

Associations between cooperation, reactive aggression and social impairments among boys with autism spectrum disorder

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Abstract

Cooperation is a fundamental human ability that seems to be inversely related to aggressive behaviour in typical development. However, there is no knowledge whether similar association holds for children with autism spectrum disorder. A total of 27 boys with autism spectrum disorder and their gender, age and total score intelligence matched controls were studied in order to determine associations between cooperation, reactive aggression and autism spectrum disorder-related social impairments. The participants performed a modified version of the Prisoner's Dilemma task and the Pulkkinen Aggression Machine which measure dimensions of trust, trustworthiness and self-sacrifice in predisposition to cooperate, and inhibition of reactive aggression in the absence and presence of situational cues, respectively. Autism spectrum disorder severity-related Autism Diagnostic Interview-algorithm scores were ascertained by interviewing the parents of the participants with a semi-structured parental interview (Developmental, Dimensional and Diagnostic Interview). The results showed that albeit the boys with autism spectrum disorder were able to engage in reciprocation and cooperation regardless of their social impairments, their cooperativeness was positively associated with lower levels of reactive aggression and older age. Thus, strengthening inhibition mechanisms that regulate reactive aggression might make boys with autism spectrum disorder more likely to prefer mutual gain over self-interest in cooperation.

Keywords

autism severity, autism spectrum disorder, cooperation, reactive aggression

Introduction

Autism spectrum disorders (ASD) are characterized by impairments in social interaction and communication, together with restricted, repetitive and stereotyped patterns of behaviour, interests and activities (Diagnostic and Statistical Manual of Mental Disorders (5th ed.; DSM-5)). Individuals with ASD have difficulties inferring the mental states and emotions of others; they have impaired 'theory of mind (ToM) skills' (Frith and Frith, 2012). In typical children, the acquisition of ToM skills facilitates the development of cooperative behaviour and hence the child's acceptance by social groups. The possession of such skills may reduce the likelihood of engagement in aggressive or disruptive behaviour. The process of social adjustment normally begins during the preschool period (Walker, 2005). Recent work has shown that same neural systems that play a role in the development of ToM skills are essential for the modulation of cooperation and inhibition of aggression (DeAngelo and McCannon, 2015; Haas et al., 2013). The design of our study was predicated on evidence that these systems are linked in typical children, in terms of both neurochemical and psychological processes.

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Cooperative behaviour is a fundamental human ability. It is defined as a joint or shared cooperative activity in which participants share an aim to which they are all committed and in which they take reciprocal or complementary roles, to achieve an agreed goal (Moll and Tomasello, 2007). Cooperation implies the motivation and willingness to help another person accomplish a task, if needed. An important aspect of cooperation is mutual trust. That is, a positive expectation that one's willingness to cooperate with another person will not be exploited (De Cremer and Stouten, 2003).

Trusting others in a group, feeling trusted by the other members and feeling part of that group experience are elements that lead to enhanced cooperation (De Cremer and Stouten, 2003). In some circumstances, defection (acting in one's self-interest, regardless of the needs of others) would provide a maximal short-term payoff. Nevertheless, the willingness of humans to cooperate with one another has been favoured in evolution and has influenced our social structures. Reputation-related reciprocal cooperation between members of a social group leads to increased personal fitness and enhances the chances of survival of that group through future generations (Moll and Tomasello, 2007; Nowak, 2006; Pennisi, 2009; Vogel, 2004; Warneken and Tomasello, 2006).

The emergence of cooperative behaviour can typically be observed very early in childhood; altruistic helping behaviour is seen at 18 months of age (Fantasia et al., 2014; Moll and Tomasello, 2007; Southgate et al., 2007; Tomasello and Carpenter, 2007). By the age of 24 months, infants can perform cooperative problem-solving tasks with peers. These skills emerge simultaneously with the child's ability to understand that self and others are separable individuals (Brownell and Carriger, 1990; Warneken and Tomasello, 2006). During later childhood, the development of increasingly complex forms of cooperative behaviour occurs, which is reflected by the integration of actions and problem-solving skills. An individual's decision whether to cooperate with another person increasingly considers issues such as the other's reputation, based on evidence of their past behaviour. For instance, cooperation might be inhibited if a potential partner had previously acted selfishly when there were choices of resource allocation to be made (Ashley and Tomasello, 1998; Brownell and Carriger, 1990; Kenward and Dahl, 2011; Li et al., 2014; Olson and Spelke, 2008).

In human evolution, altruistic cooperative behaviour towards in-group members and defensive cooperation behaviour towards out-group members may have co-evolved, to enhance the reproduction and survival of in-group individuals (Bickham, 2008; Hayes and Sanford, 2014; Li et al., 2014; Moll and Tomasello, 2007; Nowak, 2006; Pennisi, 2009; Rusch, 2014; Van Vugt et al., 2007; Vogel, 2004; Warneken and Tomasello, 2006). Cooperative and aggressive behaviours are regulated by similar neuro-modulatory systems. For instance, the serotonergic system is engaged when we decide whether to cooperate, but serotonergic dysregulation can also lead to impulsive aggressive behaviour (Crockett et al., 2010, 2008; Gollan et al., 2005; Wood et al., 2006). The neuropeptide oxytocin may modulate the development of trust. Neural systems influenced by oxytocin can influence group cohesion and foster an in-group aggressive attitude to outsiders (De Dreu, 2012; Kosfeld, 2005).

Studies of typically developing children during the pre-school period have revealed that the tendency to cooperate with another child is reduced if that partner is known to have behaved aggressively in previous social interactions. Children are typically unwilling to cooperate with another child who has previously been destructive or hurtful towards a person or object; their reluctance to cooperate is reflected in their physical and verbal responses to the offender's request (Bay-Hinitz et al., 1994; Kenward and Dahl, 2011). Adolescent males who identify themselves as having aggressive tendencies are more likely to act coercively (i.e. out of self-interest) in a structured measure of cooperation (Prisoner's Dilemma (PD)) (Gallup et al., 2010).

There have been inconsistent findings from studies designed to discover whether cooperative behaviour is reduced in ASD, which could reflect the use of diverse methodologies. Some studies have reported there is reduced cooperation among children with ASD if they have associated learning disabilities (Colombi et al., 2009; Liebal et al., 2008). Although children with ASD who lack generalized cognitive impairment may cooperate more readily, their decision-making appears to be less affected by considerations of fairness or morality than typical children (Downs and Smith, 2004; Li et al., 2014; Schmitz et al., 2015). Some have reported the inclination of children with ASD to cooperate is predicted by the degree to which their ability to imitate and to engage in joint attention are impaired, and by limitations in associated ToM abilities (Colombi et al., 2009; Downs and Smith, 2004; Hill and Sally, 2003).

Typical children who are inclined to cooperate with others are less likely to be aggressive. We do not know whether a similar association holds for children with ASD (Ambler et al., 2015; Kanne and Mazurek, 2011). Approximately 20%–30% of children and adolescents with ASD engage in maladaptive aggressive behaviour (Ambler et al., 2015; Dominick et al., 2007; Green et al., 2000; Hartley et al., 2008; Hill et al., 2014; Kanne and Mazurek, 2011; Ming et al., 2008). When maladaptive aggressive behaviour is present, children and adolescents with ASD, especially boys, tend to engage in relatively high levels of physical aggression of minor intensity, for example, pinching, biting and scratching, than typically developing children (Farmer and Aman, 2011; Kaartinen et al., 2014). Boys with ASD are less likely to respond to gender-related inhibitory cues, as they seem to react with higher levels of aggression towards girl assailants when compared to typically developing boys (Kaartinen et al., 2014). We do not know whether children with normal-range intelligence quotient (IQ) and more severe autistic traits are particularly likely to engage in aggressive behaviour, but we are

aware the strength of association could change with age (Dominick et al., 2007; Hartley et al., 2008; Hill et al., 2014; Kanne and Mazurek, 2011; Mazurek et al., 2013). However, children with ASD who have better adaptive functioning in specific social domains, such as language, show less aggressive behaviour (Connor et al., 2004; Dominick et al., 2007; Hartley et al., 2008; Ming et al., 2008).

Table 1. Characteristics of the boys with autism spectrum disorder (ASD) and their gender-, total IQ- and age-matched pairs.

	Boys						<i>p</i>	Z score
	With ASD (<i>n</i> = 27)			Without ASD (<i>n</i> = 27)				
	Mean	SD	Range	Mean	SD	Range		
Age	12.9	2.2	8.1–16.9	12.9	2.3	7.7–16.6	0.486	-0.697
IQ								
Total	102	15	77–138	105	15	75–127	0.303	-1.029
Verbal	105	14	83–140	110	20	71–150	0.082	-1.741
Performance	100	19	65–141	100	13	66–122	0.869	-0.165
Impairments in social skills								
Reciprocal Social Interaction	12.5	5.1	4.2–22.9	4.0	1.4	1.6–7.7	<0.001	-4.200
Use of Language and Other Social	12.1	5.0	3.4–19.3	2.4	2.1	0.0–9.4	<0.001	-4.257
Communication Skills								
Use of Gesture and Non-verbal Play	7.0	3.3	1.3–11.7	1.7	1.8	0.0–8.0	<0.001	-4.200
Repetitive and Stereotyped Behaviour	3.0	2.1	0.0–6.7	0.3	0.4	0.0–1.0	<0.001	-4.073
Social Expressiveness	1.8	1.0	0.0–3.25	1.3	0.5	0.6–2.8	0.006	-2.739

IQ: intelligence quotient; SD: standard deviation.

Aims of the study

Our first aim was to investigate cooperative behaviour among boys with ASD and in typically developing children that were matched for age, gender and total IQ. We hypothesized that boys with ASD would not differ from typical children in terms of their cooperative behaviour, in line with previous research findings (Downs and Smith, 2004; Li et al., 2014; Schmitz et al., 2015). A second aim was to test the hypothesis that children with ASD who had a greater tendency to engage in cooperative behaviour would possess fewer impairments in social skills. We predicted they would have better social communication and reciprocity, and that they would be less likely to engage in reactive aggression.

The sample excluded girls, as our previous work (Kaartinen et al., 2014) had shown that there is a gender difference in aggressive behaviour within the ASD population (Kopp and Gillberg, 1992). That gender difference is also observed in typically developing adolescents (Gallup et al., 2010).

Methods

Participants and procedure

The participants comprised 27 boys with ASD and 27 typically developing children. They were pairwise matched for gender, age and intelligence. Besides gender, the matching criteria for pairs included ± 6 months age and total IQ of both members of the pair within the range of 80–120 or if one pair member scored total IQ between 70 and 79 or over 120, the total IQ of the matched pair had to be within 30 units (but total IQ always over 70). There was one pair where the age difference between the children was 25 months. As the results were not changed after exclusion of that pair, it was included in the analysis. Characteristics of both groups are shown in Table 1.

The sample of children with ASD (7–17 years) was recruited from the Department of Child Psychiatry, Tampere University Hospital, Finland, where they had been diagnosed by experienced child psychiatrists using standard clinical procedures. The ICD-10 (International Classification of Diseases, Tenth Revision) diagnostic criteria were used. Five children had a diagnosis of autism (F84.0), four had atypical autism (F84.1) and 18 had Asperger syndrome (F84.5). Exclusion criteria included the presence of depression, evidence of an anxiety disorder and a full-scale IQ less than 70.

Typically developing children in the comparison group were recruited from local schools and were screened for a history of mental or neurological disorder or learning disability. The children in the ASD group and in the comparison group were all tested with the Wechsler Intelligence Scale for Children-III (WISC-III) to ascertain their IQ.

The PD task measured cooperation, and reactive aggression was measured by the Pulkkinen Aggression Machine (PAM); results were successfully obtained from all participants (27 matched pairs). The detailed clinical analysis of autistic traits provided by the Developmental, Dimensional and Diagnostic Interview (3di) (Skuse et al., 2004) was missing from one child with ASD and two children without ASD as their parents did not participate in the interview.

All participating children and their parents received information concerning the methods and aims of the study before they were interviewed and tested. They subsequently received a movie ticket as a compensation for their participation. The study was approved by the Ethics Committee of the Pirkanmaa Hospital District, and all participants and their parents gave their written informed consent.

All participants were tested individually, without a partner being physically present. This was done to avoid the risk of immediate or delayed punishment behaviour towards the other child, arising from a feeling of broken trust. Playing against an imaginary opponent has been found to correlate strongly with decision-making when an opponent is present (Knight and Kagan, 1977).

The experiments were conducted either in the Tampere University Hospital or at the home or the school of the participant. During the tasks, the children were seated in front of a laptop computer in a silent room, with only the experimenter present, who conspicuously could not see the responses chosen by the child. That was done to reduce the risk that the presence of an adult would influence the child's decision-making.

Measuring cooperation with the PD task

The PD task was adapted from Herrmann et al. (2010) (see also Herrmann and Orzen, 2008). Part 1 of the experimental design consisted of two conditional decisions (using a strategy method). The child being tested had to decide whether he wanted to cooperate or defect, with prior knowledge a partner had either cooperated or defected. Part 2 of the experimental design consisted of an unconditional decision in which a child with ASD was partnered with a typically developing child. A child had to make his decision without prior knowledge of the partner's decision. The compensation won by the child depended only on the unconditional decision and was calculated by combining the unconditional decision of the ASD child with that of his matched comparison child.

Before starting the actual game, the experimenter provided verbal and visual instructions to each child. The participants were told that another child of the same age and gender would be playing the same PD task, but at a different time. The subjects were informed that the PD task is played with imaginary tokens. Every participant would be given one token at the beginning of each of the three phases of the game. They were instructed that, when they played the game for real, they would need to decide whether they would like to give their token to an unknown child or to keep it for themselves. The participants were informed that only in the unconditional phase would they be playing an actual game with another child and that the number of tokens they received would depend on their joint decision. The children were also informed that tokens would be exchanged for small prizes (the movie tickets) afterwards. The tokens were worth approximately €5 each. In the PD game, mutual cooperation results in the greatest winnings for both parties.

There was an introductory phase in which the PD game was practiced by each participant. The experimenter verbally and visually presented all four possible outcomes of the game (keep-keep, give-keep, keep-give, give-give) in random order and asked the participants to say how much they would win from each possible outcome. If the child gave an incorrect answer, the same question was repeated. If the child again gave an incorrect answer, the experimenter explained how the decision he made would affect his winnings, in terms of both verbal and visual cues.

The game was played for real when the experimenter was sure that the child understood the rules and purpose of the game. After the practice sessions, there was a reiteration of possible choices and their outcomes before a child gave their answer in each phase of the experiment. There were customized visual instruction cards for each of the three conditions showing how outcomes are divided between the participants according to their choices (Figure 1). These cards were available to the participants while they were deciding how to respond in the respective conditions.

The winnings from the PD task were calculated by combining the unconditional decisions of each matched pair. Possible outcomes, that is, number of tokens gained, are shown in Figure 1.

Measuring retaliation to aggression with the PAM

The PAM is a computerized assessment that is designed to measure a child's propensity to engage in reactive aggression and inhibit aggressive responses in the absence and presence of situational cues (gender, size and social status of an assailant) (Juujärvi et al., 2001; Kaartinen et al., 2014). The task comprises three tasks that are administered in a fixed sequence: arbitrary responses, impulsive aggression and controlled aggression. In each of these three tasks, the child is presented with two parallel columns of icons on a computer screen; the column on the left side of the screen comprises eight stimulus icons and the one on the right side of the screen comprises nine response icons. A rectangle appears around one of the stimulus icons, and this is a signal to the participant to select a response icon (Figure 2).

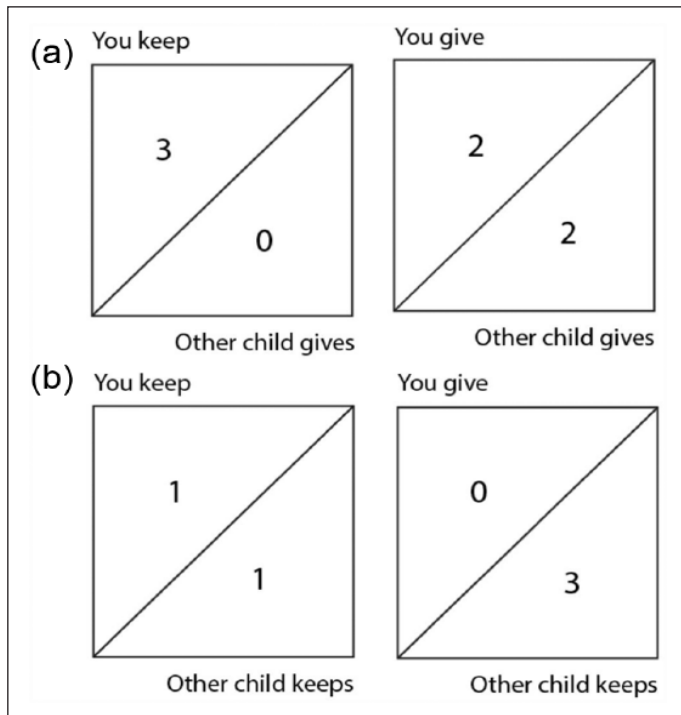


Figure 1. Picture cards presented for the participants to show the payoffs of each possible combination of choices in each of the experimental phases in the Prisoner's Dilemma task: (a) -for conditional phase 1 (whether or not to cooperate with a known cooperator), (b) -for conditional phase 2 (whether or not to cooperate with a known non-cooperator), (a and b) -for the unconditional phase (decision of cooperation had to be done without knowing the other child's decision).

The presentation of stimuli is self-paced; generation of a response triggers the next stimulus at a constant interval of 3 s after the last response. Responses are given by clicking with the mouse over one of the response icons.

The *arbitrary condition* serves as a training condition, and no aggressive content is assigned either to the stimulus or to the response icons. In this condition, the icons contain neutral black dots. Each stimulus icon is delivered once in the following predetermined order: 3-5-4-2-7-0-1-6.

In the impulsive and the controlled aggression conditions the rows of stimulus and response icons represent degrees of aggression, and of potential responses to that aggression, of varying intensity levels. These levels are scaled as follows: row 0 = a harmless interaction, row 1 = you are slightly pushed/you slightly push, row 2 = you are pinched/you pinch, row 3 = you are slapped/you slap, row 4 = you are knocked to the ground/you knock the assailant to the ground, row 5 = your hair is being pulled/you pull the assailant's hair, row 6 = you are hit with a stick/you hit with a stick and row 7 = you are punched in the face/you punch the assailant in the face. Each stimulus icon is delivered twice in a predetermined order: 3-5-4-2-7-0-1-6-2-5- 7-3-1-4-6-0. The stimulus and response icons are parallel to each other with one exception: one icon is added on to the extreme end of the response scale to deal with possible ceiling effects (i.e. row 8 = the assailant is kicked while lying on the ground).

In the *impulsive aggression* condition, participants are instructed to choose a response by which to defend themselves against aggressive attacks from an imaginary assailant. Before play commences, they are given the following instruction:

You are having a quarrel with somebody. A black rectangle around one of the icons on the left shows what the other person does to you. You may do to him or to her what you wish by touching one of the icons on the right and you do not need to worry about the consequences of your choice.

The *controlled aggression* condition is like the impulsive aggression condition with the exception that it specifies some characteristics of the assailant. In the center of the computer screen, the identity of the assailant is presented as a picture. Participants are instructed to imagine how they would behave in a real confrontation with this assailant. There are eight categories of assailant – a boy of the same size, a girl of the same size, a smaller boy, a smaller girl, a bigger boy, a bigger girl, a father and a mother. The assailant pictures appear in random order. In addition to showing them the pictures of assailants, in this condition, participants are instructed verbally during the condition about the size and the gender of their assailants. For each assailant, all eight stimuli representing aggression of varying intensity levels are presented twice in the same fixed order as in the impulsive aggression condition.

The 3di

The severity of autistic traits, in terms of social communication skills, social reciprocity and repetitive and stereotyped behaviours was measured by a standardized computerized parental interview, which had been subject to the appropriate translation. The 3di generates Autism Diagnostic Interview (ADI)-algorithm scores (Skuse et al., 2004). The 3di's concurrent validity (agreement with independent clinician formulation) is very good, criterion validity (a comparison with the Autism Diagnostic Interview) is excellent; its sensitivity is 1.0 and specificity > 0.97. The Finnish version of the interview was created by one of the authors (K.P.) together with the original developer of the instrument (David Skuse). For the study, five subscales from the interview's PDD (Pervasive Developmental Disorder) Scale were used to measure the degree of impairment in terms of subscale scores that are equivalent to those of the Autism Diagnostic Interview (Revised): Reciprocal Social Interaction, Language and Other Social Communication Skills, Gesture and Non-verbal Play, Social Expressiveness, Repetitive and Stereotyped Behaviour. The interview was used with both parents of children with ASD and parents of typically developing children.

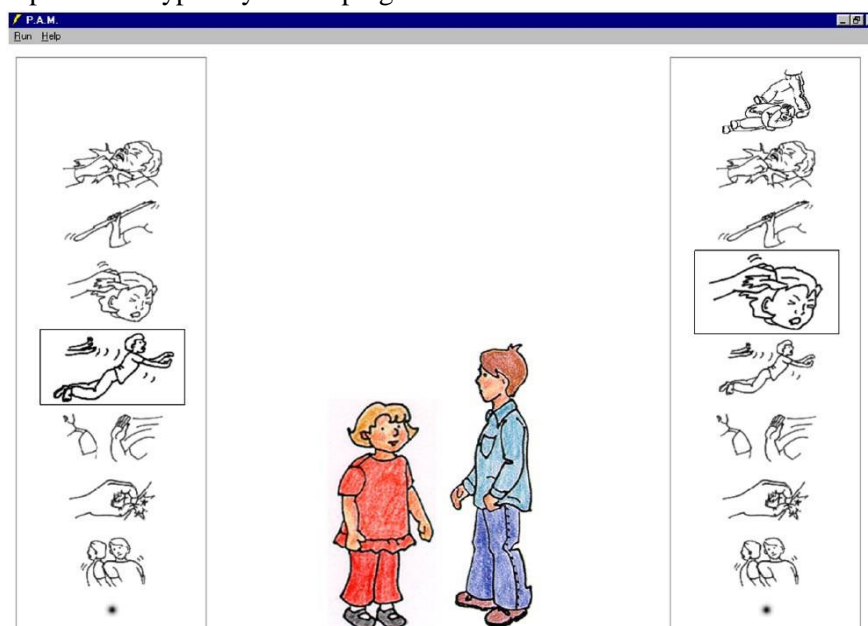


Figure 2. A screenshot of the controlled aggression condition in the Pulkinen Aggression Machine (PAM).

Statistical methods

In the PD task, the responses of the child were coded ‘cooperate’ if the child decided to give the token to his partner or ‘defect’ if the child decided to keep the token. Three different outcome scores representing degrees of cooperation were generated; one for the condition where there was prior knowledge that the ‘other keeps’, a second for the condition in which there was prior knowledge that the ‘other gives’ and a third for the unconditional condition (in which the first mover had no prior knowledge about the decision of the partner). Accordingly, each child who had participated in this experiment would acquire three scores that indexed their strategy to maximize their winnings, depending on their cooperative/non-cooperative decisions in the three phases of the PD task.

In the PAM task, the increasing intensities of the stimuli were coded in the range 0–7 and responses in the range 0–8. Three different variables were then generated; one variable for impulsive aggression, another for controlled aggression and a third for reactive aggression. For each stimulus–response pair, a difference score was calculated by subtracting the stimulus intensity score from the respective response intensity score. Because the experimental design used paired samples, the arithmetic mean of the differences of the two presentations of each pair was used as the representative of the respective stimulus–response pair in further calculations. The variable for impulsive aggression was then calculated as an arithmetic mean of the difference scores across all the eight stimulus levels (i.e. from 0 to 7). The variable for controlled aggression was calculated similarly across both all the eight stimuli and eight assailants. The variable for reactive aggression was calculated as the mean of the scores for impulsive and controlled aggression.

To study low and high levels of attack intensity separately, the stimulus variables were categorized in terms, first, of minor attacks (i.e. stimulus levels 0 = no provocation, 1 = a slight push, 2 = pinching and 3 = slapping) and, second, in terms of major attacks (i.e. levels 4 = knock to the ground, 5 = pulling hair, 6 = hitting with a stick and 7 = punching in the face).

The purpose of the analysis was not to compare the mean scores of the groups, as such, but to compare the carefully matched pairs in terms of calculated reactive aggression with regard to the way in which children with ASD differ from their comparison child. We considered it would be inappropriate to conduct a restricted analysis of the relationship between cooperation in the PD task and aggressive tendencies on the PAM tasks with the comparison sample; they had been chosen specifically to match on a case-by-case basis our ASD participants and could not be considered to be representative of typically developing individuals for that reason.

Table 2. Distribution (number of cases) of cooperative choices of the boys with ASD and their gender-, total IQ- and age-matched pairs.

PD setting	ASD cooperator		ASD non-cooperator	
	Matched pair		Matched pair	
	Cooperator	Non-cooperator	Cooperator	Non-cooperator
Conditional, with a known cooperator	19	3	4	1
Conditional, with a known non-cooperator	0	0	4	23
Unconditional	5	4	11	7

ASD: autism spectrum disorder; PD: Prisoner’s Dilemma.

To compare the severity of reactive aggression in terms of difference scores between the paired individual participants, appropriate statistical tests were used, according to the non-normality of the probability distribution of the measured variables and relatedness of samples (Wilcoxon matched pairs).

In the PD task, the groups were compared in terms of their cooperative choices (based on the decision the child made given prior knowledge of the partner’s first move and how they chose in the ‘unknown’ condition, when they did not know what decision their partner had made). These comparisons of proportion (e.g. knowing the partner had defected, what proportion of the ASD group chose ‘defect’ too) were measured using a McNemar’s test. Based on this analysis, children in both groups could be categorized as ‘cooperators’ or ‘non-cooperators’ for each phase, depending on their responses in the three conditions.

A further analysis tested the hypothesis that within the ASD sample, those who had been categorized as ‘cooperators’ or ‘non-cooperators’ would differ in terms of their propensity to engage in reactive aggression (as measured by the PAM test). Binary logistic regression analyses in two steps were carried out, with non-cooperative behaviour as outcome variable. First, only reactive aggression was entered as an explanatory

variable. Second, other explanatory variables that independently showed statistically significant association with cooperative behaviour were added into the model. Separate models for each of the three reactive aggression variables (total, impulsive and controlled reactive aggression) were fitted. The limit for statistical significance was set equal to 0.05.

Results

Cooperation

In the PD paradigm, we did not find any evidence that boys with ASD cooperated less frequently than their gender, age and total IQ matched pairs, in any of the three phases of the experiment. Most boys with ASD ($n = 22/27$) and most boys without ASD ($n = 23/27$) choose to cooperate when they had prior knowledge that the other child was a cooperator, that is, they made a choice that produces maximal mutual payoff for the pair at the expense of individual gain ($p = 1.000$).

None of the boys with ASD, and only four of the boys without ASD, cooperated with a partner who, prior knowledge had revealed, was a non-cooperator; that is, they could make a strategic decision that was rational, instead of self-sacrificing. Most of the boys with ASD ($n = 18/27$) and less than a half those without ASD ($11/27$) chose to defect (i.e. to avoid the risk their partner would not cooperate) in the third phase of the experiment, when they lacked prior knowledge of what their partner would choose to do ($p = 0.118$). For further details about the decision-making of the matched pairs in the three conditions, see Table 2.

Associations between cooperation and aggression

In the first phase of the PD experiment, none of the boys with ASD chose to cooperate with a known non-cooperator; therefore, it was not possible to investigate the association between cooperation and aggression in that situation.

Dividing the ASD sample into those who chose to cooperate with a known cooperator ($22/27$), and those who did not ($5/27$), we found no statistically significant difference between the groups in terms of their *overall aggressive reactions* ($U = 30$; $p = 0.129$) nor in terms of their *controlled aggression* ($U = 42$; $p = 0.447$) (Figure 3). However, the (5) ASD non-cooperators had a higher level of *impulsive aggression* than the (22) ASD cooperators ($U = 22$; $p = 0.039$), and they responded with relatively greater aggression than cooperative boys with ASD to attacks of minor intensity ($U = 17$; $p = 0.015$), although not to higher intensity attacks ($U = 28$; $p = 0.096$).

In the third phase of the PD task, the ‘unknown’ condition, ASD children who acted out of self-interest ($18/27$) showed more *reactive aggression* than those who responded as cooperators ($9/27$) ($U = 31$; $p = 0.009$) (Figure 3). These 18 non-cooperators also responded with greater aggression towards *minor* attacks in both the *impulsive* and *controlled* conditions of the PAM ($U = 29$; $p = 0.006$, and $U = 36$; $p = 0.020$, respectively), but they differed from the nine cooperators in their response to *major* attacks only in the *impulsive* condition ($U = 23.5$; $p = 0.002$).

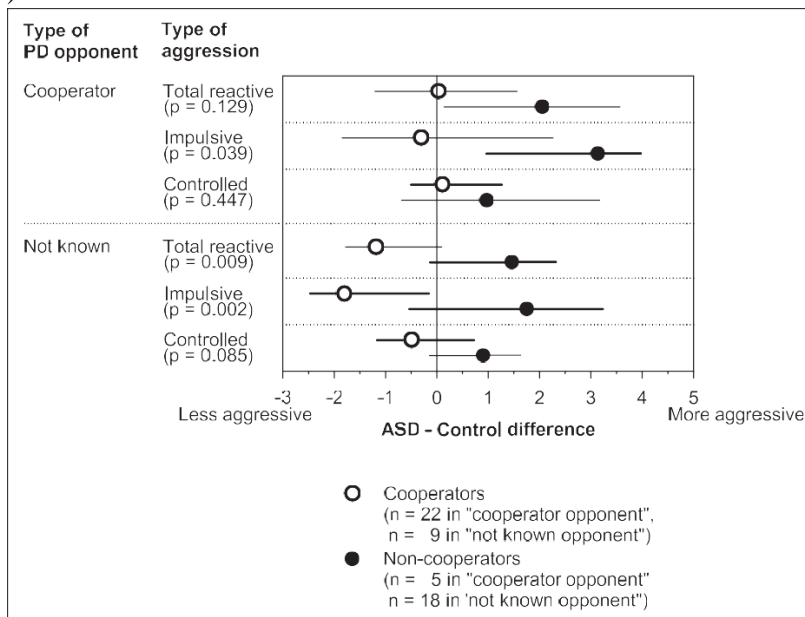


Figure 3. Associations between cooperative choices in the Prisoner's Dilemma task and aggressive responses in the Pulkkinen Aggression Machine among the boys with autism spectrum disorder (ASD).

Associations between cooperation and autism-related social impairments

Boys in the ASD sample who were categorized as cooperators (22) or non-cooperators (5) in the first two phases of the PD task did not differ statistically significantly in terms of any ADI algorithm subscale scores (Reciprocal Social Interaction $U = 36$, $p = 0.308$; Use of Language and Other Social Communication Skills $U = 31$, $p = 0.178$; Use of Gesture and Non-verbal Play $U = 28$, $p = 0.121$; Repetitive and Stereotyped Behaviour $U = 40$, $p = 0.437$; Social Expressiveness $U = 52$; $p = 0.988$). When categorized by their responses in the third phase of the PD task, a similar result was found (Reciprocal Social Interaction $U = 64$, $p = 0.683$; Use of Language and Other Social Communication Skills $U = 59$, $p = 0.495$; Use of Gesture and Non-verbal Play $U = 58$, $p = 0.461$; Repetitive and Stereotyped Behaviour $U = 53$, $p = 0.304$; Social Expressiveness $U = 64$, $p = 0.673$). The severity of their autistic traits did not predict their decision-making in this task

Associations between cooperation and age

Among the boys with ASD, the decision to cooperate or not when they had prior knowledge that their partner would be cooperative (the conditional decision) was unaffected by age ($U = 40$; $p = 0.372$). However, in the third phase of the PD, younger participants with ASD were less likely to assume that their partner would make a cooperative decision (and thus were less likely to make a decision that would maximize the payoff to both players). The median age of non-cooperative ASD boys in the unconditional decision was 11.8 years, while that of cooperative ASD boys was 14.5 years ($U = 9$; $p < 0.001$).

Associations between cooperation and intelligence

Among the boys with ASD, neither the level of total, verbal or performance intelligence correlated with the decision to cooperate, when the partner was known to be cooperative (the conditional decision; $U = 47$; $p = 0.639$; and $U = 45.5$; $p = 0.573$; and $U = 49$; $p = 0.729$, respectively). Nor did these variables predict the decision they made in the third phase of the PD task when their partner's decision was unknown ($U = 78$; $p = 0.890$; and $U = 75$; $p = 0.771$; and $U = 75$; $p = 0.772$, respectively).

Table 3. Results of logistic regression analyses examining the simultaneous impact of selected explanatory variables on the non-cooperative choice in the unconditional decision of the Prisoner's Dilemma task among the boys with autism spectrum disorder.

Explanatory variable	OR	95% CI ^a	<i>p</i>
Model 1			
Impulsive aggression ^b	2.3	0.9–6.0	0.078
Age	0.2	0.1–1.0	0.035
Model 2			
Total aggression ^c	1.9	0.7–4.9	0.175
Age Model 3	0.3	0.1–0.9	0.035
Controlled aggression ^d			
Age	0.3	0.1–0.9	0.035

OR: odds ratio; CI: confidence interval.

^aConfidence interval

^bThe level of reactive aggression in the impulsive aggression condition of the Pulkkinen Aggression Machine (PAM).

^cThe total level of reactive aggression in the Pulkkinen Aggression Machine (PAM).

^dThe level of reactive aggression in the controlled aggression condition of the Pulkkinen Aggression Machine (PAM).

Simultaneous effects of predictors of non-cooperativeness

Next, a combined analysis of the sample of ASD boys was conducted, with a view to testing the hypothesis that a combined measure of their aggression and age would predict membership of the categories 'cooperative' and 'non-cooperative'. Binary logistic regression analyses were conducted, with the level of impulsive/controlled/reactive aggression as the only explanatory variable and non-cooperativeness as the reference category. The degree of impulsive aggression significantly predicted non-cooperativeness in the third

(unknown) phase of the PD task (odds ratio (OR) = 2.1, 95% confidence interval (CI) = 1.1–4.1, $p = 0.032$). In contrast, the degree of controlled and of reactive aggression did not predict non-cooperativeness in this phase (OR = 2.2 and 1.8, CI = 1.0–4.8 and 0.8–3.7, $p = 0.054$ and 0.128 , respectively). Age, added as an explanatory variable, was a significant predictor of non-cooperativeness in all three phases of the PD task (Table 3).

Discussion

Among boys with ASD tested by this study, there was no significant difference from carefully matched comparisons in terms of their willingness to assume the trustworthiness of another individual and to engage in reciprocation and cooperation during the PD task. Those who chose to cooperate with a partner whose decision-making was unknown (33%) were less likely to engage in reactive aggression as measured by the PAM. We had hypothesized that the characteristics of ASD as measured by the severity of impairment in social communication and reciprocal social interaction skills would be associated with cooperative choices, but that was not the case. Older age (in the range 7–17 years) predicted a greater probability of being a cooperator in the third phase of the PD task, where the partner's decision was unknown.

Boys with ASD acted rationally, for the most part, to maximize mutual gain (rather than selfishly pursuing the highest individual payoff) to same degree as boys in the comparison group. Furthermore, they did not make choices that were self-sacrificing. This conclusion is in line with Down's and Smith's (2004) study of 5-9 year-olds, who played a PD game against an imaginary opponent; those with ASD did not differ in their cooperative responses from typically developing children or those with attention deficit hyperactivity disorder (ADHD)/oppositional defiant disorder (ODD). Li et al (2014) and Schmitz et al (2015) have shown that school-age children with ASD are equally likely to cooperate in the PD task and in a Social Orientation Choice Cards task as their typical peers, although their cooperative choices were less affected by considerations of fairness and morality.

Even though the evidence from the present and previous studies show that children with ASD make rational cooperative choices, they might nevertheless tend to make more self-interest choices than typically developing children when that choice does not carry a risk of harm to self or to another (Downs and Smith, 2004; Li et al., 2014; Schmitz et al., 2015). We could not test in this experiment how their decision-making is influenced by another's previous behaviour (reputation). Previous research suggests they are not influenced to the same degree as typical children by prior knowledge (e.g. a known nice vs a naughty child or a random stranger), even though they are able to make moral judgements about what constitute nice and naughty acts (Li et al., 2014). Nor are they influenced by facial appearance of trustworthiness to the same extent as typical children (Adolphs et al., 2001; Ewing et al., 2015). Children with ASD might be vulnerable to exploitation, because of undue trustworthiness, although the sample of boys in this study showed a remarkable lack of willingness to engage in self-sacrifice in the PD task, nor did their decisions in the 'unknown' phase of the task imply undue trust.

Strategies exploited in the choices of cooperation were not determined in this study. There were three possible outcomes of the PD task, including reciprocation/trustworthiness (cooperation with a known cooperator), self-sacrifice (cooperation with a known non-cooperator) and trust (cooperation with an unknown cooperator), as suggested by Gallup et al. (2010). However, the decision to cooperate might also be based upon empathy-induced altruism, mental reasoning, rational decision-making or even random selection (Batson and Ahmad, 2001; Pantelis and Kennedy, 2017; Tayama et al., 2012).

Previous research has suggested that decision-making during the PD task could differ in children with ASD and with typical development. For instance, cooperation is driven by a wish to maximize winnings in typically developing children, but children with ASD might instead make their cooperative choices according to idiosyncratic rules (Tayama et al., 2012). There is a possibility that in this study, boys' ASD based their cooperative decisions more on rational reasoning and less on intuitive processes than the comparison children (Brosnan et al., 2016).

We found some association between a propensity to be non-cooperative and the tendency to engage in reactive aggression among boys with ASD. We do not know to what extent our findings are likely to be generalizable to other children with ASD. It will be necessary for others to replicate our finding of a negative correlation between a tendency to cooperate (including the willingness to trust another individual) and reactive aggression. We speculate that by encouraging cooperation among children with ASD, we may reduce aggressive behaviour and increase prosocial behaviour (Bay-Hinitz et al., 1994).

Associations between our tendency to cooperate and our willingness to engage in violent aggressive behaviour are complex. For instance, cooperative behaviour that engages in-group members is often associated with violent confrontations with out-group members (Rusch, 2014; Van Vugt et al., 2007). Nasally

We did not find any association between dimensional measures of ASD severity and a tendency to cooperate during the PD task. Hill and Sally (2003) claimed cooperativeness, as measured by PD decision-making, was associated with mentalizing ability. This could be because cooperativeness as measured by that test is correlated with specific rather than general social skills. Liebal et al. (2008) conducted a naturalistic study of children between 24 and 60 months and found that, although those with ASD could perform some cooperative tasks, their approach to cooperation differed from typical children. They showed less partner-oriented behaviour and fewer attempts to re-engage a cooperative partner. They expressed poorly coordinated gaze and vocal expression or pointing. The degree to which children with ASD are able to engage in joint attention and imitation might explain unique variance in cooperative joint actions at this stage in development (Colombi et al., 2009).

Studies that attempt to understand the emergence of cooperation through evolution have proposed that it was the merging of joint attention and imitation skills that increased human cooperative communication, which in turn provided benefits in terms of group survival over generations (Hayes and Sanford, 2014; Li et al., 2014; Moll and Tomasello, 2007; Nowak, 2006; Pennisi, 2009; Vogel, 2004; Warneken and Tomasello, 2006). Our tendency as a species to cooperate may be influenced by neuropeptides, such as oxytocin, that can enhance emotion recognition, empathy/ToM, social communication and social reward seeking (De Dreu, 2012; De Dreu and Kret, 2016; Haas et al., 2013; Kosfeld et al., 2005). Interestingly, the administration of nasal oxytocin to people with ASD can improve eye contact, emotion recognition and processing of socially relevant cues in tests of cooperation. But it does not induce such remarkable improvements in social behaviour more generally (Andari et al., 2010; Auyeung et al., 2015; Dadds et al., 2014; De Dreu and Kret, 2016; Guastella et al., 2010; Preti et al., 2014; Watanabe et al., 2015; Yamasue, 2016; Yatawara et al., 2016).

Limitations of the study

Our study sample was of moderate size, and the generalizability of our findings cannot be assured, although it was heterogeneous in terms of age and intelligence. The decision we made to match ASD participants pairwise to typically developing children in terms of both age and total IQ to minimize bias that could have independently influenced variance in cooperation and aggression (Calkins and Fox, 2002; Hill and Sally, 2003). We only tested boys, and the results of this study apply only to those who are within normal range of intelligence. As the boys in the comparison group were individually matched to the age and total IQ of the boys in the ASD group, they could not be regarded as a representative sample of the normal population. Our study design does not permit us to discover the relationship between cooperation and reactive aggression in typically developing children.

We lack information about the degree to which our participants show aggressive behaviour in naturalistic settings. However, there is evidence from a previous work with typically developing school-aged children that responses to minor attacks as measured by the PAM task are ecologically valid and reflect maladaptive aggressive behaviour in daily life (Juujärvi et al., 2001).

Currently, we have limited evidence of the relationship between aggressive behaviour and cooperation; we do not know how these variables correlate in ASD girls or in children with learning disabilities. Future studies are also needed to investigate how these two behaviour patterns manifest and progress under conditions of typical development.

Summary

This is the first study to examine the relationship between objective measures of cooperative behaviour in children with ASD and their propensity to react with aggressive responses to others. Measures of both sets of variables were indicators of how the child responded during the experiment and may not reflect actual behaviour in real-world situations. We hypothesized that cooperative behaviour would be inversely related to the severity of autistic traits but found no supportive evidence of such an association. Nor was cooperation influenced by IQ, but there was a trend for older boys (in the age range 7–17) to be more cooperative. Although some children with ASD tend to be excessively trusting of others in everyday situations, in this study, we found a similar degree of trust was expressed by boys with ASD and by typically developing boys. The association between an inclination to cooperate with another boy to achieve a goal (to maximize winnings in the PD task) and reactive aggression was only measured in the sample of boys with ASD; there was a subtle relationship. There was a trend for those who were least cooperative during the PD task to express greater aggressive tendencies. Conversely, boys who expressed the greatest degree of impulsive aggression were more likely to act out of self-interest in a situation where the chance of their partner cooperating with them was unknown. These findings suggest that boys with ASD can cooperate with others where the benefits of doing so are clear to them.

Whether an intervention to promote cooperative behaviour would reduce a child with ASD's likelihood of reacting with aggression if threatened or upset by other people's behaviour is currently unknown, but warrants further investigation.

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Declaration of conflicting interests

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Ethical approval

All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. The study was approved by the ethics committee of the Pirkanmaa Hospital District.

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Informed consent

Informed consent was obtained from all individual participants included in the study.

References

- Adolphs R, Sears L and Piven J (2001) Abnormal processing of social information from faces in autism. *Journal of Cognitive Neuroscience* 13(2): 232–240.
- Ambler PG, Eidels A and Gregory C (2015) Anxiety and aggression in adolescents with autism spectrum disorders attending mainstream schools. *Research in Autism Spectrum Disorders* 18: 97–109.
- American Psychiatric Association (2014) *Diagnostic and Statistical Manual of Mental Disorders*. 5th ed. Washington, DC: American Psychiatric Association.
- Andari E, Duhamel JR, Zalla T, et al. (2010) Promoting social behavior with oxytocin in high-functioning autism spectrum disorders. *Proceedings of the National Academy of Sciences of the United States of America* 107(9): 4389–4394.
- Ashley J and Tomasello M (1998) Cooperative problem-solving and teaching in preschoolers. *Social Development* 7(2): 143–163.
- Auyeung B, Lombardo MV, Heinrichs M, et al. (2015) Oxytocin increases eye contact during a real-time, naturalistic social interaction in males with and without autism. *Translational Psychiatry* 5: e507.
- Batson D and Ahmad NY (2001) Empathy-induced altruism in a Prisoner's Dilemma II: what if the target of empathy has defected? *European Journal of Social Psychology* 31(1): 25–36.
- Bay-Hinitz AK, Peterson RF and Quilitch HR (1994) Cooperative games: a way to modify aggressive and cooperative behaviors in young children. *Journal of Applied Behavior Analysis* 27: 435–446.
- Bickham J (2008) The whites of their eyes: the evolution of the distinctive sclera in humans. *Lambda Alpha Journal* 38: 20–29.
- Brosnan M, Lewton M and Ashwin C (2016) Reasoning on the autism spectrum: a dual process theory account. *Journal of Autism and Developmental Disorders* 46(6): 2115–2125.
- Brownell CA and Carriger MS (1990) Changes in cooperation and self-other differentiation during the second year. *Child Development* 61(4): 1164–1174.
- Calkins SD and Fox NA (2002) Self-regulatory processes in early personality development: a multilevel approach to the study of childhood social withdrawal and aggression. *Developmental Psychopathology* 14(3): 477–498.
- Chevallier C, Kohls G, Troiani V, et al. (2012) The social motivation theory of autism. *Trends in Cognitive Sciences* 16(4): 231–239.
- Colombi C, Liebal K, Tomasello M, et al. (2009) Examining correlates of cooperation in autism: imitation, joint attention, and understanding intentions. *Autism* 13(2): 143–163.
- Connor DF, Steingard RJ, Cunningham JA, et al. (2004) Proactive and reactive aggression in referred children and adolescents. *American Journal of Orthopsychiatry* 74(2): 129–136.
- Crockett MJ, Clark L, Lieberman MD, et al. (2010) Impulsive choice and altruistic punishment are correlated and increase in tandem with serotonin depletion. *Emotion* 10(6): 855–862.
- Crockett MJ, Clark L, Tabibnia G, et al. (2008) Serotonin modulates behavioral reactions to unfairness. *Science* 320: 1739.
- Dadds MR, MacDonald E, Cauchi A, et al. (2014) Nasal oxytocin for social deficits in childhood autism: a randomized controlled trial. *Journal of Autism and Developmental Disorders* 44(3): 521–531.
- DeAngelo G and McCannon BC (2015) Theory of mind predicts cooperative behavior. West Virginia University, College of Business and Economics, Working Paper.
- De Cremer D and Stouten J (2003) When do people find cooperation most justified? The effect of trust and self-other merging in social dilemmas. *Social Justice Research* 16(1): 41–52.
- De Dreu CK (2012) Oxytocin modulates cooperation within and competition between groups: an integrative review and research agenda. *Hormones and Behavior* 61(3): 419–428.
- De Dreu CK and Kret ME (2016) Oxytocin conditions intergroup relations through upregulated in-group empathy, cooperation, conformity, and defense. *Biological Psychiatry* 79(3): 165–173.
- Dominick KC, Davis NO, Lainhart J, et al. (2007) Atypical behaviors in children with autism and children with a history of language impairment. *Research in Developmental Disabilities* 28(2): 145–162.
- Downs A and Smith T (2004) Emotional understanding, cooperation, and social behavior in high-functioning children with autism. *Journal of Autism and Developmental Disorders* 34(6): 625–635.
- Ewing L, Caulfield F, Read A, et al. (2015) Appearance-based trust behaviour is reduced in children with autism spectrum disorder. *Autism* 19(8): 1002–1009.
- Fantasia V, De Jaegher H and Fasulo A (2014) We can work it out: an enactive look at cooperation. *Frontiers in Psychology* 8: 5874.
- Farmer C and Aman M (2011) Aggressive behavior in a sample of children with autism spectrum

Frith CD and Frith U (2012) Mechanisms of social cognition.

Annual Review of Psychology 63: 287–313.

Gallup AC, O'Brien DT and Wilson DS (2010) The relationship between adolescent peer aggression and responses to a sequential Prisoner's Dilemma game during college: an explorative study. *Journal of Social, Evolutionary and Cultural Psychology* 4(4): 277–289.

Gollan JK, Lee R and Coccaro EF (2005) Developmental psychopathology and neurobiology of aggression. *Development and Psychopathology* 17(4): 1151–1171.

Green J, Gilchrist A, Burton D, et al. (2000) Social and psychiatric functioning in adolescents with Asperger syndrome compared with conduct disorder. *Journal of Autism and Developmental Disorders* 30(4): 279–293.

Guastella AJ, Einfeld SL, Gray KM, et al. (2010) Intranasal oxytocin improves emotion recognition for youth with autism spectrum disorders. *Biological Psychiatry* 67(7): 692–694.

Haas BW, Anderson IW and Smith JM (2013) Navigating the complex path between the oxytocin receptor gene (OXTR) and cooperation: an endophenotype approach. *Frontiers in Human Neuroscience* 28(7): 801.

Hartley SL, Sikora DM and McCoy R (2008) Prevalence and risk factors of maladaptive behaviour in young children with autistic disorder. *Journal of Intellectual Disability Research* 52(10): 819–829.

Hayes SC and Sanford BT (2014) Cooperation came first: evolution and human cognition. *Journal of the Experimental Analysis of Behavior* 101(1): 112–129.

Herrmann B and Orzen H (2008) The appearance of homo rivalis: social preferences and the nature of rent seeking. CeDEX Discussion Paper No. 2008–10, Centre for Decision Research and Experimental Economics. Available at: <http://www.nottingham.ac.uk/cedex/documents/papers/2008-10.pdf>

Herrmann R, Kabilin R, Nedztvesky E, et al. (2010) Emotions and cortisol reactions when cheated in a social dilemma experiment. Working paper, University of Nottingham, Nottingham.

Hill AP, Zuckerman KE, Hagen AD, et al. (2014) Aggressive behavior problems in children with autism spectrum disorders: prevalence and correlates in a large clinical sample. *Research in Autism Spectrum Disorders* 8(9): 1121–1133.

Hill E and Sally D (2003) Dilemmas and bargains: autism, theory-of-mind, cooperation and fairness. Working Paper, Social Science Research Network, University College, London. Available at: http://papers.ssrn.com/sol3/papers.cfm?abstract_id=407040

Juujärvi P, Kooistra L, Kaartinen J, et al. (2001) An Aggression Machine V. Determinants in reactive aggression revisited. *Aggressive Behavior* 27(6): 430–445.

Kaartinen M, Puura K, Helminen M, et al. (2014) Reactive aggression among children with and without autism spectrum disorder. *Journal of Autism and Developmental Disorders* 44(10): 2383–2391.

Kanne S and Mazurek M (2011) Aggression in children and adolescents with ASD: prevalence and risk factors. *Journal of Autism and Developmental Disorders* 41(7): 926–937.

Kenward B and Dahl M (2011) Preschoolers distribute scarce resources according to the moral valence of recipients' previous actions. *Developmental Psychology* 47(4): 1054–1064.

Knight GP and Kagan S (1977) Development of prosocial and competitive behaviors in Anglo-American and Mexican-American children. *Child Development* 48: 1385–1394.

Kopp S and Gillberg C (1992) Girls with social deficits and learning problems: autism, atypical Asperger syndrome or a variant of these conditions. *European Child & Adolescent Psychiatry* 1(2): 89–99.

Kosfeld M, Heinrichs M, Zak PJ, Fischbacher U, Fehr E (2005) Oxytocin increases trust in humans. *Nature* 435(7042): 673–676.

Li J, Zhu L and Gummerum M (2014) The relationship between moral judgment and cooperation in children with high-functioning autism. *Scientific Reports* 4: 4314.

Guastella AJ, Einfeld SL, Gray KM, et al. (2010) Intranasal oxytocin improves emotion recognition for youth with autism spectrum disorders. *Biological Psychiatry* 67(7): 692–694.

Haas BW, Anderson IW and Smith JM (2013) Navigating the complex path between the oxytocin receptor gene (OXTR) and cooperation: an endophenotype approach. *Frontiers in Human Neuroscience* 28(7): 801.

Hartley SL, Sikora DM and McCoy R (2008) Prevalence and risk factors of maladaptive behaviour in young children with autistic disorder. *Journal of Intellectual Disability Research* 52(10): 819–829.

Hayes SC and Sanford BT (2014) Cooperation came first: evolution and human cognition. *Journal of the Experimental Analysis of Behavior* 101(1): 112–129.

Herrmann B and Orzen H (2008) The appearance of homo rivalis: social preferences and the nature of rent seeking. CeDEX Discussion Paper No. 2008–10, Centre for Decision Research and Experimental

- Kaartinen et al. (2010) Emotions and cortisol reactions when cheated in a social dilemma experiment. Working paper, University of Nottingham, Nottingham.
- Herrmann R, Kabin R, Nedztesky E, et al. (2010) Emotions and cortisol reactions when cheated in a social dilemma experiment. Working paper, University of Nottingham, Nottingham.
- Hill AP, Zuckerman KE, Hagen AD, et al. (2014) Aggressive behavior problems in children with autism spectrum disorders: prevalence and correlates in a large clinical sample. *Research in Autism Spectrum Disorders* 8(9): 1121–1133.
- Hill E and Sally D (2003) Dilemmas and bargains: autism, theory-of-mind, cooperation and fairness. Working Paper, Social Science Research Network, University College, London. Available at: http://papers.ssrn.com/sol3/papers.cfm?abstract_id=407040
- Juujärvi P, Kooistra L, Kaartinen J, et al. (2001) An Aggression Machine V. Determinants in reactive aggression revisited. *Aggressive Behavior* 27(6): 430–445.
- Kaartinen M, Puura K, Helminen M, et al. (2014) Reactive aggression among children with and without autism spectrum disorder. *Journal of Autism and Developmental Disorders* 44(10): 2383–2391.
- Kanne S and Mazurek M (2011) Aggression in children and adolescents with ASD: prevalence and risk factors. *Journal of Autism and Developmental Disorders* 41(7): 926–937.
- Kenward B and Dahl M (2011) Preschoolers distribute scarce resources according to the moral valence of recipients' previous actions. *Developmental Psychology* 47(4): 1054–1064.
- Knight GP and Kagan S (1977) Development of prosocial and competitive behaviors in Anglo-American and Mexican-American children. *Child Development* 48: 1385–1394.
- Kopp S and Gillberg C (1992) Girls with social deficits and learning problems: autism, atypical Asperger syndrome or a variant of these conditions. *European Child & Adolescent Psychiatry* 1(2): 89–99.
- Kosfeld M, Heinrichs M, Zak PJ, Fischbacher U, Fehr E (2005) Oxytocin increases trust in humans. *Nature* 435(7042): 673–676.
- Li J, Zhu L and Gummerum M (2014) The relationship between moral judgment and cooperation in children with high-functioning autism. *Scientific Reports* 4: 4314.
- Liebal K, Colombi C, Rogers SJ, et al. (2008) Helping and cooperation in children with autism. *Journal of Autism and Developmental Disorders* 38(2): 224–238.
- McClintock K, Hall S and Oliver C (2003) Risk markers associated with challenging behaviours in people with intellectual disabilities: a meta-analytic study. *Journal of Intellectual Disability Research* 47(6): 404–416.
- Mazurek MO, Kanne SM and Wodka EL (2013) Physical aggression in children and adolescents with autism spectrum disorders. *Research in Autism Spectrum Disorders* 7(3): 455–465.
- Ming X, Brimacombe M, Chaaban J, et al. (2008) Autism spectrum disorders: concurrent clinical disorders. *Journal of Child Neurology* 23(1): 6–13.
- Moll H and Tomasello M (2007) Cooperation and human cognition: the Vygotskian intelligence hypothesis. *Philosophical Transactions of the Royal Society of London: Series B: Biological Sciences* 362(1480): 639–648.
- Nowak MA (2006) Five rules for the evolution of cooperation. *Science* 314(5805): 1560–1563.
- Olson KR and Spelke ES (2008) Foundations of cooperation in young children. *Cognition* 108(1): 222–231.
- Pantelis PC and Kennedy DP (2017) Autism does not limit strategic thinking in the 'beauty contest' game. *Cognition* 160: 91–97.
- Pennisi E (2009) Origins. On the origin of cooperation. *Science* 325(5945): 1196–1199.
- Preti A, Melis M, Siddi S, et al. (2014) Oxytocin and autism: a systematic review of randomized controlled trials. *Journal of Child and Adolescent Psychopharmacology* 24(2): 54–68.
- Rusch H (2014) The evolutionary interplay of intergroup conflict and altruism in humans: a review of parochial altruism theory and prospects for its extension. *Proceedings of the Royal Society B: Biological Sciences* 281(1794): 20141539.
- Schmitz EA, Banerjee R, Pouw LB, et al. (2015) Better to be equal? Challenges to equality for cognitively able children with autism spectrum disorders in a social decision game. *Autism* 19(2): 178–186.
- Skuse D, Warrington R, Bishop D, et al. (2004) The Developmental, Dimensional and Diagnostic Interview (3di): a novel computerized assessment of autism spectrum disorders. *Journal of the American Academy of Child and Adolescent Psychiatry* 43(5): 548–558.
- Southgate V, van Maanen C and Csibra G (2007) Infant pointing: communication to cooperate or communication to learn? *Child Development* 78(3): 735–740.
- Tayama M, Tateno M, Park TW, et al. (2012) The study of cognitive characteristics in Asperger's

Tomasello M and Carpenter M (2007) Shared intentionality. *Developmental Science* 10(1): 121–125.

Tomasello M, Carpenter M and Liszkowski U (2007) A new look at infant pointing. *Child Development* 78(3): 705–722.

Tsakanikos E, Costello H, Holt G, et al. (2007) Behaviour management problems as predictors of psychotropic medication and use of psychiatric services in adults with autism. *Journal of Autism and Developmental Disorders* 37(6): 1080–1085.

Van Vugt M, De Cremer D and Janssen DP (2007) Gender differences in cooperation and competition: the male-warrior hypothesis. *Psychological Science* 18(1): 19–23.

Vogel G (2004) Behavioral evolution. The evolution of the golden rule. *Science* 303(5661): 1128–1131.

Walker S (2005) Gender differences in the relationship between young children's peer-related social competence and individual differences in theory of mind. *Journal of Genetic Psychology* 166(3): 297–312.

Warneken F and Tomasello M (2006) Altruistic helping in human infants and young chimpanzees. *Science* 311(5765): 1301–1303.

Watanabe T, Kuroda M, Kuwabara H, et al. (2015) Clinical and neural effects of six-week administration of oxytocin on core symptoms of autism. *Brain* 138(11): 3400–3412.

Wood RM, Rilling JK, Sanfey AG, et al. (2006) Effects of tryptophan depletion on the performance of an iterated Prisoner's Dilemma game in healthy adults. *Neuropsychopharmacology* 31(5): 1075–1084.

Yamasue H (2016) Promising evidence and remaining issues regarding the clinical application of oxytocin in autism spectrum disorders. *Psychiatry and Clinical Neurosciences* 70(2): 89–99.

Yatawara CJ, Einfeld SL, Hickie IB, et al. (2016) The effect of oxytocin nasal spray on social interaction deficits observed in young children with autism: a randomized clinical cross-over trial. *Molecular Psychiatry* 21(9): 1225–1231.