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ORIGINAL ARTICLE

The importance of working memory updating in the Prisoner's dilemma

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Abstract Successful cooperation requires that humans can flexibly adjust choices to their partner's behaviour. This, in turn, presupposes a representation of a partner's past decisions in working memory. The aim of the current study was to investigate the role of working memory processes in cooperation. For that purpose, we tested the effects of working memory updating (Experiment 1) and working memory maintenance demands (Experiments 2 and 3) on cooperative behaviour in the Prisoner's dilemma game. We found that demands on updating, but not maintenance, of working memory contents impaired strategy use in the Prisoner's dilemma. Thus, our data show that updating a partner's past behaviour in working memory represents an important precondition for strategy use in cooperation.

Introduction

Evolutionary accounts of altruism assume that the existence of social cooperation in human primates presupposes the evolution of specific cognitive abilities. Among others, it is necessary that humans can reliably discriminate between cooperative partners and selfish free-riders to protect themselves from being exploited (Axelrod & Hamilton, 1981; Trivers, 1971). An effective strategy to avoid exploitation by free-riders is to use a tit-for-tat strategy: an individual should reciprocate cooperation only if her partner cooperates, whereas she should defect if being confronted with a defective partner. Although a large number of theoretical and empirical studies examined strategic decision-making in social cooperation (Axelrod & Hamilton, 1981; Nowak & Sigmund, 1993a, b; Trivers, 1971), it remains unclear which cognitive abilities are involved in strategic decision-making in social interactions. Because playing tit-for-tat requires representing the interaction partner's last choice in order to adjust one's own strategy to it, it is reasonable to assume that working memory processes are involved in social cooperation. The goal of the current study was to provide evidence for the importance of working memory processes in cooperative behaviour.

In game theory, social cooperation is often examined by analysing behaviour in the Prisoner's dilemma game (PDG): In the PDG, a player A chooses whether to either cooperate (C) or defect (D) with a second player B. The payoffs in the PDG are arranged such that, independently of player B's decision, player A can maximise her outcome if she defects: If player B cooperates, then player A's outcome is higher if she defects, too (unreciprocated defection; DC), compared if she cooperates (mutual cooperation; CC). Importantly, also in the case that player B defects, player A's payoff is higher if she defects (mutual defection; DD) compared to if she cooperates (unreciprocated cooperation; CD). As a consequence of this arrangement of payoffs, mutual defection is the Nash-equilibrium in the PDG because changing the strategy (i.e., starting to cooperate) leads to worse outcomes under the condition that the partner continues with defection. Importantly, however, both partners' payoff would be higher in the case of mutual cooperation compared to mutual defection (i.e., CC is pareto-superior). If the PDG is played iteratively, this discrepancy

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between the Nash-equilibrium (mutual defection) and the pareto-superior solution (mutual cooperation) results in the following dilemma: on the one hand, cooperation leads to the better long-term outcome than defection because CC > DD. On the other hand, mutual cooperation is no stable solution of the dilemma (no Nash-equilibrium) because DC > CC. The use of a tit-for-tat strategy allows resolving this dilemma (Axelrod & Hamilton, 1981; Trivers, 1971): a player should start cooperating if her partner has cooperated in the preceding round in order to establish mutual cooperation. However, if a partner has defected in the previous round, then a player should respond with defection to avoid being exploited by a free-rider.

From a cognitive perspective, playing tit-for-tat in the PDG requires working memory (WM) processes: a player must encode the partner's last decision in WM in order to be able to adjust her own decisions accordingly. In line with this assumption, a previous study showed memory demands to impair strategic decision-making in the PDG (Milinski & Wedekind, 1998): while playing the PDG, participants performed a supplementary memory task in which they should search for identical pairs among a set of 32 cards. After each PDG choice, participants uncovered two cards: if these were identical, they were removed from the set of cards; if they showed different pictures, they were returned. Importantly, this memory task required dissociable different memory processes, namely the updating as well as the maintenance of WM contents (Braver et al., 1997; Morris & Jones, 1990). While WM updating processes include monitoring for task-relevant new information and replacing old, irrelevant WM contents with new, relevant ones (e.g., the motives of the currently uncovered cards), demands on WM maintenance are dependent upon the number of items which are currently stored in WM (e.g., the motives of all cards that had been uncovered in previous rounds). Consequently, it remains an open question whether the observed impaired strategy use in the PDG was caused by demands on WM updating or on WM maintenance. Moreover, since PDG performance in the memory group was compared with a control group playing only the PDG, it is also possible that not WM processes per se but the demands of performing two tasks simultaneously (the PDG and the memory task) are responsible for the observed effects.

The current study addressed this issue and tested how WM updating, WM maintenance, and dual-task processing demands affect decision-making in the PDG. Similar to the study of Milinski and Wedekind (1998), we applied a dual-task approach in which participants played the PDG and simultaneously performed a WM task exposing selective demands on updating or maintenance processes. Subjects played the PDG against a computer partner which used a tit-for-tat strategy (see below for details), allowing us to test how participants strategically adjust their choices to the partner's behaviour in an experimentally controlled way. Although subjects appear to show quite similar behaviour when playing the PDG against a computer or a human partner (Rilling et al., 2002), we are aware that playing the PDG with a human partner may involve further social processes which cannot be measured with a computer-variant of the PDG. However, both real "social" and computer-based PDGs require adjusting one's own strategy to the partner's behaviour, such that the current paradigm allowed us to assess the impact of WM demands on strategic decision-making in the PDG in general.

Experiment 1 examined the effects of WM updating and dual-task processing on the PDG, whereas Experiments 2 and 3 tested whether high demands on WM maintenance impair strategy use in the PDG.

Experiment 1

Experiment 1 tested the involvement of WM updating processes in cooperation in the PDG. For that purpose, participants played an iterative PDG and, simultaneously, performed a variant of the *n*-back task in which a stream of letters was sequentially presented to the participants. The *n*-back task allows manipulating the demands on the updating and monitoring of WM contents in an experimentally controlled way (Braver et al., 1997). We administered the *n*-back task in two difficulty levels: While in the 1-back condition, participants should decide whether the currently presented letter is identical with the letter presented in the previous trial, they were instructed to respond only to a pre-defined letter in the 0-back condition, without the need to update WM contents on every trial. While only the 1-back condition required updating WM contents, both the 0-back and the 1-back task required maintaining one item in WM (i.e., the pre-defined target latter in case of the 0-back condition and the lastly presented letter in the 1-back condition). Thus, the *n*-back task allowed us to manipulate updating demands while controlling for load on WM maintenance. We hypothesized that, if playing tit-for-tat requires WM updating in order to adjust one's decisions to the partner's behaviour, then the demands of the 1-back task on updating should impair participants' ability to use a tit-for-tat strategy. In particular, we expected that participants use a tit-for-tat strategy less often in the 1-back relative than in the 0-back condition.

In addition, we administered also a control condition in which participants played the PDG without a supplementary *n*-back task. This manipulation allowed us to test for effects of dual-task processing on the PDG: if the demands of performing two tasks simultaneously interfere with strategy use in the PDG, then this should result in different PDG choices between the control and the 1-back condition.

Methods

Participants

Nineteen right-handed volunteers (14 female; $M_{\text{age}} = 23.7$, $\text{SD}_{\text{age}} = 4.6$) who were recruited at the Humboldt-Universität participated in Experiment 1 after having given informed consent. All participants were naïve to the purpose of the study and were paid 8 euro per hour plus a performance-dependent bonus (see below).

Experimental design and procedure

Participants performed two tasks simultaneously: an iterated PDG and an *n*-back task. In the PDG, participants should choose between cooperating and defecting with a virtual opponent. As cover story, we told participants that, for organisational reasons, they would play the PDG against a computer instead of a human partner, and asked them to make their decisions as if playing against a human partner. We also stressed that the computer would simulate the behaviour of real partners and that the computer's decisions to cooperate or defect would partly depend on their own choices, as is the case for human partners (however, no details about the algorithms used by the computer were specified). In fact, the computer played a tit-for-tat strategy and cooperated or defected with a probability of 80 % depending on whether the player had cooperated or defected, respectively, in the preceding trial (Rilling et al., 2002; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004a). We used the following payoff matrix: Participants received two cent in case of mutual cooperation (CC), whereas they lost one cent in case of unreciprocated cooperation (CD). Mutual defection (DD) and unreciprocated defection (DC) were rewarded with zero and three cent, respectively. We informed participants that they would receive the cumulated outcomes in addition to their basic payment.

The second task was a letter-version of the *n*-back paradigm in which white letters were presented on the screen centre between two rounds of the PDG (Braver et al., 1997; Soutschek, Strobach, & Schubert, 2013).We used phonologically similar letters in German (B, D, P, T, and W) to increase task difficulty. In the 0-back condition, we instructed participants to press the left shift-key with the left index finger if a specific, pre-defined letter (e.g., B) was presented. The target letter in the 0-back condition was defined in the instruction before the start of a 0-back block. In the 1-back condition, participants should respond only if the currently presented letter was identical with the letter presented in the preceding trial (e.g., if the letter "D" was presented in two subsequent trials). Thus, while both the 0-back and the 1-back condition required the maintenance of one item in WM, only the 1-back task demanded, in addition, WM updating processes.

On each trial, subjects performed first the *n*-back task and then played one round of the PDG. Every trial started with the presentation of a letter for the *n*-back task for 1000 ms, followed by a fixation cross (1500 ms). If the *n*-back letter was a target stimulus, then the response had to be executed while the letter or the fixation cross was presented. Next, participants were asked whether they would like to cooperate or to defect in the PDG (1500 ms). During this interval, participants should indicate their decision by pressing the keys "N" (for cooperation) or "M" (for defection) with the right index or middle finger, respectively, on a QWERTZ keyboard. After an interval of 500 ms, participants received a visual feedback on their own and their opponent's outcome in the current trial (1000 ms). Following an inter-trial interval of 500 ms, the next trial started, again with the presentation of a letter for the *n*-back task (Fig. 1).

The experimental design included three different task conditions: control, 0-back, and 1-back condition. In the control condition, participants were instructed to play only the PDG and to ignore the letters presented for the *n*-back task. In contrast to that, we advised participants to play the PDG and to perform also the 0-back or the 1-back task in the 0-back or the 1-back condition, respectively. Three blocks were administered for every task condition, resulting in a total of nine blocks which were presented in randomised order. Every block contained a total of 15 trials. In the 0-back and 1-back conditions, three target stimuli were presented per block.

Statistical analysis

We analysed cooperation rates (i.e., number of cooperation decisions/number of cooperation and defection decisions) in the PDG and hit rates (number of correctly detected targets/number of targets) in the *n*-back task. For tests of significance, we calculated ANOVAs and planned comparisons with a significance threshold of 5 %.

Results

PDG

We analysed cooperation rates in the PDG with a repeated-measures ANOVA including the factors Previous decision (partner cooperated vs. partner defected) and *n*-back (control vs. 0-back vs. 1-back). While the factors Previous decision and *n*-back showed no significant effects, $F(1,18)\text{s} < 3.06$, $p\text{s} > 0.098$, $\eta_p^2\ \text{s} < 0.145$, we found a significant Previous decision × *n*-back interaction, $F(1,18) = 3.30$, $p < 0.05$, $\eta_p^2 = 0.155$, suggesting that participants' responses to the behaviour of their partners

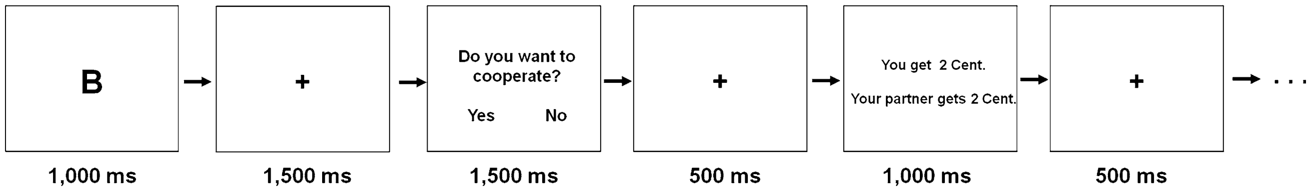
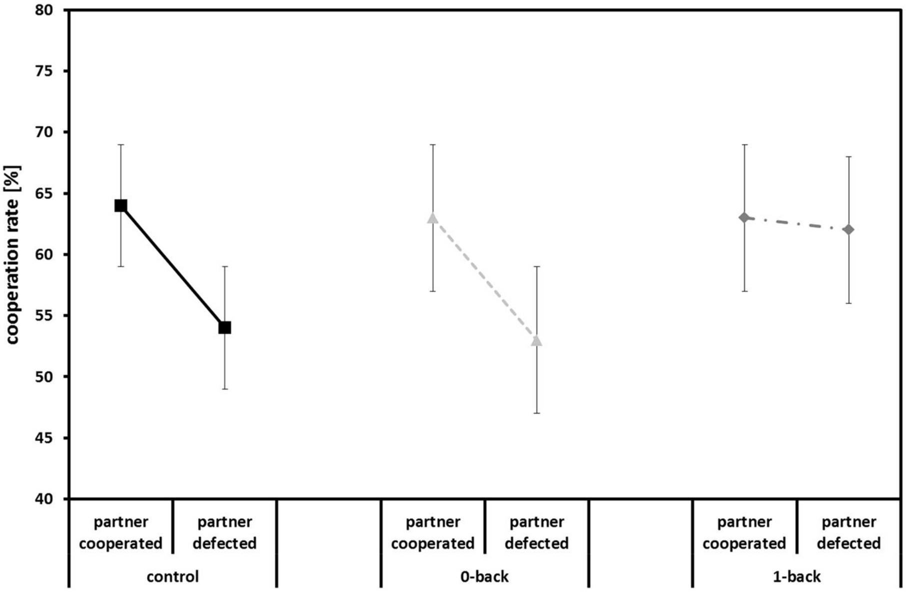


Fig. 1 Example trials of the Prisoner's dilemma game (PDG) and the *n*-back task of Experiment 1: on each trial, first a letter for the *n*-back task was presented. Then, participants were asked whether they would like to cooperate or to defect. Finally, participants received a feedback regarding their own and their partner's outcome before the next trials started with the presentation of the next *n*-back stimulus

Fig. 2 Cooperation rates (%) in Experiment 1, plotted as a function of Previous decision (partner cooperated vs. partner defected) and *n*-back condition (control vs. 0-back vs. 1-back). *Error bars* indicate standard error of mean



differed between the *n*-back conditions. To examine this effect in more detail, we tested whether participants played tit-for-tat, i.e. cooperated more often when the partner had cooperated vs. defected in the preceding trial, in the different *n*-back conditions. We found higher cooperation rates when the partner had cooperated compared to when the partner had defected in the control and the 0-back condition, $t(18)$s > 2.17, ps < 0.05, but not in the 1-back condition, $t < 1$, $p > 0.87$. This suggests that participants adjusted their decisions to their partner's behaviour (i.e., played tit-for-tat) in the control and the 0-back but not in the 1-back condition. While cooperation rates did not differ between the *n*-back conditions when the partner had defected in the preceding round, ts < 1, ps > 0.52, cooperation rates were significantly higher in the 1-back condition than in the control and the 0-back condition when the partner had defected in the preceding round, $t(18)$s > 2.10, ps < 0.05 (Fig. 2).

N-back task

We compared hit rates (i.e., correct responses to *n*-back targets) with a paired-samples *t* test. We found a significantly reduced *n*-back performance in the 1-back (77 %) compared to the 0-back (88 %) condition, $t(18) > 2.10$, $p < 0.05$.

Discussion

The aim of Experiment 1 was to test the role of WM updating in the PDG. We found that no tit-for-tat strategy was used in the PDG when participants simultaneously performed the 1-back task, whereas participants played tit-for-tat in the control and the 0-back condition. Since playing tit-for-tat is considered to be an effective strategy in the PDG (Axelrod & Hamilton, 1981), these results show that WM updating is an important cognitive precondition for successful cooperation. Cooperation requires the ability to flexibly adjust one's behaviour to the partner's decision in order to avoid being exploited by free-riders. Our data suggest that the flexible adjustment of behaviour, in turn, presupposes the updating of the partner's last decision in WM.

In addition, the results of Experiment 1 provide no evidence for an effect of dual-task processing demands per se on choices in the PDG because no significant differences occurred between the control and the 0-back condition. This suggests that the demands on WM updating, and not on dual-task processing per se, impaired the use of tit-for-tat strategies in the 1-back condition. We would like to note that the comparison between the control condition and the 0-back condition does not allow drawing conclusions regarding the impact of WM maintenance demands on the PDG because the maintenance demands in the 0-back condition (maintain the target letter in WM) are confounded with task-switching processes (switching between PDG and 0-back task). Therefore, we conducted a further experiment in order to test the impact of WM maintenance demands on choices in the PDG.

Experiment 2

Experiment 2 examined whether demands on WM maintenance affect decision-making in the PDG. Participants played the PDG together with a memory task which required maintaining either one or six items in WM (Soutschek et al., 2013). We presented participants one or six numbers before the start of a PDG block and they should reproduce the numbers after the block. Thus, this memory task required only the maintenance but not the updating of WM contents during the PDG, allowing us to test whether high demands on WM maintenance, similar to demands on WM updating, interfere with playing tit-for-tat in the PDG. We would like to note that maintaining items in WM may involve some kind of "refreshing" process which directs attention to the items stored in WM (Vergauwe & Cowan, 2014). Such a "refreshing" of contents stored in WM may, at a first glance, appear to be conceptually similar to the updating WM of contents However, while updating involves monitoring for new relevant information and replacing old (irrelevant) WM contents with new relevant ones, "refreshing" only operates on items already maintained in WM. Thus, contrary to the *n*-back task in Experiment, the memory task of Experiment 2 did not require WM updating processes.

Methods

Participants

Fifteen right-handed volunteers (8 female; $M_{\text{age}} = 26.7$, $\text{SD}_{\text{age}} = 3.5$) who were recruited at the Humboldt-University took part in Experiment 2. All volunteers were naïve to the purpose of the study and gave informed consent before participating. Importantly, we recruited only subjects who had not taken part in Experiment 1. We paid them 8 euro per hour plus a performance-dependent bonus.

Experimental design and procedure

Participants played the PDG in the same way as in Experiment 1. In addition, they performed a WM task in which they had to memorize either one digit (low load condition) or six digits (high load condition) between zero and nine at the start of each PDG block; the numbers were presented for 5,000 ms. At the end of a block, i.e., after seven rounds of the PDG, participants had to enter these numbers on the keyboard (without time limit).

Participants performed seven blocks of the low load and seven blocks of the high load condition in randomised order.

Statistical analysis

Performance in the PDG was analysed in the same way as in Experiment 1. In the WM task, we analysed the percentage of correctly reproduced numbers in the low load and the high load condition. In the high load condition, an answer was considered as correct only if all digits were reproduced in the correct order.

Results

PDG

Cooperation rates were analysed by an ANOVA including the factors Previous decision (partner cooperated vs. partner defected) and WM load (low load vs. high load). The significant main effect of Previous decision, $F(1,14) = 7.64$, $p < 0.05$, $\eta_p^2 = 0.353$, indicated that cooperation rates were higher when the partner had cooperated (74 %) compared to when the partner had defected (54 %) in the preceding trial; hence, participants used a tit-for-tat strategy. Planned comparisons revealed that participants played tit-for-tat both in the low load and the high load condition, $ts(14) > 2.14$, $ps < 0.05$. Neither the factor WM load alone nor the Previous decision × WM load interaction yielded a significant result, $F(1,14)\text{s} < 1.11$, $ps > 0.31$, $\eta_p^2\text{ s} < 0.073$ (Fig. 3).

WM task

A paired-samples *t* test showed that the correct number was reproduced more often in the low load (95 %) than in the high load (84 %) condition, $t(14) = 4.00$, $p < 0.01$.

Discussion

Experiment 2 provided no evidence for an effect of high WM maintenance demands on cooperation in the PDG because participants used a tit-for-tat strategy both in the low load and

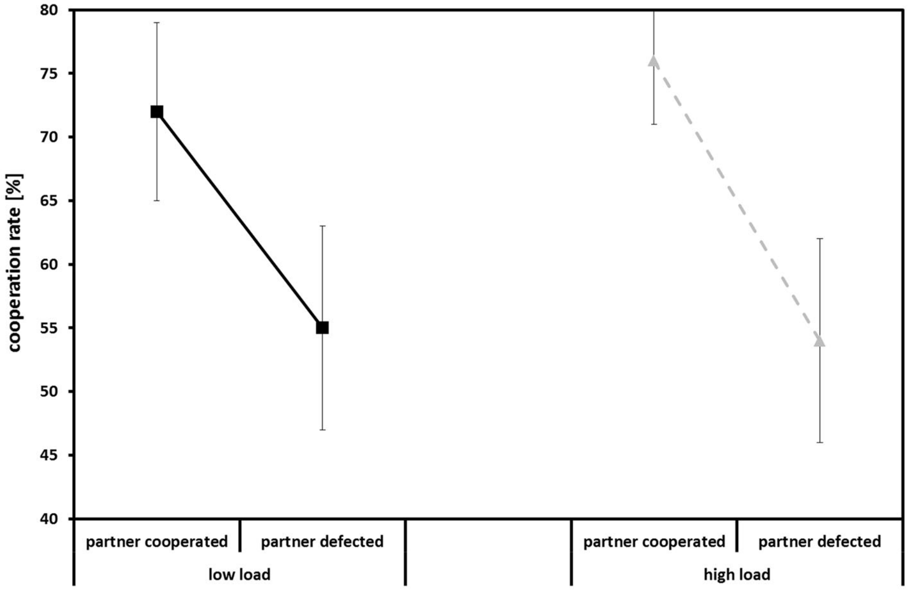


Fig. 3 Cooperation rates (%) in Experiment 2, plotted as a function of Previous decision (partner cooperated vs. partner defected) and WM load (low load vs. high load). *Error bars* indicate standard error of mean

the high load condition. Importantly, the finding that more errors occurred (i.e., less numbers were correctly reproduced) in the high load compared to the low load condition of the WM task indicates that demands on WM maintenance were higher in the high load than in the low load condition, showing the effectiveness of the WM load manipulation. Taken together, the results of Experiment 2 suggest that, contrary to WM updating, the maintenance of WM contents per se does not interfere with playing tit-for-tat in the PDG. This is in line with previous findings showing WM capacity to be uncorrelated with flexible strategic decision-making (Schunn, Lovett, & Reder, 2001).

Against our conclusion that maintenance demands have no effect on the use of tit-for-tat strategies, one may argue that the demands of the maintenance task were not sufficiently high in order to interfere with maintenance processes in the PDG. This is because WM storage capacity is thought to allow the maintenance of seven items simultaneously in WM (Miller, 1956), whereas the high load condition of our WM task required the maintenance of only six items. To rule out this potential counterargument, we conducted a third experiment in which we tested the impact of even more extreme maintenance demands on decision-making in the PDG.

Experiment 3

In Experiment 3, participants played the PDG and simultaneously performed a WM task requiring the maintenance of ten numbers in WM. This allowed us to test the effect of even more extreme WM maintenance demands than in Experiment 2 on strategic decision-making in the PDG.

Methods

Participants

We recruited eighteen right-handed volunteers (11 female; $M_{\text{age}} = 24.8$, $\text{SD}_{\text{age}} = 4.5$) who were naïve to the purpose of the study and had not taken part in Experiment 1 or Experiment 2. All volunteers gave informed consent before participating in the study. We paid them 8 euro per hour plus a performance-dependent bonus.

Experimental design and procedure

Participants played the PDG and performed a WM task similar as in Experiment 2. However, in the high load condition of the WM task, participants had to memorize and recall ten numbers (instead of six, as in Experiment 2). The numbers were presented for 20 s before the start of a block.

Participants performed ten blocks of the low load and ten blocks of the high load condition in randomised order.

Statistical analysis

Performance in the PDG and the WM task was analysed in the same way as in Experiment 2.

Results

PDG

Cooperation rates were analysed by an ANOVA including the factors Previous decision (partner cooperated vs. partner defected) and WM load (low load vs. high load). The significant main effect of Previous decision, $F(1,17) = 11.01, p < 0.01$,

$\eta_p^2 = 0.393$, indicated that participants used a tit-for-tat strategy because cooperation rates were higher when the partner had cooperated (72 %) compared to when the partner had defected (54 %) in the preceding trial. Planned comparisons revealed that participants played tit-for-tat both in the low load and the high load condition, ts(17) > 2.80, ps < 0.05. Importantly, the Previous decision × WM load interaction was not significant, F(1,14)s < 1.11, ps > 0.31, $\eta_p^2 = 0.027$ (Fig. 4), providing no evidence for an effect of WM maintenance demands on behaviour in the PDG.

One potential counterargument requires to be addressed: one may argue that in blocks in which participants solved the high load task correctly, they had sufficient WM capacities available both to perform the WM maintenance task (e.g., by using an efficient chunking strategy) and to play tit-for-tat in the PDG. Therefore, we tested whether participants played tit-for-tat both in those blocks in which they solved the high load task correctly and in those in which participants failed to reproduce the numbers in the correct order (suggesting that these blocks may have been too demanding for their WM capacities). Importantly, we found that participants played tit-for-tat both in correct, $t(17) = 2.20$, $p < 0.05$, as well as in incorrect high load blocks, $t(17) = 2.66$, $p < 0.05$, with no significant difference occurring between these conditions, $t < 1$. Thus, participants were able to use a tit-for-tat strategy even in blocks in which they did not manage to maintain all ten numbers in WM.

WM task

A paired-samples t test showed that the number of correctly reproduced items was significantly reduced in the high load (59 %) compared to the low load (98 %) condition, $t(17) = 7.62$, $p < 0.001$.

Discussion

Experiment 3 confirmed the results of Experiment 2: participants applied tit-for-tat strategies even under very high demands on WM maintenance processes, providing no evidence for an impact of high WM load on cooperation in the PDG. Note that participants managed to correctly recall the ten numbers in the high WM load condition only in 59 % of all blocks, suggesting that the demands of the high load WM task were close to maximum WM capacity. Thus, the data suggest that even high demands on WM maintenance, contrary to WM updating demands, do not interfere with the use of tit-for-tat strategies in the PDG.

Between-experiment analysis

While the results of Experiment 1 suggested that WM updating demands interfere with the use of tit-for-tat strategies in the PDG, the results of Experiments 2 and 3 showed no evidence for an effect of WM maintenance demands on behaviour in the PDG. To provide conclusive support for such dissociable effects of updating versus maintenance demands, we conducted a between-experiment ANOVA on cooperation rates including the within-subject factors Previous decision (partner cooperated vs. partner defected) and WM load (low load vs. high load) as well as the between-subject factor Experiment (Experiments 1 vs. 2 vs. 3). As low load and high load conditions, we used the 0-back and 1-back conditions of Experiment 1 and the low load and high load

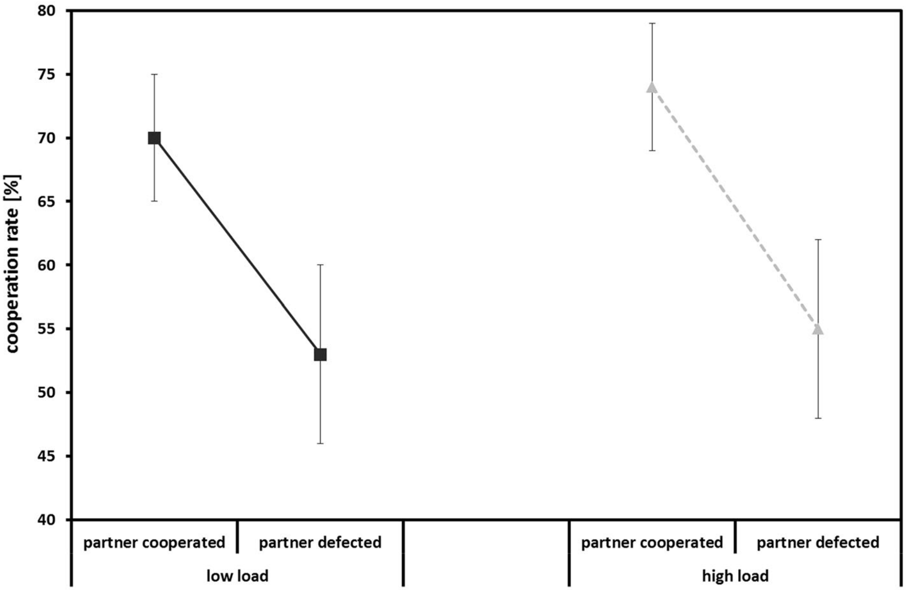


Fig. 4 Cooperation rates (%) in Experiment 3, plotted as a function of Previous decision (partner cooperated vs. partner defected) and WM load (low load vs. high load). *Error bars* indicate standard error of mean

conditions of Experiments 2 and 3. This allowed us to test whether the manipulation of updating demands in Experiment 1 and the manipulation of WM maintenance in the Experiments 2 and 3 demands have dissociable effects on choices in the PDG. The main effect of Previous decision, $F(1,49) = 19.90$, $p < 0.001$, $\eta_p^2 = 0.289$, replicated the finding that cooperation rates were higher when the partner had cooperated compared to when the partner had defected in the preceding trial, i.e. participants used a tit-for-tat strategy. Importantly, we also found a significant experiment × WM load × Previous decision interaction, $F(2,49) = 3.24$, $p < 0.05$, $\eta_p^2 = 0.117$: This suggests that, in line with the single experiment analyses, WM demands had dissociable effects on the use of tit-for-tat strategies in the different experiments. In fact, when comparing the use of tit-for-tat strategies (cooperation rate after partner's cooperation/cooperation rate after partner's defection) between the experiments, we found no significant differences between the three experiments in the low load condition, $t\text{s} < 1$. In the high load condition, however, participants applied a tit-for-tat strategy significantly less frequently in Experiment 1 than in Experiments 2 and 3, both $t\text{s} > 2.544$, $p\text{s} < 0.05$. This confirms the hypothesis that updating demands interfere with the use of a tit-for-tat strategy in the PDG relative to WM maintenance demands.

General discussion

The goal of the current study was to examine the importance of WM processes for cooperative behaviour in the PDG. Our findings show that demands on WM updating, but not WM maintenance, impair the use of tit-for-tat strategies. In particular, we found that participants used no tit-for-tat strategy if they simultaneously had to perform a 1-back task exposing demands on WM updating processes. In contrast to that, participants played tit-for-tat (i.e., cooperated more often when the partner had cooperated vs. defected in the previous round) independently of the demands on WM maintenance. Note that the difficulty of the WM tasks per se cannot be the decisive factor for the observed effects because participants committed less error in the 1-back condition of Experiment 1 (77 %) than in the high load condition of Experiment 3 (59 %). This suggests that the high load condition of Experiment 3, in which we observed no effect on cooperation rates, was more demanding than the 1-back condition of Experiment 1.

The finding that the use of a tit-for-tat strategy was impaired when participants simultaneously were performing a task with WM updating demands indicates that updating processes play a crucial role in strategic decision-making in the PDG. In order to play tit-for-tat, it is necessary to form a WM representation of the partner's last choice; after every round of the PDG, this WM representation must be updated. The performance of a supplementary task with high demands on WM updating interferes with the monitoring of the partner's choices and, thus, impairs the ability to play tit-for-tat. WM updating belongs to the broader category of executive functions (Miyake et al., 2000). Thus, the current study contributes to the existing literature showing executive functions to be involved in decision-making in game-theoretic paradigms (De Neys, Novitskiy, Geeraerts, Ramautar, & Wagemans 2011; Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006; Soutschek & Schubert, 2014).

We would like to stress that the applied paradigm did not measure cooperative behaviour in a real "social situation" because participants played the PDG against a computer. However, irrespective of whether the PDG is played against a human or a computer partner, tit-for-tat strategies always require to represent and update the partner's last decision in WM. Therefore, we assume that the current findings can be extended also to social variants of the PDG.

The proposed role of WM updating in strategic decision-making in the PDG is supported also by neuroanatomical findings suggesting that WM updating and social cooperation are related to activity in the lateral prefrontal cortex (Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004b; Schumacher et al., 1996; Smith & Jonides, 1999). Since two tasks with overlapping neural correlates are likely to involve also common cognitive processes (Poldrack et al., 2011), these functional imaging results suggest a functional relationship between WM updating and social cooperation. The results of the current study confirm this prediction and suggest that the DLPFC activity observed during PDG performance may reflect WM updating processes.

Moreover, our data also support the assumption that WM updating processes are important for strategic decision-making in general. For example, WM updating has been shown to contribute to context-sensitive adjustments of cognitive control during conflict processing (Soutschek et al., 2013), to voluntary emotion regulation (Schmeichel, 2007), and to strategy use in mental arithmetic (Imbo, Duverne, & Lemaire, 2007). WM updating allows representing the current task context; this mental representation of the current situation enables humans to flexibly adjust the current strategy to changing environmental demands. Thus, the availability of WM updating capacities constrains flexible social and non-social behaviour.

In sum, the current study shows that demands on WM updating, but not WM maintenance, impair the use of tit-for-tat strategies in the PDG. Thus, it provides evidence for the importance of updating processes in strategic decision-making in the PDG. Interestingly, executive functions like updating are supposed to have developed relatively lately in phylogenesis (Barkley, 2001). Therefore, the current data are in line with the assumption that different levels of cognitive development correspond to different levels of cooperation (Brosnan, Salwiczek, & Bshary, 2010). Thus, in turn, may help us to understand why social cooperation among non-relatives occurs so rarely in the animal kingdom: only species with highly developed executive functions are able to use effective tit-for-tat strategies, which allow minimising the risk of being exploited by free-riders in social cooperation.

Conflict of interest The authors declare no conflicting financial interests.

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