unilateral defection benefits the most, followed by mutual cooperation, then unilateral cooperation, and finally mutual defection. More specifically, the PD game encourages people to defect with others, because mutual defection is a dominant-strategy equilibrium although

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mutual defection is worse for both players than mutual cooperation.⁴ However, there is no dominating strategy in the CD game. It forces people to make hard decisions between the balance of cooperation and defection. Defection in the CD is a high-risk decision situation with considerable outcome variance, which may cause the best or worst outcome. On the other hand, the risk level for choosing cooperation in the CD is relatively low, because the player may receive or lose intermediate pay-offs. Compared with PD, the mutual defection payoff in the CD is worse than the payoff for cooperation from just player.⁵ Therefore, the CD game may be more dynamic and ubiquitous than the PD game because players get immediate benefits from cooperation and costs of cooperation are shared.⁶

Cooperation is essential for social interaction, but people do not always cooperate with each other due to the universality and complexity of social dilemmas. Prior studies revealed that cooperation relies on reputation or potential future interactions, as well as propensity toward risk.^{7,8} Recent studies applied two-person prisoner's games with gambles and found that risk-seeking had a positive correlation with cooperation,^{9,10} which is contradictory to earlier research suggesting no relationship between cooperation and risk preference.¹¹ In addition, the relationship between risk-seeking and cooperation may be more influential in the CD than in the PD. De Heus and colleagues (2010) found a decreased rate of cooperative behavior in the CD caused by risk-seeking but not in the PD.⁵ Therefore, risk-taking preferences may play different roles in cooperative behavior with different social dilemmas.

Sleep loss has detrimental effects on a wide array of psychological functions including alertness, emotion, working memory, and reasoning.^{12,13} In the past decade, the effect of

sleep loss on human social behavior has attracted increasing attention in the domain of sleep research. Although sleep loss significantly impairs an individual's performance, several studies consistently found that the social interaction or collaboration might be helpful to counter the adverse effect of sleep loss and partially improve individual's outcomes.^{14–16} In 2010, Anderson and Dickinson explored sleep deprivation and its effect on decision-making by using social economic games and observed lower trustworthiness and increased unfairness when people were sleep deprived.¹⁷ A recent study further demonstrated that chronic sleep loss significantly reduced people's trustworthiness and altruistic behavior.¹⁸

However, social relationships in daily life involve perceptions of others, such as trustworthiness and fairness, and also interaction with mutual interests and conflicts. Social dilemmas are the important approach to investigate cooperative behaviors based on the conflict of "individual needs and desires versus the benefit of the group."¹⁹ To date, no single study investigated the effect of acute sleep deprivation on cooperation with social dilemmas. In the current study, we applied two social dilemmas with different payoff matrixes (see Figure 1), in which the PD game leads to a win or nothing (zero gain) and the CD game leads to a win or loss (subtraction of money), to investigate whether sleep deprivation alters cooperative behaviors.

The other aim was to explore potentially influential factors underlying cooperative behaviors and sleep deprivation, including objective alertness, subjective sleepiness, mood, and risk-seeking. Numerous studies demonstrated that sleep loss strongly affected individual's alertness and sleepiness,^{20–26} as well as mood¹² and risk-seeking.^{27–29} Those factors may also influence cooperative behavior due to insufficient resources to regulate cognitive and affective control after sleep loss.³⁰ Based on these considerations,

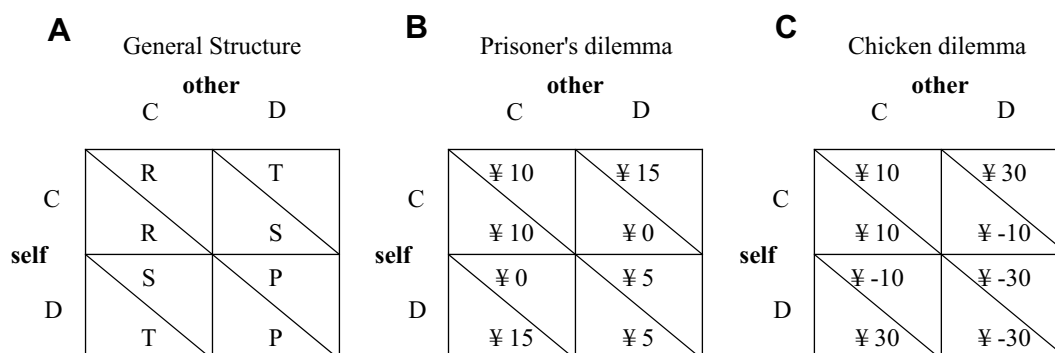


Figure 1 (A) Payoff matrix for general structure. (B) Payoff matrix for the prisoner's dilemma. (C) Payoff matrix for the chicken dilemma.

Abbreviations: C, cooperation; D, detection; P, punishment; R, reward; S, sucker; T, temptation.

we hypothesized that sleep deprivation might impair cooperative behaviors to different degrees in the CD and PD. The change of objective and subjective indicators (including objective alertness, subjective sleepiness, mood, and risk-seeking) may influence cooperative behaviors between normal sleep and sleep deprivation.

Methods and Materials

Participants

Twenty-four healthy adults ($M_{age} = 21.38 \pm 2.14$ years old, 16 females) with normal body mass index ($19.97 \pm 1.86 \text{ kg/m}^2$) and normal or corrected-to-normal vision participated in this study, which was conducted in the Center for Sleep Research at the South China Normal University. All study procedures were approved by the Ethical Committee of the South China Normal University, and were conducted in accordance with the Declaration of Helsinki. All participants provided written informed consent and were financially compensated for their time.

All the participants were nonsmokers. They had no acute or chronic physical or psychological conditions, as established by interviews, clinical history, questionnaires, and physical examinations. Participants had habitual 6.5–8 hrs sleep duration and habitual awake times between 06:00 am and 09:00 am, as assessed by sleep diary and actigraphy (Actiwatch Spectrum, Philips) within 2 weeks before the in-laboratory experiment. Individuals with sleep disorders were excluded by the sleep adaptation night of laboratory polysomnography (PSG) and oximetry measurements (Grael HD PSG, Compumedics). Participants had no transmeridian travel or shift work (in any pattern, including evening or night shifts, early morning shifts, and rotating shifts) or irregular sleep-wake routines in 60 days prior to the in-lab experiment. No caffeine, alcohol, or medications were permitted 3 days before and during the in-laboratory study.

Experimental Procedures

All participants were required to come to the Center for Sleep Research twice, one time for normal sleep condition, the other for sleep deprivation condition. The condition sequence was counter-balanced. If the experiment started with normal sleep, the sleep deprivation session was carried out after 1 week to minimize the practice effects of behavioral tasks. If the session of sleep deprivation started first, the normal sleep session was after at least 1 month to ensure participants fully recovered from the effect of one-night acute sleep deprivation, and to minimize the practice effects of behavioral tasks as well.

Participants were continuously monitored in a semi-isolated living area and only had contact with research staff during the stay in the lab. They were given meals at regular, pre-specified hours (7:30 am for breakfast, 12:00 pm for lunch, and 18:00 pm for dinner). Meals contained no caffeinated products. During their free time, participants were permitted to read books and magazines and converse with the study monitors. They were not allowed to do any physically demanding tasks. Participants were not allowed to use light-emitting electronic equipment, such as smartphones or tablets, during the whole experiment. They were only allowed to use desktop computers during behavioral tests on the study time schedule.

For the in-laboratory protocol (Figure 2), during the normal sleep condition, participants arrived at the laboratory in the evening around 19:00 pm and had around 8 hrs of time in bed (normally starting from 23:00 pm, the duration of normal sleep was 7.99 ± 0.28 hrs according to the PSG data) for baseline sleep. During the sleep deprivation condition, participants did not sleep for the whole night under monitoring by the research staff. In addition, all the participants were required to have around 8 hrs of time in bed as adapting sleep in the laboratory the night before the experiment (normally starting from 23:00 pm, the duration of normal sleep was 8.07 ± 0.32 hrs according to PSG data) to familiarize participants with

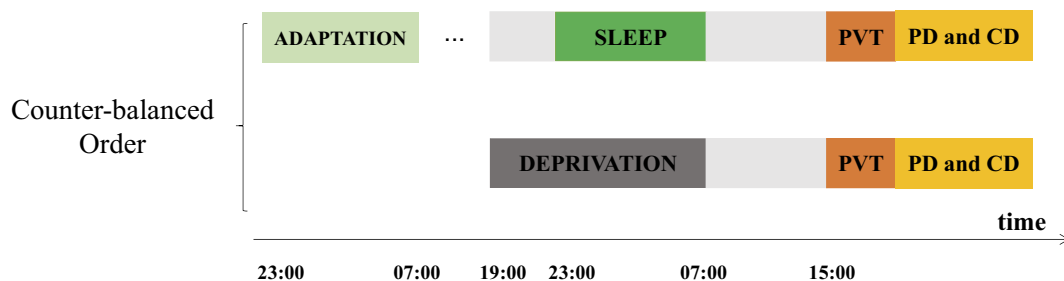


Figure 2 Experimental protocol of normal sleep and sleep deprivation conditions.

the experimental environment and avoid potential factors influencing their sleep. In the afternoon following the normal sleep or sleep deprivation night, participants filled in the Positive and Negative Affect Schedule (PANAS), Risk Orientation Questionnaire (ROQ), and Karolinska Sleepiness Scale (KSS) scales and then performed a psychomotor vigilance task followed by the PD and CD. The task sequence of PD and CD was counterbalanced between conditions (Normal sleep/Sleep deprivation) and participants.

Experimental Paradigms and Instruments Prisoner's Dilemma (PD) and the Chicken Dilemma (CD)

In both the PD and CD games, participants were told that they would be paid each round based on the decisions made by themselves and their partners, who were 30 different people that only contacted them via the computer (but their partners were actually fictive and randomly selected by computer, and the participants did not know that their partners were fictive). The participants had to make a choice between A (cooperation) or B (defection), but the words “cooperation” and “defection” were never used. Participants were asked to make their own choice without being informed about the partner's choice. To avoid potential influence of the prior response on the next decision, there was no feedback about the outcome during the experiment.

The instructions for both games with the payoff matrix (see Figure 2) were always shown on the screen during the game.⁵ To make sure the participants understood the games, we also explained the implications of the payoff matrix for both the PD and CD to the participants before the experiment. In the PD game, the B option always leads to a better outcome for oneself than the A option. However, if both of the players choose B, both will get worse outcomes than if both chose A. In the CD game, one may get the best possible gain with option B (if the other chooses A) but may also get the worst loss (if the other chooses B). Option A always leads to an intermediate outcome, either a gain or a loss.

Psychomotor Vigilance Test (PVT)

Under both normal sleep and sleep deprivation conditions, participants were administered a 10 mins version of the PVT before the cooperation tasks.³¹ This sustained attention task is based on visual reaction time, which is highly sensitive to the circadian and homeostatic influences on cognitive

decrements due to sleep loss.^{20–23} Participants were asked to focus their attention on a red, rectangular box subtending 2 x 1.3 degrees of visual angle in the middle of a black screen and monitor that space for the appearance of a millisecond counter, which appeared at random intervals ranging from 2–10 s. They were instructed to stop the counter as quickly as possible with a button press, after which they would be able to view their reaction time. Participants were also instructed to avoid anticipating the stimuli so as not to register “false starts,” or responses when no stimulus was present on the screen.

Subjective Sleepiness, Mood and Risk-Seeking Preference

Subjective sleepiness was assessed by the KSS.³² The KSS is a 9-point, verbally anchored scale ranging from 1 (extremely alert) to 9 (extremely sleepy).

The PANAS is a 5-point scale with two subscales (positive and negative affect) was applied to measure participants' affective state. It was developed by Watson and colleagues and adapted to the Chinese population in 2008.^{33,34} We used the Chinese version, which includes 20 items with 10 positive affect and 10 negative affect items.

We also used the ROQ to assess individuals' risk-seeking level under normal sleep and sleep deprivation conditions.³⁵ The ROQ is a 7-point scale containing 12 items to evaluate how different people deal with risky situations and assess their attitude toward risk decision.

Results

Differences of Objective Alertness and Subjective Ratings of Sleepiness, Mood, and Risk-Seeking Preference Between Normal Sleep and Sleep Deprivation

The number of PVT lapses (reaction time >500 ms) and the reciprocal of mean reaction time are two common indicators to assess alertness attention after sleep deprivation. The increased number of PVT lapses (paired *t*-test: $t = -4.71$, $p < 0.001$, Cohen's $d = 1.34$) and the decreased reciprocal of mean reaction time (paired *t*-test: $t = 6.48$, $p < 0.001$, Cohen's $d = -0.98$) indicated impaired participant alertness due to sleep insufficiency (Table 1).

We used paired *t*-tests to investigate whether sleep deprivation altered the ratings of subjective sleepiness, as well as negative affect (Table 1). As expected, compared to the normal sleep condition, the sleepiness rating was marginally increased ($t = -1.890$, $p = 0.071$, Cohen's $d = -0.39$) after

Table 1 Objective Measurements and Subjective Ratings During Normal Sleep and Sleep Deprivation

	Normal Sleep	Sleep Deprivation	p
PVT			
1/mean RT	3.24 ± 0.34	2.12 ± 0.74	<0.001
Number of lapses	3.46 ± 2.78	17.00 ± 15.18	<0.001
Cooperation Rate (%)			
PD	28.69 ± 29.54	30.49 ± 31.51	0.992
CD	80.19 ± 26.75	58.01 ± 37.76	0.007
Subjective Rating			
Sleepiness	4.78 ± 1.21	6.42 ± 1.64	0.061
PANAS (P)	28.92 ± 7.64	25.58 ± 9.44	0.020
PANAS (N)	14.25 ± 6.04	18.17 ± 6.79	0.004
ROQ	44.70 ± 3.21	47.00 ± 6.59	0.057

Abbreviations: CD, chicken dilemma; PANAS, Positive and Negative Affect Schedule; PD, prisoner's dilemma; PVT, Psychomotor Vigilance Test; ROQ, Risk Orientation Questionnaire; RT, response time.

sleep deprivation. Analysis of PANAS scores showed that positive affect (paired *t*-test: *t* = 2.51, *p* = 0.02, Cohen's *d* = 0.51) and negative affect (paired *t*-test: *t* = -3.22, *p* = 0.004, Cohen's *d* = -0.66) were significantly reduced due to sleep loss.

Paired *t*-tests were used to assess risk seeking by comparing ROQ ratings between normal sleep and sleep deprivation. The result showed a marginal difference (*t* = -2.00, *p* = 0.057, Cohen's *d* = -0.409) between normal sleep and sleep deprivation conditions.

Cooperation Performance Affecting by Sleep Deprivation

Repeated measures analysis of variance revealed that a significant main effect between different cooperative tasks (*F* = 20.1, *p* < 0.001, partial η^2 = 44.0%). Participants

chose to cooperate at a higher rate in the CD task than in the PD task, regardless of sleep state. The main effect of sleep state was also significant (*F* = 4.93, *p* = 0.037, partial η^2 = 17.7%), and there was a significant interaction effect (*F* = 6.99, *p* = 0.014, partial η^2 = 23.3%). A post hoc comparison revealed that the rate of cooperation decreased after sleep deprivation in the CD tasks (*t* = 3.438, *p* = 0.007) but not in the PD tasks (*t* = -0.279, *p* = 0.992, Table 2, Figure 3).

Correlations Analysis Between Cooperation and Objective/Subjective Indicators

To clarify the processes underlying different cooperative tasks after normal sleep and sleep deprivation, we analyzed the relationship between the change of cooperative tasks and objective alertness (PVT performance), as well as with subjective ratings (subjective sleepiness, positive/negative affect, and risk preference). However, the analysis did not reveal any significant correlation (Table 2).

Discussion

The present study investigated whether sleep deprivation affects cooperative behavior in two social dilemmas, the PD and CD. In line with previous studies, the CD had a higher level of cooperation than the PD. Moreover, sleep deprivation decreased the cooperation rate in the CD task but not the PD task, and the impairment of cooperation in CD by sleep deprivation was not associated with differences of objective alertness, subjective fatigue, mood, or risk-seeking between normal sleep and sleep deprivation.

In the two classic social dilemmas, an individual makes the decision based on his/her own will and the other's choice. Generally speaking, in the PD task, people may have an optimal strategy, which is defection regardless of the other's choice, to ensure stable payoff for himself/

Table 2 Correlations Between Cooperation Changes and Indicators' Changes

			Indicators (Normal Sleep vs Sleep Deprivation)					
			Number of Lapses	1/Mean RT	Sleepiness	PANAS (P)	PANAS (N)	ROQ Ratings
Cooperation (normal sleep vs sleep deprivation)	PD	<i>r</i>	-0.008	-0.067	0.291	0.028	-0.014	0.326
		<i>p</i>	0.972	0.755	0.167	0.895	0.587	0.119
	CD	<i>r</i>	0.057	0.260	0.373	0.075	-0.062	0.002
		<i>p</i>	0.793	0.221	0.073	0.732	0.770	0.992

Abbreviations: CD, chicken dilemma; PANAS, Positive and Negative Affect Schedule; PD, prisoner's dilemma; ROQ, Risk Orientation Questionnaire; RT, response time.

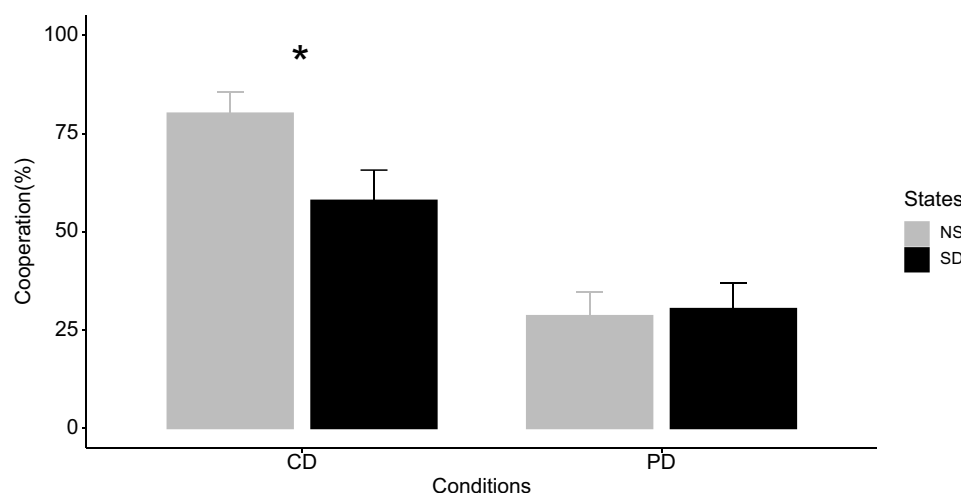


Figure 3 Cooperation rates for CD and PD under normal sleep and sleep deprivation condition.

Note: * $p=0.007$.

Abbreviations: CD, chicken dilemma; PD, prisoner's dilemma.

herself. However, in the CD task, there is no such strategy to keep stable payoff if one only considers his/her own interests and ignore the other's choice.⁶ In this way, it is reasonable for people to choose cooperation in the CD task more than in the PD task, which is in line with the current results. In addition, the rate of cooperation did not change much in the PD task but decreased significantly in the CD task after sleep deprivation. It seems that sleep deprivation did not alter the rate of defection much in the PD game, but it decreased cooperative behavior in the CD game. In addition, the CD game involves greater risk (more is at stake and more can be won or lost), compared to the PD game that is either a win or nothing. That is, it seems that sleep deprivation has a greater effect when the stakes are higher.

The influence of sleep deprivation on human cooperation may be related to several factors. First, decreased cooperative behavior may result from enhanced risk-seeking.^{5,9,10,36} In the current study, we tested the level of risk-seeking with the ROQ and found only marginal differences between the normal sleep and sleep deprivation conditions. Some studies demonstrated that acute sleep-deprived individuals are more sensitive to gain and less sensitive to loss, compared with the well-rested condition,^{37,38} which might be explained by elevated risk propensity and attenuated risk aversion after sleep loss.^{27–29} However, other evidence indicated that risky decision-making did not affect by sleep loss robustly.^{39–42} These inconsistent findings may indicate that risk-seeking is not strongly impaired by sleep deprivation and helps to explain why the change in risk-seeking did not correlate

with differences in cooperation rates in the PD and CD tasks between normal sleep and sleep deprivation. Second, numerous studies have indicated that sleep deprivation decreases objective alertness and dramatically enhances subjective sleepiness.^{20–26} Low alertness and fatigue make it difficult to carefully process information, which may influence cooperative behavior. However, decreased alertness (the number lapses and reciprocal of mean reaction time of PVT) and increased sleepiness (KSS scores) were not significantly correlated with the change in the rates of cooperation in PD and CD tasks. Moreover, we also found that the differences in the two tasks between normal sleep and sleep deprivation were not affected by mood, although both negative and positive affect were significantly changed due to sleep insufficiency. This indicated that differences of objective and subjective indicators might not influence cooperation in the dilemmas after sleep deprivation.

Limitations and Future Directions

The present study demonstrated that sleep deprivation selectively impairs cooperative behaviors in social dilemmas, but the results should be considered in the context of several limitations. First, the sample size was relatively small. Individual differences in how people respond to sleep deprivation may partially explain why the present study did not uncover the influential factors (e.g., risk-seeking, objective alertness, subjective sleepiness, and mood), which may be related with the change in cooperation after sleep loss. Additionally, the time of day effect on objective performance and subjective ratings may also need more attention. Although

objective PVT performance significantly declined after sleep deprivation, subjective sleepiness was only marginally decreased. This may be related with the time when the measurements were taken. All the behavioral tasks and rating were performed at 15 pm in the afternoon. According to the two-process model of sleep regulation,^{43,44} individuals may perform worse in the afternoon even with enough sleep, as well as provide higher sleepiness ratings. This may explain why the KSS results were only marginally different after sleep deprivation. Correspondingly, this may also influence the correlation between sleepiness and cooperative behavior. Future studies need to recruit larger samples and consider different time points to further clarify how sleep deprivation affects cooperation.

Secondly, most of the variables we used to examine potential influences on cooperative behavior after sleep deprivation were subjective evaluations, such as questionnaires about risk-seeking, positive and negative mood, and sleepiness. Subjective measurements may not sufficiently reflect the status or performance of individuals after sleep deprivation. Specially, the ROQ applied in the current study was mainly used for measuring the stable propensity of risk, which may be not suitable to test state effects. This could explain the marginal state difference of risk-seeking between the normal sleep and sleep deprivation conditions. It is better to investigate impaired effects of risk-taking propensity after sleep deprivation by both self-report and behavioral measurement⁴⁵ and to consider assessing differences in other types of behavioral performance (e.g., trust propensity) to explore potential influences on cooperative behavior between normal sleep and sleep deprivation.

Thirdly, sensitivity of gain and loss is crucial for promoting cooperation in social dilemmas. Several studies have verified that sleep deprivation impairs human incentive processing, and neuroimaging evidence suggests that sleep loss causes diminished medial prefrontal cortex responses to gain outcomes and increased anterior insula responses to loss outcomes.^{12,46} Future studies may apply functional neuroimaging techniques to investigate if the change in cooperative behavior after sleep deprivation correlated with sensitivity of gain and loss.

Last but not least, the findings of the current study need further verification by actual face-to-face interactions in real-world contexts. We explicitly controlled potential confounders, such as face-to-face interactions and feedback after single trials, to try to reduce the effects of other factors. However, social interactions are very common and clearly interesting components in real-world life. Future study is

needed to explore the effects of sleep loss on social behavior with better ecological approaches.

Conclusion

The present study suggested that sleep deprivation selectively impairs cooperative behavior, demonstrated by the decreased rate of cooperation in the CD but not in the PD after sleep loss. In addition, the differences of cooperation between normal sleep and sleep deprivation in the CD game were not correlated with changes in objective alertness, subjective sleepiness, negative affect, or risk preference. Unfortunately, the current study did not uncover the mechanism by which sleep deprivation affects people's cooperation, but it may help rule out several possible factors (e.g., risk-seeking level, alertness, sleepiness, and mood). Future investigations should recruit larger sample with better ecological approaches to verify the current findings with other potential mediators affecting cooperation (e.g., trustworthiness, sensitivity of gain and loss) and use neuroimaging techniques to further explore human cooperative behaviors after sleep loss.

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Author Contributions

All authors contributed to design of the study, data analysis, drafting or revising the article, gave final approval of the version to be published, and agree to be accountable for all aspects of the work.

Disclosure

The authors report no conflicts of interest in this work.

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