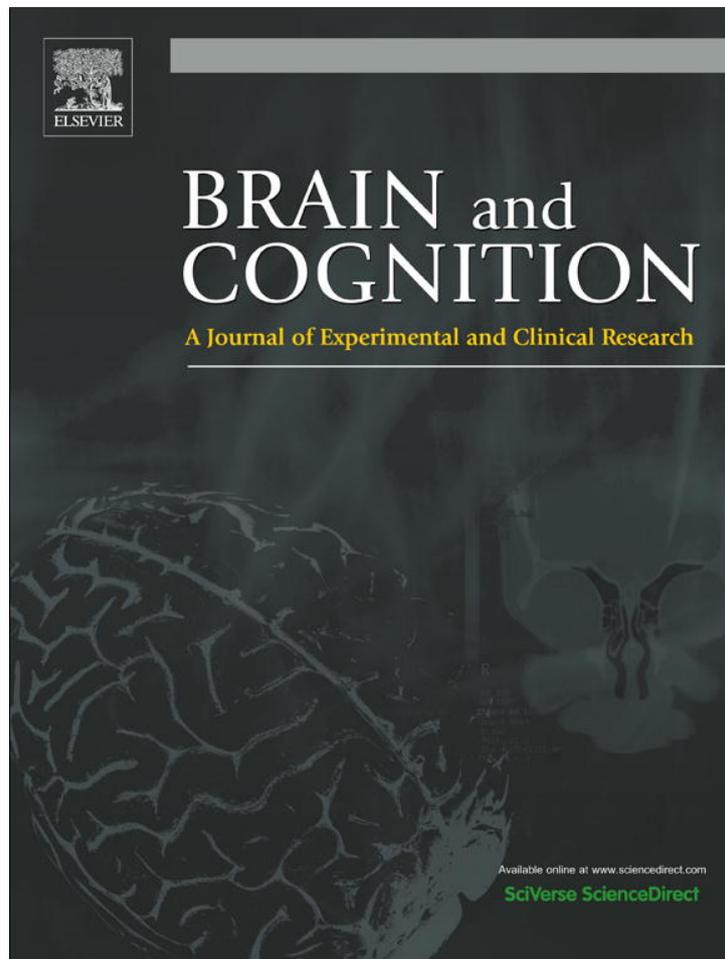


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/authorsrights>

Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

Neural correlates of Machiavellian strategies in a social dilemma task

Tamas Bereczkei^{a,*}, Anita Deak^a, Peter Papp^a, Gabor Perlaki^b, Gergely Orsi^b^a Institute of Psychology, University of Pécs, Hungary^b MTA-PTE Clinical Neuroscience MR Research Group, University of Pécs, Ifjúság u. 6., Pécs H-7624, Hungary

ARTICLE INFO

Article history:

Accepted 19 February 2013

Keywords:

Functional MRI

Trust Game

Manipulative behavior

Inferior and middle frontal gyrus

Thalamus

ABSTRACT

In spite of having deficits in various areas of social cognition, especially in mindreading, Machiavellian individuals are typically very successful in different tasks, including solving social dilemmas. We assume that a profound examination of neural structures associated with decision-making processes is needed to learn more about Machiavellians' abilities in exploiting other people. More specifically, we predicted that high-Mach people would show elevated activity in the brain areas involved in reward-seeking, anticipation of risky situations, and inference making. To test this hypothesis, we used an fMRI technique to examine individuals as they played the Trust Game. In accordance with our predictions, we found consistent activation in high-Machs' thalamus and anterior cingulate cortex (player 1), and dorsal anterior insula/inferior frontal gyrus (player 2). We suggest that Machiavellians conduct specific neural operations in social dilemma situations that make them successful in exploiting others. Machiavellians may have cognitive heuristics that enable them to make predictions about the future reward in a basically risky and unpredictable situation.

© 2013 Elsevier Inc. All rights reserved.

1. Introduction

Machiavellianism refers to interpersonal strategies that advocate self-interest, deception, and manipulation (Fehr, Samsom, & Paulhus, 1992; Jones & Paulhus, 2009). A person high in Mach is likely to exploit others and less likely to be concerned about other people beyond his or her own self-interest. It has been argued that advanced human computational power would be a necessary precondition for the ability to manipulate others (Byrne, 1995; Dunbar, 1998). Particularly, mindreading ability would be an important cognitive device for successful manipulation. This is because good mind readers – that is, people who can easily understand the others' intentions, beliefs and knowledge – are one step ahead of others and can mislead them more easily than those with poor mindreading ability. It appears that the manipulative behavior characteristic of Machiavellianism cannot work efficiently without the refined use of a theory of mind (ToM) (McIlwain, 2003; Repacholi, Slaughter, Pritchard, & Gibbs, 2003).

However, surprisingly, the first study did not find any relationship between Machiavellianism (measured on Mach-IV scale) and theory of mind (measured on a verbal comprehension test) (Paal & Bereczkei, 2007). Furthermore, later studies, using tests for ToM differences in comprehension of stories, in the eye region, and in facial expressions found a significant but negative relationship – that is, people having high scores on the Mach IV test proved

to be weak mindreaders (Ali & Chamorro-Premuzic, 2010; Lyons, Caldwell, & Shultz, 2010). Moreover, other studies have revealed that high-Machs show a lower level of empathy, less advanced emotional intelligence, and worse skill in understanding emotions than low-Machs (Austin, Farrelly, Black, & Moore, 2007; Barlow, Qualter, & Stylianou, 2010; McIlwain, 2003; Nettle & Liddle, 2008; Wastell & Booth, 2003).

Therefore, rather than having a superior understanding of others, Machiavellian individuals appear to have deficits in various areas of social cognition, especially in attributing mental states and emotions to others. Nevertheless, as a matter of fact, Machiavellians are smart; many studies have demonstrated that Machiavellians are very successful in various tasks, including social dilemma situations (Gunnthorsdottir, McCabe, & Smith, 2002). In experimental settings, high-Machs frequently outperform low-Machs, whether in bargaining and alliance forming or assuming leadership in group situations (Cherulnik, Way, Ames, & Hutto, 1981; Christie & Geis, 1970). A study using the Trust Game found that high-Mach people did not reciprocate the favor they received from their partner and gained a higher profit than low-Machs (Gunnthorsdottir et al., 2002). A more recent study found that high-Mach players in a modified Ultimatum game of 24 trials earned higher income by the end of the game than did low-Machs (Spitzer, Fischbacher, Herrnberger, Gron, and Fehr (2007)).

Recent evidence suggests that one of the crucial Machiavellian characters underlying successful adaptation to the social environment is flexibility. Machiavellian people are frequently described as rational, cold, impersonal, aloof, and practical; they can stay

* Corresponding author. Fax: +36 72 501516.

E-mail address: bereczkei.tamas@pte.hu (T. Bereczkei).

emotionally detached from a situation (Christie & Geis, 1970; Fehr, Samsom, & Paulhus, 1992). They can calmly identify the optimal strategy in each situation and behave in a self-interested way if it is to their advantage (Gunnthorsdottir et al., 2002). Because of this opportunism, they easily leave an alliance when it is advantageous for them, and are likely to steal from someone who trusts them (Christie & Geis, 1970; Harrell & Hartnagel, 1976; Wilson, Near, & Miller, 1998). A recent study using a modified Ultimatum game found a positive correlation between overall earnings and Machiavellian score. This finding appeared to result from the Machiavellians' flexible adaptation to the social context: they earned most in the non-punishing condition of the game, whereas they escaped punishment in the punishment condition (Spitzer et al., 2007).

As a means of flexibility, Machiavellians frequently conceal their intentions in order to achieve their goals (Wilson, Near, & Miller, 1996). In a recent study, subjects were asked to volunteer and offer a less and a more costly charity service in both public and anonymous conditions (Bereczkei, Birkas, & Kerekes, 2010). Subjects with high scores on Mach-IV were not likely to give assistance when they were not observed by the others but increased their help to others when their group members could observe their behavior. High-Mach persons seemed to give specific responses to different social circumstances: they disguised their selfishness and pretended altruism in the presence of others, but realized their self-interest when others could not observe their behavior.

Another recent study, using Public Goods Game, found that situational factors like the other players' behavior proved to be more predictive for the high Mach people's final payoff, compared to that of low-Machs (Czibor & Bereczkei, 2012). Machiavellians offered significantly less in every round and gained a higher profit by the end of the game than non-Machiavellians. Regression analyses have revealed that high-Machs track the previous movements of others and adjust their contributions to the behavior of their group mates. The authors concluded that Machiavellians are highly sensitive to signals in a social dilemma situation and capable of making flexible decisions. Therefore, they successfully exploit others in spite of their deficits in social cognition.

Now, the question is, what abilities and their neural correlates are involved in their behavior? In the present experiment we used an event-related fMRI paradigm during Trust Game for analyzing cooperative and non-cooperative strategies and the underlying brain areas. In this bargaining game, the first player (investor) has the chance of choosing a costly trusting action, that is transferring some of the money she/he possesses. Then the player 2 (trustee) is informed about the investor's action and can honor it by reciprocating a part of her/his payoffs. Trusting is always risky given the unpredictability of the intentions of the partner (player 2) in a social exchange. The decision to reciprocate, on the other hand, is dependent on evaluating consequences for the second player's personal outcomes and the others' previous behavior. Consequently, player 1 faces unpredictability and potential threat from the partner, whereas player 2 is expected to consider the norm of reciprocity.

Recently, several studies, using Trust Game, have demonstrated the neural correlates of the participants' responses to various conditions of social dilemma situations. One found that the breaking of the promise, that the participants made before playing, was associated with elevated activities in dorsolateral prefrontal cortex (dlPFC), anterior cingulate cortex, and amygdala (Baugmgartner, Fischbacher, Feierabend, Lutz, & Fehr, 2009). Another study have demonstrated ventromedial and dorsomedial PFC when the participants decided not to honor the partner's trust (Chang, Smith, Dufwenberg, & Sanfey, 2011). Different types of trust evoke different activity patterns: conditional trust (one's partner is self-interested) selectively activated the ventral tegmental area, whereas

unconditional trust (one's partner is trustworthy) activated the septal area (Krueger et al., 2007). Also individual differences in social value orientation were found to modulate activation in temporal-parietal-junction, bilateral anterior insula, and anterior cingulate cortex (van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2009).

We propose that an examination of neural structures associated with decision-making processes in a social dilemma task, such as Trust Game, is needed to learn more about the motives underlying the Machiavellians' behavior. We hypothesize that instead of having an advanced theory of mind, general intelligence, and emotional intelligence, Machiavellians have specific cognitive skills that allow them to evaluate the most important factors associated with the situation around them and other people's behavior. In the light of evidence, Machiavellians can change their tactics creatively and flexibly as the social games changes (Bereczkei et al., 2010; Christie & Geis, 1970; Czibor & Bereczkei, 2012; Spitzer et al., 2007). They are characterized by practical problem-solving, flexibility, and risk-taking (Jones & Paulhus, 2009).

We predict that Machiavellians as first players show an elevated activity in the brain regions associated with reward-seeking and anticipation of a risky situation involving a gain or a loss of money (thalamus, caudate nucleus). They may feel intense conflict between their long-term interest to obey the social norms and wish to desert the partner that is expected to activate anterior cingulate cortex. High-Machs as second players are expected to show increased activities in brain areas involved in making inferences and skills such as planning and mental flexibility (inferior and middle frontal gyrus).

2. Methods

2.1. Participants

Thirty right-handed healthy volunteers participated in the study. Three participants were excluded from the analysis after data collection due to motion artifacts, previous knowledge about the study and claustrophobia. The final sample included 27 participants, 13 males and 14 females aged between 19 and 30 (mean age: 23 years, standard deviation: 2.42 years). The participants were selected from a large sample of our previous studies ($N = 620$) on the basis of their scores on the Mach-IV scale. From this sample we retained extreme values below and above one standard deviation ($SD = 13.04$) of the mean score of 101.08. Individuals who obtained scores lower than 88 were defined as low Mach (LM) persons, whereas subjects who scored higher than 114 were defined as high-Mach (HM) persons. The LM group consisted of seven males and eight females, while the HM group was made up by six males and six females. No subject had any neurological, medical or psychiatric disorder.

2.2. The Trust Game

During fMRI scanning, participants were playing a Trust Game. In this game, a player (the Investor) must decide how much of his or her initial capital of 1000 HUF (about \$5) to transfer to a partner (Trustee). Once transferred, this money is tripled by the experimenter, and the Trustee will have the opportunity to return all, some, or none of the money to the Investor. From a purely economic point of view, the Investor's interest is not to trust in the partner and – consequently – transfer only a small amount of money. Similarly, the Trustee gains when he or she does not reciprocate but keeps the major part of the money for him- or herself (Fehr & Rockenbach, 2003).

Throughout the course of the game the participants were given continuous feedback about their partner's and their own transactions on the screen. Carrying out responses was made possible by the use of two-key MR-compatible response devices placed in their right and left hand.

2.3. Procedure and experimental design

Subjects were told that they would play several rounds of the Trust Game online with other individuals who were in a separate room. In fact, there were no real peers during the game: the other players' decisions were provided by a premade computer script. As it turned out from the postscanning debriefing, the participants had no doubts about the identity of their actual game partners. The computer script adjusted the amount of the return to the amounts offered by the player. We defined a $\pm 10\%$ range, and the computer randomly selected the answer (e.g. -3% ; -8% ; -10% ; 4% ; 5% ; 10%). When, for example, a subject as a first player offered 600 HUF, and if the computer used a 7% return rate, the subject received 642 HUF back.

Before scanning, the subjects played practice rounds of the Trust Game on a laptop computer, then were trained in how to use the response panel in the scanner to ensure that they understood the task and could respond within the allotted time. We explained to the participants that they could make their offers by using an adjustable scale shown on the screen. As the default position for each game round, the cursor was set randomly to any of the nine possible locations of the scale. Pressing the right response button, the cursor moved to the right increasing the amount to be transferred to the peer. Respectively, pressing the left button decreased the amount to offer. One press in either direction changed the offer with a fixed proportion. The left end of the scale represented 0 to offer, while the maximum amount appeared at the right end. The available amount of money in each round was equally divided between the different cutpoints of the scale. Every time the participant pressed a button in the second round as a Trustee, s/he received a visual feedback about the motor action: the cursor changed its position on the scale in colors, and the exact offer appeared in numbers.

Before entering the scanning room, written informed consent was acquired from each participant and all metallic objects were removed in accordance with MRI safety rules.

The whole procedure consisted of 48 rounds. Once in the magnet, participants saw an instruction slide for 15 s, then a black screen with a centered white fixation cross for 3 s in order to direct their attention to the upcoming event. 48 blocks (rounds) were presented next. We used two types of blocks: a Trust Game block and a control block. A Trust Game type block consisted of an 8-s trial (GAME) followed by an information screen for 15-s with a short description of actual balance of both players (FEEDBACK, ending with an additional 3-s black screen with the fixation cross). The round commenced with another 8-s trial (GAME) followed by an 18 (15 + 3)-s feedback screen with both players' final balance of the round (FEEDBACK). Therefore, each Trust Game round contains two different trials because participants make decisions either as first (Investor) or second player (Trustee). Across the total of 48 rounds participants were playing 12 times as the Investor, and 24 times as the Trustee. Participants took the two different roles randomly. The control condition consisted of 12 rounds lasting for 26 s each. One round consisted of an 8-s decision where participants were presented a number in letters between 100 and 900 (e.g. three hundred), and the cursor on the scale was required to be set to the appropriate unit (e.g. 300), and a 15-s black screen, with the centered white fixation cross appearing for another 3 s (15 + 3-s).

In sum, the time window spanning a total of 26 s comprises three different phases: 8 s of a game phase, during which the active

player considers the amount of money to transfer to his/her peer, 15 s of receiving feedback on the balances of both players after the transfer has been made, and 3 s of viewing a blank screen with a centrally presented white fixation cross. The actual decision window in our analyses was the 8 s-long period that the players used to make decisions on the amount of money to be transferred (game phase). Thus, we modeled the decision processes in this 8 s window and compared it to the related 8 s phase of the control condition (which involved the adjustment of the scale's cursor to the amount shown on the screen). The whole process is presented in Fig. 1.

In the post-scanning debriefing at the end of the experiment, we asked the participants about their experiences during the Trust Game, and paid them the amount of money they earned during the game.

2.4. Data acquisition and analysis

MRI data were acquired on a 3T scanner (TrioTim, Siemens Healthcare, Erlangen, Germany) at the Diagnostic Center of Pécs (Pécs, Hungary) equipped with a standard head-coil. Functional MRI was based on a gradient-echo EPI sequence (TR/TE = 2000/36 ms, flip angle 76°) with spatial resolution of $2.5 \times 2.5 \times 4$ mm (23 sections) in an axial orientation parallel with the AC-PC plane. Motion correction was performed as offered by the manufacturer.

Image processing was carried out using SPM5 (<http://www.fil.ion.ucl.ac.uk/spm>) implemented in MATLAB (Version 7.0.1.24704 [R14] Service Pack 1) (Mathworks Inc., Sherborn, MA). Images were corrected for motion, registered to the standard space at $2 \times 2 \times 2$ mm, and smoothed with a FWHM Gaussian kernel at 5 mm.

A first level analysis was computed subjectwise, using a general linear model with a hemodynamic response function modeling the GAME > CONTROL, AS FIRST PLAYER (INVESTOR) > CONTROL and AS SECOND PLAYER (TRUSTEE) > CONTROL conditions. For the analysis we used the 12 control rounds, the 12 Investor rounds, and 12 from the 24 Trustee rounds randomly-selected.

First-level contrasts of low-Mach and high-Mach groups were introduced to a two-sample *t* test at the second level. A voxelwise statistical significance of $p < 0.001$ (uncorrected) was applied.

2.5. Behavioral measures

We logged the output of players' decisions and calculated how much money they earned by the end of the game as an indicator of their success in the Trust Game. Additionally, we computed the mean offers as investor and as trustee.

SPSS 17.0 statistical software was used for analyzing the behavioral measures of the two groups by means of independent sample *t* test. We compared the Mach-IV scores, the amounts of money they transferred as a first player and as a second player, and their final profits they received after the Trust Game.

3. Results

3.1. Behavioral measures

Compared to low-Mach (LM) individuals, high-Machs (HM) transferred a smaller amount of money to the trustee ($t(25) = 3.29$, $p < 0.01$) ($M_{LM} = 548$ HUF, $SD_{LM} = 176.9$ HUF; $M_{HM} = 330$ HUF, $SD_{HM} = 163.82$ HUF) and, as second player, reciprocated less to the investor ($t(25) = 4.72$, $p < 0.001$) ($M_{LM} = 229$ HUF, $SD_{LM} = 43.44$ HUF; $M_{HM} = 153$ HUF, $SD_{HM} = 40.5$ HUF). High-Mach people gained a significantly higher profit at the end of the game than low-Machs (LM) ($t(25) = -4.59$,

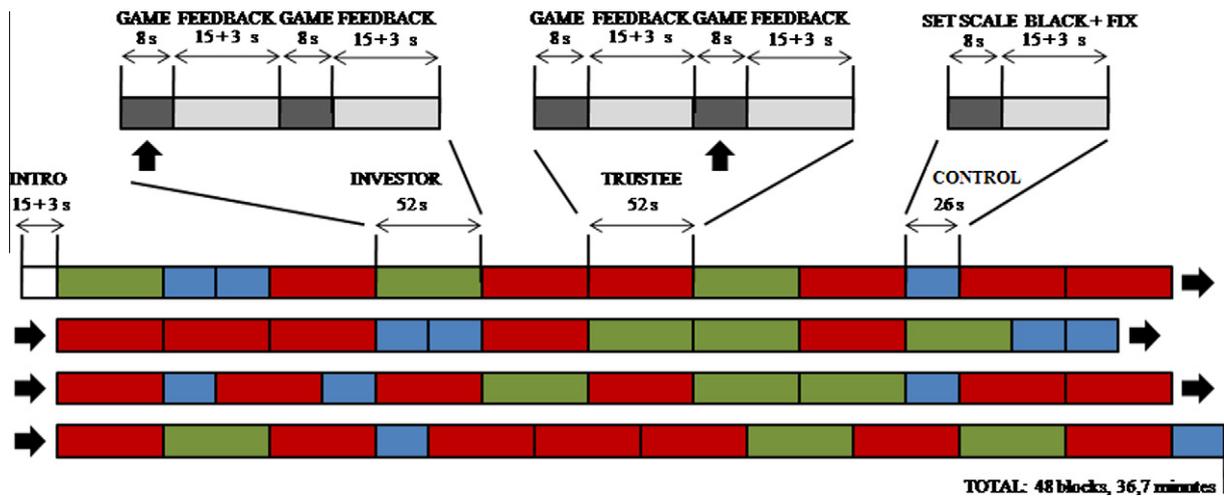


Fig. 1. Time course of the Trust Game (TG). The fMRI session consisted of 12 investor blocks, 24 trustee blocks and 12 control blocks. One TG unit started with the Partner's offer (8 s) followed by a feedback (15 s) after the experimenter has tripled the invested money. A fixation cross lasted 3 s, then the player in the scanner could make his/her offer from his account (8 s). In the end of the unit, the outcome of the Trust Game was presented (15 s), and closed with a fixation cross as a preparatory signal for the following game (3 s). One control unit consisted of a task in which participants had to set the cursor on the response scale to a specific number written out as text on the screen (8 s), then a black screen appeared for 15 s and a fixation cross for 3 s.

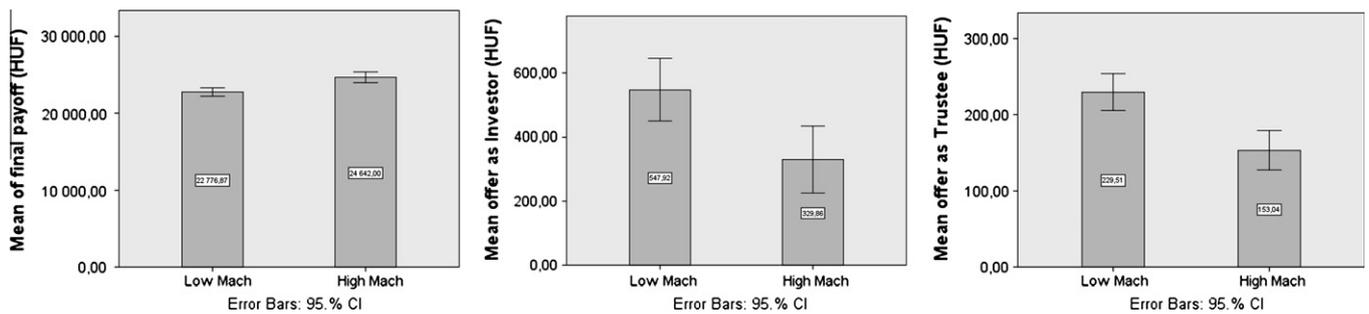


Fig. 2. (a) High-Mach and low-Mach players' means of final payoffs, and offers as (b) first and (c) second player during the Trust Game.

$p < 0.001$) ($M_{LM} = 22,777$ HUF, $SD_{LM} = 997.23$ HUF; $M_{HM} = 24.642$ HUF, $SD_{HM} = 1110.5$ HUF). Fig. 2 shows the final payoff and the players' offers as the Investor, the Trustee.

3.2. Functional imaging data

We compared the group activation of high-Mach and low-Mach participants during the decision-making process in the Trust Game, contrasted to the control phase. Whole-brain two-sample t test revealed a significantly higher activation during GAME > CONTROL condition for the HM group in comparison with the LM group (see Figs. 3–5 and Table 1).

Bilateral neural response was found in the superior frontal and middle frontal gyrus. Right hemispheric activation was detected in the anterior insula, inferior frontal gyrus, precuneus, and cerebellum. In the left hemisphere, the lingual gyrus and the globus pallidus showed elevated activation (see Table 1).

The contrast examining the brain activation as a first player (investor > control) yielded bilateral response in the superior frontal, middle frontal gyrus, middle temporal gyrus and the globus pallidus. Significant activation was found in the right middle occipital gyrus, fusiform gyrus, precuneus and anterior cingulate cortex, as well as in the right thalamus and putamen. In the left hemisphere, activation was detected in the lingual gyrus, cuneus and the superior occipital gyrus. When the trustee role was contrasted to the baseline (Trustee > Control), increased activation was

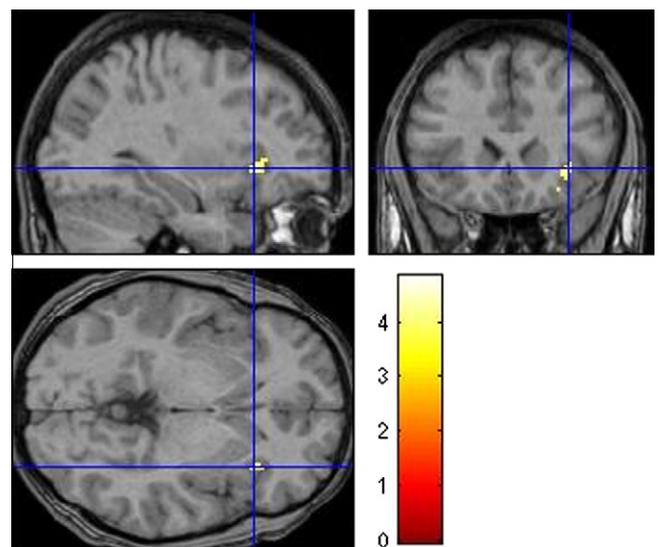


Fig. 3. Significantly higher activation in the right anterior insula and inferior frontal gyrus (32, 22, -2) during GAME > CONTROL condition for the HM group in comparison with the LM group.

detected in the left superior frontal and middle frontal gyrus, in the right anterior insula, inferior frontal gyrus and parahippocampal gyrus.

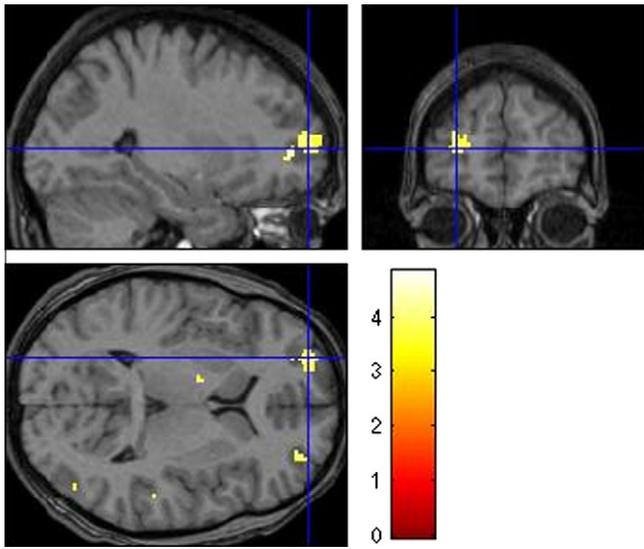


Fig. 4. Significantly higher activation in the middle frontal gyrus bilaterally (right hemisphere: 28, 12, 54; left hemisphere: -26, 62, 12) during INVESTOR > CONTROL condition for the HM group in comparison with the LM group.

Given that an increased activity in the high-Mach subjects' anterior cingulate cortex (ACC) was found, and given that this brain area is responsible for monitoring cognitive conflicts, we wondered if there was a relationship between reaction times and ACC. We expected that high-Mach people who may be involved in a larger conflict between their short-term and long-term interests than low-Machs, will show a longer reaction times pertaining to greater conflict. In order to demonstrate any possible links between neural activity in the ACC and behavioral measures, we introduced the first level contrasts into a regression analysis on the second level, using the participants' averaged button-press reaction times as a regressor. This analysis revealed multiple clusters of ACC activation along the trustee > control condition (left hemisphere, 0, 32, -12; right hemisphere 4, -36, 32). We then extracted weighted beta values from the first level contrasts of each participant as a representation of the intensity of brain response at the above coordinates. A strong positive association between these intensity values and subjects' button-press reaction times was discovered at both clusters (0, 32, -12: $r = 0.81$, $p < 0.05$; 4, -36, 32: $r = 0.799$, $p < 0.05$) (Fig. 6).

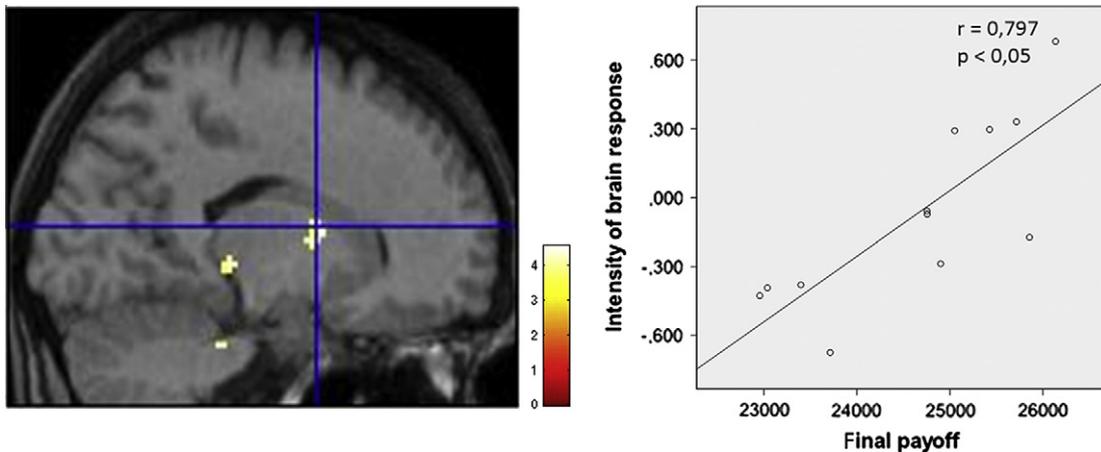


Fig. 5. Right-hemispheric activation of the thalamus identified in high-Mach participants (vs. low-Machs) while playing the Trust Game. Clusters are superimposed on sagittal ($x = 14$), coronal ($y = 0$) and axial ($z = 6$) MRI sections. A strong positive association was discovered between high-Mach players' thalamic neural activity and their final payoffs.

Other strong links were found between behavior and brain activity. If the increased thalamus activity in high-Machs may relate to the processing of reward and the anticipation of success following a risky decision (see below), we expect a relationship between activity in this brain region and the financial payoff at the end of the game. Indeed, we found that the more profit the high-Mach players gained during the game the higher activity in their thalamus was measured (left hemisphere, -6, -16, 18; $r = 0.79$, $p < 0.01$).

4. Discussion

Our behavioral data show that subjects with higher scores on Mach-IV scale transferred (both as investor and trustee) a smaller amount of money to the partner and gained a higher profit by the end of the game, compared to low-Mach persons. These results suggest that Machiavellians may be successful in social dilemma situations even in the long term if exploitation has a low cost, that is, no punishment is used and anonymity is guaranteed; as in our experimental condition.

When comparing brain activity differences (brain activity during decisions in the Trust Game minus control brain activity) between high-Mach and low-Mach people, higher activities in certain brain regions were characteristic of Machiavellians. In other words, decisions in social dilemma situations elicited higher neural response in high-Machs than in low-Machs. We suggest that a social environment involving opportunities for exploiting the others may be more demanding for persons with higher manipulative attitudes. Due to their specific cognitive abilities, Machiavellian people may take advantage of social relationships that imply potential deceptions and cheating. What abilities and what particular brain regions are involved in the Machiavellian people's success in exploiting others?

Considering first players, we found an increased activity in the high-Mach subjects' bilateral middle frontal gyrus, compared to low-Machs. This region of the brain is important in abstract reasoning, including reasoning about social situations (Reverberi, Shallice, D'Agostini, Skrap, & Bonatti, 2009). It is also known to be a core component of executive control and mental flexibility, and related to the anticipation of beneficial decisions. Several authors suggest that middle frontal gyrus plays a role in the manipulation and the active maintenance of information in working memory as required for high level planning (Cairo, Liddle, Woodward, & Ngan, 2004; Liu et al., in press; Vidal, Mills, Pang, & Taylor, 2012). It plays a crucial role in cognitive controls in the processing of logical relationships and learning

Table 1

Brain activations registered in the high-Mach group relative to the low-Mach group, while playing the Trust Game (based on the following first level contrasts: GAME > CONTROL; AS INVESTOR > CONTROL; AS TRUSTEE > CONTROL).

Region	Brodmann area	Active voxels	Z-score	Voxel coordinates (MNI)		
				x	y	z
<i>GAME > CONTROL</i>						
R inferior frontal gyrus	BA11/47	22	3.86	32	22	-2
R insula	BA13	3	3.86	32	22	-2
R middle frontal gyrus	BA6/8	9	3.68	28	50	6
R superior frontal gyrus	BA6/8	20	4.02	28	14	56
L middle frontal gyrus	BA10	58	3.67	-26	56	6
L superior frontal gyrus	BA10	34	3.25	-18	50	4
R precuneus		3	3.5	14	-36	50
L lingual gyrus		4	3.15	-16	-70	-6
L globus pallidus		4	3.69	-14	-6	4
R cerebellum		4	3.56	18	-46	-28
<i>AS INVESTOR > CONTROL</i>						
R middle frontal gyrus	BA6/8	24	3.83	28	12	54
R superior frontal gyrus	BA6/8	31	3.83	28	12	54
L middle frontal gyrus	BA10	18	3.39	-26	62	12
L superior frontal gyrus	BA10	4	3.25	-28	55	5
R middle occipital gyrus	BA19	36	3.56	46	-76	6
L superior occipital gyrus	BA19	5	3.87	-30	-88	28
L lingual gyrus	BA18/19	28	3.49	-8	-70	-4
R fusiform gyrus	BA20	10	3.85	50	-58	-16
L cuneus	BA 19	8	3.87	-30	-88	28
R precuneus		4	3.33	14	-40	50
R middle temporal gyrus	BA39	9	3.24	40	-76	-2
L middle temporal gyrus	BA37	4	3.48	-64	-54	-4
R cingulate gyrus	BA24	4	3.29	10	-16	44
R thalamus		12	3.72	14	0	6
R putamen		8	3.72	14	0	6
L globus pallidus		4	3.54	-12	-4	0
R globus pallidus		6	3.72	14	0	6
<i>AS TRUSTEE > CONTROL</i>						
R inferior frontal gyrus	BA47	22	3.69	30	22	-6
R insula	BA13	3	3.69	30	22	-6
L middle frontal gyrus	BA10	9	3.6	-30	60	12
L superior frontal gyrus	BA10	4	3.22	-26	58	4
R parahippocampal gyrus	BA36	3	3.56	32	-22	-28

$P < 0.001$ uncorrected.

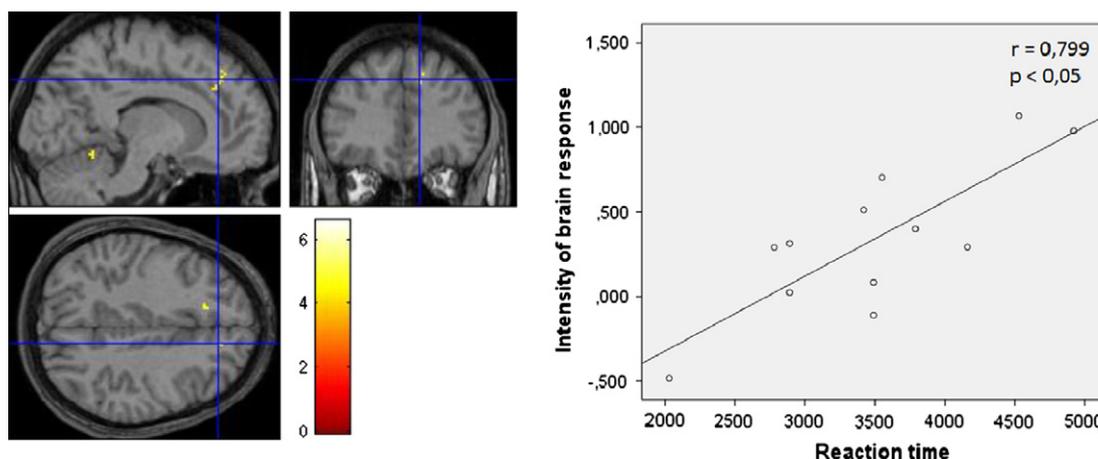


Fig. 6. Subjects with higher activation in the ACC exhibit longer reaction times prior to the first button press during the decision phases.

new rules (Geake & Hansen, 2005; Liu et al., in press). It is also related to inhibitory control in terms of inhibiting a tendency to do something, filtering irrelevant information, and in a virtual situation of competition (Goel & Dolan, 2004; Picton et al., 2007; Polosan, Baci, Perrone, Pichat, & Bougerot, 2011).

These results may coincide with high-Mach people's flexible and opportunistic character: they exploit interpersonal strategies,

bend the rules and improvise. They thrive when they have more decision power, fewer rules, and low structural organization (Jones & Paulhus, 2009). In the Trust Game, as first player, they can easily ignore social rules concerning fairness and equity in order to increase their payoff.

We also found an increased activity in the right thalamus in high-Mach persons, compared to low-Machs. The thalamus is

supposed to play an essential role in processing of reward, including monetary reward (Delgado et al., 2000). A recent meta-analysis shown that this brain region is especially involved in reward anticipation (Liu, Hairston, Schrier, & Fan, 2011). A study has shown that thalamus was required for a high-risk-assessment concerning winning or losing money in a blackjack scenario (Miedl, Fehr, Meyer, & Hermann, 2010). Other studies suggest that thalamus is one of the brain areas that support active instrumental avoidance that involves selecting, controlling and modifying risky external situations (Schlund et al., 2010). A more recent study has revealed that thalamus is involved in error detection and feedback processing associated with uncertain reward (Winkler, Hu, & Li, 2012).

Social dilemma tasks, as represented in the Trust Game, always have an element of unpredictability and risk, especially when players exert no control over their partner's decisions. This situation compels players to make predictions about the future reward, and evaluate the reward value and potential risk of obtaining it. It is highly probable that Machiavellians who are well-known to permanently search for possible short-term benefits show a higher skill at reward-related decision making (Gunnthorsdottir et al., 2002). Since they are egoistically motivated, they are also expected to have a good ability for detecting and evaluating threats to their self-interest (Jones & Paulhus, 2009). The increased thalamus activity in high-Machs, therefore, may relate to the anticipation of success following a risky decision. This interpretation was supported by our other result showing a strong relationship between thalamus activity and the amount of profit in high-Mach people. Machiavellians' financial success may be influenced by neural processes that are involved in processing monetary reward.

It has to be emphasized that not the reality of risk, in itself, what eventually counts. Machiavellians characteristically attribute negative intentions to others and do not expect cooperation from them; they start out from the assumption that others will exploit them, if they themselves fail to do so (Repacholi et al., 2003). Therefore, they are likely to perceive any social exchange as a socially threatening situation, independent of the degree of the actual risk.

We found additional elevated activities in high-Machs', as first players', anterior cingulate cortex (ACC). It is involved in reward-based decision making, and plays a specific role in the performance of novel (non-automatic) tasks (Etkin, Egner, & Kalisch, 2011; Weston, 2011). Additionally, this region of the brain is known to monitor cognitive conflicts and particularly to eliminate conflicts between brain modules. It monitors for response conflicts in the ongoing processing stream and signals the need for additional cognitive control to the executive unit (Dulebohn, Conlon, Sarinopoulos, Davison, & McNamara, 2009; Rilling et al., 2002). A recent study has revealed that ACC evaluates especially negative performance outcome which then used as an avoidance signal for future action selection (Dreisbach & Fischer, 2012).

In the present experiment a higher activation of the ACC was detected in high-Mach persons. As a possible interpretation, we argue that because Machiavellian people do not trust others, they are likely to transfer a low amount of money as the first and the second player. At the same time, however, they must be aware that they break the norm of cooperation that may be disadvantageous for them on a long run. Therefore they may feel an intense conflict between their long-term interest to obey the social norms and wish to desert the partner, which may be the reason why their ACC has a higher activity at the moment of their decision.

This interpretation was supported by our results on reaction times. We found a positive correlation between high-Mach persons' reaction times and ACC activity. This is what we expected: if Machiavellians experience a more intensive conflict between their short-term interest (desert their partners) and long-term interest (benefit

from a repeated cooperation) than low-Machs, they will have a longer reaction time pertaining to the greater conflict.

However, the findings of one study may weaken the strength of this explanation. King-Casas et al. (2005) found that "intention to trust" signal was correlated with average ACC signal in trustee. The ACC of the trustee (player 2) was strongly activated when an investor's (player 1's) decision was revealed. Whereas increased ACC activity may be related to the anticipation of trust, it is also possible that plays a role in matching opposite motivations: in spite of her/his wish to gain, trustee wants to follow the norm of reciprocity that gradually develops over the game. Indeed, reciprocity was found to be the strongest predictor of subsequent increases or decreases in trust. It is also possible that, as King-Casas' experiment involved a multiround format where the same two individuals played consecutive rounds (in contrary to our experiment), subjects might engage in a reputation building, as they developed models of one other through iterated exchange.

Decisions during the social dilemma task also evoked stronger activities in several additional brain regions in high-Machs, compared to LMs. The right fusiform gyrus has been classically reported for face perception processes, but more recent studies also suggest the implication of this region in social interactions (Iacoboni et al., 2004). The right superior frontalis gyrus is involved in executive functions, including monitoring of one's moves in relation to the others, and attentional control in responding conflict situation. (Decety et al., 2004; Aarts, Roelofs, & Turennout, 2009). The middle occipital gyrus is required in sensory inhibition processing, e.g. blocking attention from returning to the previously attended location (Tian & Yao, 2008). Lingual gyrus plays a crucial role in language processing and the integration of sentences into the mental representation of the text (Jin et al., 2009). We speculate that in the hope of the successful manipulation, Machiavellians pay a larger attention to the texts on the screen that inform them about the possible movements (transferring a certain amount of money to the partner) during the game. It is possible that, compared to low-Machs, social dilemma task imposes a greater attentional and executive demands on Machiavellian persons, who strive for exceeding the others' material benefit. A recent study shown that high-Mach people permanently monitor their play mates. They start with a relatively low amount of contribution and do not exceed the others' contributions over the game. As a result, by the end of the game they are capable of gaining a higher profit, compared to low Machs (Czibor & Bereczkei, 2012).

High-Mach people, as second players, shown an elevated activity in the overlapping brain areas of dorsal anterior insula and right inferior frontal gyrus (IFG), compared to low-Machs. The anterior insula activation is reported in a broad range of cognitive domains, including interoception, emotional and arousal processing, reward anticipation, and uncertainty assessment (Chang, Yarkoni, Khaw, & Sanfey, 2012; Craig, 2009; Kuhnen & Knutson, 2005). A meta-analysis has shown that anterior insula was consistently involved in risk possessing, especially in anticipation of loss (Mohr, Biele, & Heekeren, 2010). A study has revealed that relative to judgments about safe personal activities, judgments of risky activities activated the anterior insula/left inferior frontal gyrus (BA 13/45) (Qin & Han, 2009). Another study reported that subjects who behaved dishonestly (broke promise in a Trust Game) reacted to the unpredictable and thus emotional and stressful situation with increased activation in the same brain regions of right anterior insula and right inferior frontal gyrus (Baugmgartner et al., 2009). These results suggests that social exchange situations associated with a lack of control and uncertainty may be more pronounced and more intensively experienced in the Machiavellian subjects who intend to behave dishonestly. Since they are known to attribute negative characteristics to others, they are expected to feel

mistrust toward partners, and anticipate a negative outcome of the social transaction.

The dorsal anterior insula is activated in many different tasks that require the capacity to sustain attention, monitor goals, and modulate arousal level (Chang et al., 2012; Nelson et al., 2010; Yarkoni, Barch, Gray, Conture, & Braver, 2009). The inferior frontal gyrus (IFG, BA 47) has similar functions in terms of goal-directed cognition. It is known to be engaged in making predictive inferences during various tasks (Liakakis, Nickel, & Seitz, 2011). Virtue, Haberman, Clansy, Parrish, and Beeman (2006) found that participants with high working memory capacity showed greater fMRI signal in the left IFG area, compared to participants with low working memory capacity. Given that people with high working memory capacity are more likely to draw inferences, the authors indicated that this area plays a critical role in bridging inference generation. Another study manipulated the likelihood that a particular event can be predicted from the content of various sentences and revealed that predictive stories (from which novel statements could be inferred) evoked stronger activities in the left inferior frontal gyrus and the right lingual gyrus, relative to reading control studies (Jin et al., 2009). However, more recent studies suggest that the function of IFG goes beyond verbal communication and probably extends to nonverbal social interaction (Liakakis et al., 2011). For example, a study, using a conflict resolution task, found that right inferior frontal gyrus may be related to reward-expectancy required in social competition as the participant played in order to win. The activation of this area may reflect the subjects' effort to observe the competitors' action (Potosan, Baciu, Perrone, Pichat, & Bougerot, 2011).

Since inference making plays a crucial role in complex interpersonal situations, inferior frontal gyrus may be involved in selection of information among competitive alternatives in a social dilemma situation. It may play a crucial role in adjusting the Machiavellians' decisions to the others' actions in a social dilemma situation. Recently, Czibor and Bereczkei (2012) demonstrated that high-Mach people are more skilled in making inferences from the behavior of the others participating in a competitive version of Public Goods Game. Regression analysis revealed that Machiavellians can evaluate the clues related to the previous movements of group mates and adjust their actual behavior accordingly. They appear more sensitive to signals in a social situation and more ambitious to monitor the others than low Machs. They permanently give less amount of money than the partner do and, as a result, gain a higher profit by the end of the game, compared to low-Mach persons.

This flexibility of the Machiavellians' behavior may correspond with our additional finding: an elevated activation was found in the left middle frontal gyrus in high-Machs, compared to low-Machs, as players 2 (trustee). As we have seen, this brain region is involved in high-level controls in the processing of logical relationships (Liu et al., in press). It is also related to inhibitory control, in terms of inhibiting a tendency to do something (e.g. verify a statement), or inhibiting the effect of irrelevant information (e.g. rejecting one option of the others). (Goel & Dolan, 2004; Picton et al., 2007). A more recent study shown that this neural circuit is required during successful inhibitory control in a virtual situation of competition (Polosan et al., 2011). It is possible that Machiavellians are more willing than low-Machs to inhibit their former decisions (transferring money as a player 1 to the partner) and rather opt for giving little or nothing as player 2. This inhibition mechanism may serve their context-dependent strategy since high-Mach people were found to be highly sensitive to the signals of social relationships in the PGG and took the behavior of their partners into consideration to a greater extent when making a decision than did non-Machiavellians (Czibor & Bereczkei, 2012; Spitzer et al., 2007).

5. Conclusions

We found that high-Mach people, compared to low-Machs, gain a higher profit by the end of the game and show a higher activation in specific brain regions during decision-making processes in a social dilemma task. Previous studies have revealed that Machiavellians successfully exploit others in interpersonal relationships, in spite of their deficits in cognitive abilities, such as mindreading, empathy and emotional intelligence. The recent fMRI findings coincide with these results. Compared to low-Machs, high-Mach people did not show elevated activities in any brain regions linked to mentalization and empathy, such as the medial and ventromedial prefrontal cortices, the inferior parietal cortex, and the superior temporal sulcus. Instead we found increased neural activation in areas that are involved in inference making and reward-related decision making, that is inferior and middle frontal gyrus, anterior insula, thalamus, anterior cingulate cortex.

These results suggest that in spite of their poor performance in mentalization and emotional intelligence, Machiavellians may have cognitive heuristics that enable them to make predictions about the future reward in a basically risky and unpredictable situation. Their success in exploiting others may result from their skill at inferring possible actions from the others' behavior and anticipating reward and threat to their self-interest, that may yield a relatively large final payoff for them. Using these cognitive devices and the underlying neural activities they can utilize the movements of others during a social dilemma situation, and make beneficial decisions to maximize their profit (Czibor & Bereczkei, 2012). Future studies are needed to obtain more information about the neural correlates of their responsiveness to the more specific contextual variables of the social environment (e.g. the presence of other defectors).

Acknowledgments

This work was supported by the grants from Hungarian Scientific Foundation (OTKA K101762) and from SROP (TÁMOP 4.2.1.B-10/2konv-2010-0002).

References

- Aarts, E., Roelofs, A., & Turenout, M. (2009). Attentional control of task and response in lateral and medial frontal cortex: Brain activity and reaction time distributions. *Neuropsychologia*, *47*, 2089–2099.
- Ali, F., & Chamorro-Premuzic, T. (2010). Investigating theory of mind deficits in nonclinical psychopathy. *Personality and Individual Differences*, *49*, 169–174.
- Austin, E. J., Farrelly, D., Black, C., & Moore, H. (2007). Emotional intelligence, Machiavellianism and emotional manipulation: Does EI have a dark side? *Personality and Individual Differences*, *43*, 179–189.
- Barlow, A., Qualter, P., & Stylianou, M. (2010). Relationships between Machiavellianism, emotional intelligence, and theory of mind in children. *Personality and Individual Differences*, *48*, 78–82.
- Baugmgartner, T., Fischbacher, U., Feierabend, A., Lutz, K., & Fehr, E. (2009). The neural circuitry of a broken promise. *Neuron*, *64*, 756–770.
- Bereczkei, T., Birkas, B., & Kerekes, Zs. (2010). The presence of others, prosocial traits, Machiavellism. A personality X situation approach. *Social Psychology*, *41*, 238–245.
- Byrne, R. (1995). *Thinking Ape. Evolutionary Origins of Intelligence*. Oxford: Oxford University Press.
- Cairo, T. A., Liddle, P. F., Woodward, T. S., & Ngan, E. T. C. (2004). The influence of working memory load on phase specific patterns of cortical activity. *Brain Research. Cognitive Brain Research*, *21*, 377–387.
- Chang, L. C., Yarkoni, T., Khaw, M. W., Sanfey, A. G. (2012). Decoding the role of the insula in human cognition: Functional parcellation and large-scale reverse inference. *Cerebral Cortex*, <<http://cercor.oxfordjournals.org>>.
- Chang, L. J., Smith, A., Dufwenberg, M., & Sanfey, A. G. (2011). Triangulating the neural, psychological, and economic bases of guilt aversion. *Neuron*, *70*, 560–572.
- Cherulnik, P. D., Way, J. H., Ames, S., & Hutto, D. B. (1981). Impressions of high and low Machiavellian men. *Journal of Personality*, *49*, 388–400.
- Christie, R., & Geis, F. (1970). *Studies in Machiavellianism*. New York: Academic Press.
- Craig, A. D. (2009). How do you feel – now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, *10*, 59–70.

- Czibor, A., & Bereczkei, T. (2012). Machiavellians people's success results from monitoring their partners. *Personality and Individual Differences*, *53*, 202–206.
- Decety, J., Jackson, P. L., Sommerville, J. A., Chaminade, T. C., & Meltzoff, A. N. (2004). The neural bases of cooperation and competition: An fMRI investigation. *NeuroImage*, *23*, 744–750.
- Delgado, M. R., Nystrom, L. E., Fissell, C., Noll, D. C., & Fiez, J. A. (2000). Tracking the hemodynamic responses to reward and punishment in the striatum. *Journal of Neurophysiology*, *84*, 3072–3077.
- Dreisbach, G., & Fischer, R. (2012). Conflicts as aversive signals. *Brain and Cognition*, *78*, 94–98.
- Dulebohn, J. H., Conlon, D. E., Sarinopulus, I., Davison, R. B., & McNamara, G. (2009). The biological bases of unfairness: Neuroimaging evidence for the distinctiveness of procedural and distributive justice. *Organizational Behavior and Human Decision Processes*, *110*, 140–151.
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, *6*, 178–190.
- Etkin, A., Egner, T., & Kalisch, R. (2011). Emotional processing in anterior cingulate and medial prefrontal cortex. *Trends in Cognitive Sciences*, *15*, 85–93.
- Fehr, E., & Rockenbach, B. (2003). Detrimental effects of sanctions on human altruism. *Nature*, *422*, 137–140.
- Fehr, B., Samsom, B., & Paulhus, D. L. (1992). The construct of Machiavellianism: Twenty years later. In C. D. Spielberger & J. N. Butcher (Eds.), *Advances in personality assessment* (pp. 77–116). Hillsdale, NJ: Erlbaum.
- Geake, J. G., & Hansen, P. C. (2005). Neural correlates of intelligence as revealed by fMRI of fluid analogies. *NeuroImage*, *26*, 555–564.
- Goel, V., & Dolan, R. J. (2004). Differential involvement of left prefrontal cortex in inductive and deductive reasoning. *Cognition*, *93*, 109–121.
- Gunnthorsdottir, A., McCabe, K., & Smith, V. (2002). Using the Machiavellianism instrument to predict trustworthiness in a bargaining game. *Journal of Economic Psychology*, *23*, 49–66.
- Harrell, W. A., & Hartnagel, T. (1976). The impact of Machiavellianism and the trustfulness of the victim on laboratory theft. *Sociometry*, *39*, 157–165.
- Iacoboni, M., Lieberman, M. D., Knowlton, B. J., Molnar-Szakacs, I., Moritz, M., et al. (2004). Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. *NeuroImage*, *21*, 1167–1173.
- Jin, H., Liu, H., Mo, L., Fang, S., Zhang, J. X., & Lin, C. (2009). Involvement of the left inferior gyrus in predictive inference making. *International Journal of Psychophysiology*, *71*, 142–148.
- Jones, D. N., & Paulhus, D. L. (2009). Machiavellianism. In M. R. Leary & R. H. Hoyle (Eds.), *Individual differences in social behavior* (pp. 93–108). New York: Guilford.
- King-Casas, B., Tomlin, D., Anen, C., Camerer, C. F., Quartz, S. R., Quartz, S. R., et al. (2005). Getting to know you: Reputation and trust in two-person economic exchange. *Science*, *308*, 78–83.
- Krueger, F., McCabe, K., Moll, J., Kriegeskorte, N., Zahn, R., Strenzi, M., et al. (2007). Neural correlates of trust. *Proceedings of the National Academy of Sciences*, *104*, 20084–20089.
- Kuhnen, C. M., & Knutson, B. (2005). The neural basis of financial risk taking. *Neuron*, *47*, 763–770.
- Liakakis, G., Nickel, J., & Seitz, R. J. (2011). Diversity of the inferior frontal gyrus – A meta-analysis of neuroimaging studies. *Behavioral Brain Research*, *225*, 341–347.
- Liu, J., Zhang, M., Jou, J., Wu, X., Li, W., Qiu, J. (in press). Neural bases of falsification in conditional proposition testing: Evidence from an fMRI study. *International Journal of Psychophysiology*.
- Liu, X., Hairston, J., Schrier, M., & Fan, J. (2011). Common and distinct networks underlying reward valence and processing stages: A meta-analysis of functional neuroimaging studies. *Neuroscience and Biobehavioral Reviews*, *35*, 1219–1236.
- Lyons, M., Caldwell, T., & Shultz, S. (2010). Mind-reading and manipulation – I Machiavellianism related to theory of mind? *Journal of Evolutionary Psychology*, *8*, 261–274.
- McIlwain, D. (2003). Bypassing empathy: A machiavellian theory of mind and sneaky power. In: B. Repacholi, V. Slaughter, (Eds.), *Individual differences in theory of mind. Macquarie monographs in cognitive science*. Hove, E. Sussex: Psychology Press, pp. 39–66.
- Miedl, S. F., Fehr, T., Meyer, G., & Hermann, M. (2010). Neurobiological correlates of problem gambling in a quasi-realistic blackjack scenario as revealed by fMRI. *Psychiatry Research: Neuroimaging*, *181*, 165–173.
- Mohr, P. N., Biele, G., & Heekeren, H. R. (2010). Neural processing of risk. *The Journal of Neuroscience*, *30*, 6613–6619.
- Nelson, S. M., Dosenbach, N. U., Cohen, A. L., Wheeler, M. E., Schlaggar, B. I., & Petersen, S. E. (2010). The role of the anterior insula in task-level control and focal attention. *Brain Structure and Function*, *21*, 669–680.
- Nettle, D., & Liddle, B. (2008). Agreeableness is related to social-cognitive but not social-perceptual theory of mind. *European Journal of Personality*, *22*, 323–335.
- Paal, T., & Bereczkei, T. (2007). Adult theory of mind, cooperation, Machiavellianism: The effect of mindreading on social relations. *Personality and Individual Differences*, *43*, 541–551.
- Picton, T. V., Stuss, D. T., Alexander, M. P., Shallice, T., Binns, M. A., & Gillingham, S. (2007). Effects of focal frontal lesions on response inhibition. *Cerebral Cortex*, *17*, 826–838.
- Polosan, M., Baci, M., Perrone, M., Pichat, T., & Bougerot, T. (2011). An fMRI study of the social competition in healthy subjects. *Brain and Cognition*, *77*, 401–411.
- Qin, J., & Han, S. (2009). Neurocognitive mechanisms underlying identification of environmental risk. *Neuropsychologia*, *47*, 397–405.
- Repacholi, B., Slaughter, V., Pritchard, M., Gibbs, V., 2003. Theory of mind, Machiavellism, and social functioning in childhood. In: B. Repacholi, V. Slaughter (Eds.), *Individual differences in theory of mind. Macquarie monographs in cognitive science*. Hove, E. Sussex: Psychology Press, pp. 99–120.
- Reverberi, C., Shallice, T., D'Agostini, S., Skrap, M., & Bonatti, L. L. (2009). Cortical bases of elementary deductive reasoning: Inference, memory, and metaduction. *Neuropsychologia*, *47*, 1107–1111.
- Rilling, J. K., Gutman, D. A., Zeh, T. R., Pagnoni, G., Berns, G. S., & Kilts, C. D. (2002). A neural basis for social cooperation. *Neuron*, *35*, 395–405.
- Schlund, M. W., Siegle, G. J., Ladouceur, C. D., Silk, J. S., Cataldo, M. F., Forbes, E. E., et al. (2010). Nothing to fear? Neural systems supporting avoidance behaviour in healthy youths. *NeuroImage*, *52*, 710–719.
- Spitzer, M., Fischbacher, U., Herrnberger, B., Gron, G., & Fehr, E. (2007). The neural signature of social norm compliance. *Neuron*, *56*, 185–196.
- Tian, Y., & Yao, D. (2008). A study on the neural mechanism of inhibition of return by the event-related potential in the Go/Nogo task. *Biological Psychology*, *79*, 171–178.
- van den Bos, W., van Dijk, E., Westenberg, M., Rombouts, S. A., & Crone, E. A. (2009). What motivates repayment? Neural correlates of reciprocity in the Trust Game. *Social Cognitive and Affective Neuroscience*, *4*, 294–304.
- Vidal, J., Mills, T., Pang, E. W., & Taylor, M. J. (2012). Response inhibition in adults and teenagers: Spatiotemporal differences in the prefrontal cortex. *Brain and Cognition*, *79*, 49–59.
- Virtue, S., Haberman, J., Clancy, Z., Parrish, T., & Beeman, T. (2006). Neural activity of inferences during story comprehension. *Brain Research*, *1084*, 104–114.
- Wastell, C., & Booth, A. (2003). Machiavellianism: An alexithymic perspective. *Journal of Social and Clinical Psychology*, *22*, 63–68.
- Weston, C. S. E. (2011). Another major function of the anterior cingulate cortex: The representation of requirements. *Neuroscience and Biobehavioral Reviews*.
- Wilson, D. S., Near, D., & Miller, R. R. (1996). Machiavellianism: A synthesis of the evolutionary and psychological literatures. *Psychological Bulletin*, *119*, 285–299.
- Wilson, D. S., Near, D. C., & Miller, R. R. (1998). Individual differences in Machiavellianism as a mix of cooperative and exploitative strategies. *Evolution and Human Behavior*, *19*, 203–212.
- Winkler, A. D., Hu, S., & Li, C. R. (2012). The influence of risky and conservative mental sets on cerebral activations of cognitive control. *International Journal of Psychophysiology*.
- Yarkoni, T., Barch, D. M., Gray, J. M., Conture, T. E., & Braver, T. S. (2009). BOLD correlates of trial-by-trial reaction time variability in gray and white matter: A multi-study fMRI analysis. *PLoS One*, *4*, e4257.