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Coordination Strategies of Chimpanzees and Human Children in a Stag Hunt Game

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Abstract

Much of human cooperation takes place in mutualistic contexts in which the main challenge for individuals is how to coordinate decisions. In the current studies we compared the abilities of chimpanzees and young children to coordinate with a partner in two versions of a Stag Hunt game. When risks were low (the hare was of low value) and information was cheap (the partner's behaviour was readily observable) partners of both species were able to successfully coordinate on the higher value stag more than 90% of the time. In contrast, when the risks were raised and observing the partner was more difficult, the chimpanzees became less successful, whereas the children compensated, and so remained highly successful, by communicating more often and more specifically. This pattern of results is consistent with the hypothesis that humans evolved unique skills of coordination and communication in the context of especially risky coordination problems.

Introduction

Human cooperation is most often studied in the framework of ‘social dilemmas’ such as the Prisoner’s Dilemma and the Public Goods Game in which the individual must pay a cost to cooperate e.g. [1];[2];[3]. But much of human cooperation is mutualistic and so better described by coordination games in which cooperation benefits all, and there is no temptation to defect [4]; [5]. A particularly realistic game is the Stag Hunt [6]. In this game two hunters may each safely pursue their own low-value prey (hare) or they may coordinate to pursue a higher value prey (stag). They both know that they need a partner to capture the stag so that pursuing it alone means losing both options. To solve this problem the hunters need to be able to coordinate their decisions and subsequent actions so that both either go for the stag (the risky, payoff dominant solution) or both go for hare (the safe, risk dominant solution). The most straightforward way for humans to coordinate on the stag, in particular, is to communicate with each other [7].

Humans’ closest living relatives, chimpanzees (*Pan troglodytes)* and bonobos (*Pan paniscus),* both engage in the group hunting of small mammals, mostly monkeys. The typical situation for chimpanzees (the species about whom much more is known) is that several males coordinate their behaviours to surround and capture the prey [8] [9]. In going for the monkey, individuals forsake time and energy that they could have spent foraging for other, lower value, food sources. Chimpanzee group hunting could thus be modelled as a Stag Hunt game. In two recent studies, Brosnan and colleagues gave pairs of primate conspecifics (capuchin monkeys, Rhesus macaques, chimpanzees, and human adults) a choice between two types of tokens (or symbols on a computer screen) in a Stag Hunt game: one represented the stag option and the other the hare option [10, 11]. In order to standardise procedures across species minimal instructions or training was provided, and so none of the participants were aware of the pay-off structure prior to testing. Under these conditions, all species struggled to coordinate on the high pay-off stag option (humans became successful when they were allowed to communicate with each other).

The results from these two studies suggest that coordination in the Stag Hunt game is challenging for all primates. However, chimpanzees have also demonstrated the ability to coordinate actions with a partner to solve cooperative tasks in a number of experimental settings e.g. [12-15]. This raises the question of whether their performance would be different in a Stag Hunt game in which, unlike the studies of Brosnan et al., the pay-off structure is clear to subjects. Bullinger et al. [16] presented pairs of chimpanzees with a Stag Hunt game using a foraging task. Subjects were given the choice between collecting a completely safe low value food (hare) individually or cooperating with a partner to acquire higher value food (stag). Importantly, they received training to ensure they understood that if they attempted to acquire the high value reward alone, they would not only fail but also lose access to the low value food. Therefore, to be maximally successful subjects needed to take a risk and coordinate their decisions with one another on the stag.

The chimpanzees were highly successful in coordinating to acquire the stag, doing so in 91% of trials. However, they did so with very little communication or visual monitoring of their partner (communication only occurred after a subject was at the stag exhorting their partner to join). Bullinger et al. [16] suggest that subjects were using a simple ‘leader-follower’ strategy. Once one individual takes the risk and goes for stag, the best decision for the second individual is to follow so that they are successful on the stag. This strategy is employed by a wide range of species encountering coordination problems. A common example is deciding on travel direction for species that travel in large groups (e.g. pigeons) in which case some individuals (leaders) have disproportionate influences on the chosen direction according to factors such as their motivation or knowledge (see [17] for a review). While the reason for the follower to abandon the hare is clear, the mechanism of leadership in the Stag Hunt game is more difficult to discern, since leaders would seem to be taking on all the risk. Theorists such as Schelling [18] and Lewis [19] have argued that the solution is mutual knowledge. If both hunters know that each of them would prefer the stag and that they need a partner to succeed (i.e. they both know that they both understand the game and pay-off structure) then, once mutual knowledge of the presence of the stag is established both hunters should abandon their hare in pursuit of the stag. This can be accomplished by communication prior to decision-making.

Our aim was to directly compare coordination strategies used by chimpanzees and humans in solving an evolutionary relevant coordination problem (the Stag Hunt). In Experiment 1 we presented pairs of 4-year-old children (who conceivably have less experience and less conventionalised solutions to such problems than adults would) with the Stag Hunt game of Bullinger et al. [16]. In a previous study, using a different Stag Hunt game, 4 year olds had to decide between hare and stag without knowledge of their partner's decision and without any verbal or gestural communication. However, in one condition the partner (as adult experimenter) made eye contact with and smiled at the child prior to the decision being made, and this minimal communication was enough to increase cooperation, presumably because it established mutual knowledge about the arrival of the stag [20]. We were interested in whether 4 year old children would solve our version of the Stag Hunt problem by actively establishing mutual knowledge to coordinate their decisions. If this were the case we would expect that they would do so by communicating with their partner prior to going for the stag. Alternatively, it may be that, in this low risk situation, children would employ a leader-follower strategy, similar to chimpanzees.

In Experiments 2a and 2b we investigated how pairs of chimpanzees and pairs of children, respectively, coordinated in a higher risk Stag Hunt game. Risk was increased in two ways: (1) by increasing the value of the hare in relation to the stag, so that there were greater losses incurred through a failed attempt to cooperate; and (2) by reducing the auditory and visual information participants have about their partner's decision, thus rendering the leader-follower strategy ineffective. In this high risk Stag Hunt we would expect individuals of both species to mitigate the risk through increases in communication and visual monitoring before going for the stag. If they are unable to do so, then we would expect them to be less likely to take the risk of going for the stag.

Experiment 1: Low Risk Stag Hunt with Children

In this experiment, pairs of 4 year old children participated in a low risk Stag Hunt game based on Bullinger et al. [16]. During the game, children began by collecting a low value food reward (hare) alone. While they were doing this a high value food reward (stag) appeared, which they knew required cooperation with a partner to acquire. Children therefore had to decide either to continue collecting their low-value reward, or to try to obtain the high value option. The latter choice entailed the risk that if their partner did not also try to cooperate, they would then lose both rewards. We recorded children's decisions and their communication, with a particular focus on the use of communication prior to making a decision.

Material and Methods

Subjects

Forty children (20 girls, mean age: 50 months, range 45-56 months) were included in the final sample. An additional seven children took part, but were excluded from the analysis either because they failed pre-tests (see below, *N* = 3), or because their motivation wavered during testing (*N* = 4). Children were paired into 20 same-sex dyads, which belonged to the same kindergarten group, or were known to play together. All testing took place at kindergartens.

Materials

Hare boxes. Each child was assigned their own hare box (denoted by colour and location), containing low value food (sweet rice puffs) which they could retrieve alone, but that required some time to do so. The front face of the box could be accessed by opening a transparent door, behind which were six tubes (6cm deep) containing the hare reward. An elastic hinge ensured that the door would close automatically when let go, and once the door closed a magnet held it shut so children were unable to re-open it until it was re-set by the experimenter.

Stag box. The stag box contained the high value food (gummibears) and required both children to work together to acquire the reward. The apparatus consisted of a large wooden box (approx. 100x70x30cm) containing a sliding tray that could be set to three positions (operated surreptitiously by E3, who pretended to read). When released to the mid-way position the contents of the tray could be seen by the children. In this position, a loud ticker sounded for 15 seconds, during which children could pull simultaneously on ropes at either side of the box to release the tray to the final position and retrieve one reward each. A bell sounded at the end of the 15 seconds, if the dyad had not retrieved the rewards, and the tray was fully retracted to the start position. The hare and stag boxes were positioned at opposite ends of the testing room (approx. 300cm apart, see Figure 1).

Barrier. An opaque curtain (150x150cm) was positioned between the hare boxes for barrier test trials. This barrier meant that children could not see each other while they were both at hare, although they could look around the barrier if they repositioned themselves, as well as see their partner if one was waiting at the stag box already.

Design and Procedure

Dyads participated in two conditions (within subjects). In *no-barrier trials,* partners were able to see each other throughout the trial. In *barrier trials*, visual monitoring was restricted by the barrier so that partners could not see each other whilst were both at hare (unless they repositioned themselves). Each dyad received one block of 3 no-barrier trials and one block of 3 barrier trials (with order counterbalanced across dyads).

Training and pre-tests. Children were trained individually by the first experimenter (E1) so that they understood the apparatuses and the relationships between them. They never experienced the full test set-up prior to test trials with their partner (for full details of the training see ESM). Each child then received two types of pre-test. The *social pre-test* trials ensured that children were motivated to coordinate when a willing partner was available, and children could see this (i.e. they preferred the stag over the hare reward). The child started collecting the hare and E1 waited beside the stag box, so that when the stag appeared, the child had to decide whether to continue collecting hare, or abandon it and attempt to get to the stag together with E1. To pass the social pre-test children were required to go for the stag. The *non-social pre-test* was designed to ensure that children did not attempt to retrieve the stag payoff indiscriminately, and that they valued the hare enough to collect it when the stag was unavailable. Once the child had begun to collect the hare, E1 made an excuse to leave the room. The stag then appeared, and in order to pass the children had to stay at the hare. Pre-tests were presented in a block of 6 alternating trials, which was repeated if they did not pass the first block. To pass, children needed to respond correctly in at least 2 out of 3 trials for each trial type.

Test trials. The dyad now played together for the first time. Each was guided to her respective hare box by E1, who then left the room. The trials began when the children had opened the door to their hare boxes and the stag appeared (accompanied by an exclamation of "Oh, wow" by E3 and the onset of the ticking sound). At this point the children had 15 seconds to decide whether to stay on their hares or try to retrieve the stag. The trial ended once the stag had been acquired, or, if unsuccessful, until the stag was removed. If they were still collecting hare at the end of the trial the children were allowed to continue until they had emptied their hare box. Both children left the room with E1 while E3 re-set the apparatuses for the next trial.

Coding

Based on the coding in Bullinger et al. (2011), we coded several aspects of participants' behaviour in order to determine a) how likely individuals were to decide to go for the stag; b) how well these decisions were coordinated with their partner's decisions; and c) the role of communication and visual monitoring of partners in successful coordination. All testing sessions were video recorded and the following variables were coded from the tapes. We coded:

Decisions to leave hare. For each individual on every trial we coded whether or not individuals left their hare to go for stag during the trial.

Coordination success. Trials were coded as successful coordination when both partners left hare to go for stag, as a measure of whether dyads coordinated their decisions.

Communication. Each individual on every trial was given a communication score (1 or 0) for the two phases of a trial a) while still at hare, and b) after leaving hare, to denote whether or not they communicated during each of these phases. Communication was defined as: verbal communication related to the objects, actions, or players in the game, directed towards their partner (as indicated by either looking towards them while talking, addressing them directly, or otherwise indicated by the context of the utterance).

Visual monitoring. Each individual on each trial was given a visual monitoring score (1 or 0) for each of the two phases of a test trial a) while still at hare, and b) after leaving hare, to denote whether they looked in the direction of their partner's face during these phases.

Reliability. An independent observer who was blind to the hypotheses of the study coded a random sample of 20% of children (4 pairs) for reliability. As some of the behaviours coded occurred infrequently we used Prevalence-Adjusted Bias-Adjusted Kappa (PABAK, [21]) to determine reliability (this was the measure used for all subsequent calculations of inter-rater reliability). Agreement on whether dyads acquired the stag was 100% (K =1.00); whether individuals went for stag 99% (K =0.96); communication at hare 96% (K =0.91); communication after leaving hare 88% (K =0.71); monitoring at hare was 90% (K =0.77); monitoring after leaving hare was 85% (K =0.62).

Results

All of the following analyses (including analysis for Experiments 2a and 2b) used Generalized Linear Mixed Models (GLMM; [22]), with significant set at $p < 0.05$. See ESM for details of model construction and results.

Children overwhelmingly decided to go for stag, with no effect of condition (no-barrier condition: 96.7% of decisions; barrier condition: 98.3%; χ^2=3.284, df= 4, p= 0.51,

N=240). This corresponded to high levels of successful coordination in both conditions (no-barrier condition: 95.0% trials; barrier condition: 96.7%; χ^2=2.27, df= 3, p=0.52, N=120).

These high levels of coordination were achieved with very little verbal communication prior to making their decisions (i.e. before leaving hare), with no effect of condition or order (no-barrier condition: 7.5% trials; barrier condition: 4.2%; χ^2= 5.81, df= 7, p =0.56, N=240). Most verbal communication occurred after leaving hare, when children were running for the stag or waiting for their partners to join them, and also did not differ between conditions (no-barrier condition: 32.8% trials; barrier condition: 38.1%; χ^2= 4.26, df= 3, p =0.23, N=234).

Visual monitoring of the partner showed a pattern similar to that of verbal communication. There was some monitoring while individuals were still at hare, with no effect of condition (no-barrier condition: 13.3% trials; barrier condition: 11.7%; χ^2=2.63, df= 3, p=0.45, N=240); but there was more after leaving the hare, again with no effect of condition (no-barrier condition: 72.4% trials; barrier condition: 66.9%; χ^2= 6.821, df= 4, p=0.146, N=234).

Discussion

Four year-old children achieved high rates of successful coordination, directly comparable to those of the chimpanzees in Bullinger et al. [16], with coordination in both species at or above 90% of the trials. Communication and monitoring also showed a largely similar pattern between species: like the chimpanzees, the children in our study produced little pre-decision communication and monitoring, especially compared to their post-decision production. Thus, under these particular conditions, the coordination of young children - and the strategies they used to achieve this - appears quite similar to that seen in chimpanzees under similar conditions.

These results are consistent with children also using a ‘leader-follower strategy’. They could use this strategy in the current experimental set-up because (i) leaders could rely on followers hearing their hare door closing and see them once they reached the stag, and (ii) the hare was of such low value that leaving it was no real risk.

Alternatively, the value of the hare was not high enough for its loss in a failed coordination attempt to present a real cost. However, children were motivated to collect the hare when there was no partner available, indicating that the rewards were of some value to them. A richer alternative is that children assumed mutual knowledge of the stag. The stag was accompanied by auditory signals, the salience of which might have been enough for children to not only assume that their partner was also aware of the stag but was making the same assumptions of them. Thus, if the cues were removed, we would expect the children to use other means to actively establish mutual knowledge of the stag.

To test these potential explanations Experiments 2a and 2b presented chimpanzees and children with a modified version of the Stag Hunt game used in Experiment 1 and Bullinger et al. (2011). We increased the value of the hare, which increased the risk of pursuing the stag. We also eliminated auditory cues associated with the stag and visual cues (by extending the barrier all the way up to the stag), which meant that the leader-follower strategy was no longer viable (without something like blind faith). Under these conditions, if either species attempted to continue using a leader-follower strategy, we would expect them mostly to fail – unless they compensated with some pre-decision communication.

Experiment 2a: High Risk Stag Hunt with Chimpanzees

Material and Methods

Subjects

Ten chimpanzees (*Pan troglodytes*) (eight of which took part in Bullinger et al.); four males and six females were included in the final sample (mean age=20.1 years, range: 7 -35 years, see ESM for full subject table). Three additional subjects did not complete the training or pre-tests and thus did not take part in the test trials. Subjects could choose to stop participating at any time. They were never food deprived and water was available ad libitum throughout testing. Animal husbandry and research comply with the EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria and the WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquarium.

Materials

The materials were adapted from Bullinger et al. [16]and had the same properties as in Experiment 1, with minor exceptions. First, the hare boxes contained a drinking bottle with a weak mixture of fruit syrup and water. Secondly, the stag apparatus consisted of a platform and rope spanning a booth between two cages. When two individuals pulled simultaneously on ends of the rope, the platform lifted and the stag rewards (6cm of banana for each) became accessible. In Bullinger et al. sounds cued the arrival of the stag and the time it was available; these cues were removed and a sound that mimicked the closing of hare box door played throughout pre-tests and test trials. Thus this cue could not be used as a reliable indicator of their partner’s decision. Finally, the barrier (several plastic panels) was positioned so that dyads could see each other only when they were both at the stag apparatus.

Subjects were tested in two adjacent cages ($8.05m^2$ and $6.75 m^2$) separated by wire mesh. Each had a hare box in their own cage and the stag apparatus was situated between the two cages, at the opposite end to the hares (see Figure 2).

Design and Procedure

Subjects were divided into two groups of five; balanced for sex and age and to maximise the number of dyads that were not previously paired together in Bullinger et al. (see subject table in ESM for details). Individuals were paired with all other members of the group (10 pairs per group) in a within subjects design with two conditions. In the *no-*

barrier condition subjects were able to visually monitor their partner throughout the trial. In the *barrier condition* the barrier was placed such that subjects had no visual access to their partners (and thus their partner's decisions) until both were already at stag. Each pair had 12 trials per condition, conducted across 2-3 testing days. Each subject completed one condition with all of their partners before moving on to the next condition (order counterbalanced across groups).

Training and pre-tests. As in Experiment 1 and Bullinger et al., subjects completed several training phases and pre-tests (see ESM for full details of all training phases and attainment). After training, subjects were also given *social* and *non-social pre-tests* (though in this case E1 was replaced by a conspecific stooge) before each new testing session. A set of pre-tests consisted of one social and one non-social pre-test trial. Subjects could only participate in test trials if they responded correctly to both trial types in a set. If they did so in either the first or the second set, subjects could go on to test. If not, a third set was presented as training and testing was discontinued for that day. Subjects were given another opportunity to pass pre-test in the following session.

Test trials. Test trials were the first time subjects were paired together. The trial started when both subjects opened their own hare boxes, and the stag reward was placed on the stag apparatus. The trial ended when the stag was retrieved. If the stag was not retrieved within 20 seconds, E1 pulled a rope from outside the room to cause the stag to fall out of reach of the subjects and end the trial. If a subject was still at hare at this point they were allowed to finish the contents.

Coding

The coding scheme was identical to that used in Exp. 1 with the following modifications: communication was defined as gestural attention-getters (e.g. clapping) and vocalisations. Visual monitoring includes 'checking back' from the hare to either the stag, or their partner's cage.

Reliability. A second coder, unaware of the hypotheses coded one randomly selected trial per condition per dyad (8.33% of total trials). Agreement on whether dyads acquired the stag, and whether they left hare before the stag disappeared was 100% (*K* =1.00); checking back at hare was 91% (*K* =0.81); there was also 100% agreement that there was no communication at hare (*K* =1.00), and 98% (*K* =0.97) on communication after leaving hare.

Results

We directly compared the behaviour of the chimpanzees in Experiment 2a with their behaviour in Bullinger et al. ([16], hereafter the low risk game). Our main aims were to compare how likely individuals were to take the risk to go for stag on a given trial; how well dyads coordinated their decisions; and the role of communication and visual monitoring in these interactions.

Subjects responded to the game modifications in the high risk game by being less likely to leave hare than in the low risk game (low risk: 94.3% of decisions, high risk: 69%), though this reduction was greatest in the barrier condition, when this was experienced after the no-barrier condition (3-way interaction between game, condition and condition order; χ^2=5.79, *df*=1, *p*=0.02, *N*=1536). The reduced likelihood of going for stag in the high risk game was reflected in a reduction in successful coordination (low risk: 91% both leaving hare, high risk: 53%; see Figure 3; 3-way interaction between game, condition and condition order χ^2=6.63, *df*=1, *p*=0.01, *N*= 768). Additionally, leaving hare and coordination were both more likely in later trials (leaving hare: χ^2=8.02, *df*=1, *p*<0.01, *N*=1536; coordination: χ^2=5.84, *df*=1, *p*=0.02, *N*= 768).

The reduction in successful coordination on stag in the high risk game could have been due to both individuals coordinating on hare, the safe, risk dominant option. However, even when we consider coordination failures to be trials in which one individual stayed at hare while their partner went for the stag (and therefore successful coordination to include trials in which both individuals stayed at hare or both went for stag), coordination failures were generally more likely in the high risk game (low risk game: 6.6% trials, high risk game: 31.7%; except in the no-barrier trials for the no-barrier first group, they were equally likely to fail to coordinate in the low and high risk games; 3-way interaction between game, condition and order: χ^2=5.82, *df*=1, *p*=0.02, *N*= 768). This supports our conclusion that pairs were worse at coordinating decisions in high risk contexts.

The overall pattern of communication did not differ between the low and high risk games. That is, there was no pre-decision communication in either game. However, in both games subjects did occasionally communicate while they were at stag waiting for their partner (low risk: on 7.9% of trials the leader communicated; high risk: 11.5%; no significant difference between games; see Figure 4); with leaders being more likely to communicate the longer they waited (χ^2=34.96, *df*=1, *p*<0.01, *N*=686).

While subjects did not communicate at hare, they did visually monitor the situation (‘check back’ from their hare to either the stag or their partner’s cage). They did so more often in the high risk game (31.7% of trials) than low risk game (5.7% of trials; χ^2=4.79, *df*=1, *p<0.01*, *N*=1536). However, subjects were no more likely to check back when they could get information about their partner (no-barrier condition) as when only information about the presence of the stag was available (barrier condition), suggesting that increased checking may not have been motivated by coordination with a partner but monitoring the presence of the stag.

Discussion

These results suggest that chimpanzees did not adapt their coordination strategy to the new situation. As in the Bullinger et al. study, communication was rare overall (at the highest: 11% trials in the high risk game); did not differ in frequency between the two risk contexts; and never occurred pre-decision. This indicates that chimpanzees’ use of communication for coordination purposes may be fairly inflexible and restricted to attempting to get the attention of their partners post-decision, once they have already made their decision for the stag and time is running out. Bullinger et al. argued that a leader-follower strategy could best account for their findings. This account predicted coordination failure in the barrier condition of the high risk game. This was supported to a certain extent: a reduction in the barrier condition for those individuals that started with the no-barrier condition suggests that at least they may have been using a leader-follower strategy. Alternatively, subjects could have based their decisions on the predicted likelihood of a partner to go for stag (e.g. by projecting their own preferences as in [23]) and thus the likelihood of success. This is consistent with sensitivity to risk in group hunting frequency observed in the wild: males are more likely to hunt during times of fruit abundance (reduced loss in unsuccessful attempts; [24-26]).

In sum, rather than mediating risk through pre-decision communication, chimpanzees responded by adjusting their likelihood to cooperate. In Experiment 2b we examine how young children respond to our high-risk Stag Hunt game.

Experiment 2b: High Risk Stag Hunt with Children

Material and Methods

Subjects

Forty-eight children (24 girls, mean age: 54 months, range 46-58 months) were included in the analysis. Ten children were not tested because they either failed the pre-tests or were able to reach both sides of the stag-ropes. Children were paired into 24 same-sex dyads. All children were recruited from a database of middle-class children and brought by their parents to an institute for testing.

Materials

The apparatuses from the low risk experiment were re-used with some alterations. The value of the hare was increased so that the hare boxes now contained larger chocolate cereal balls rather than rice puffs. In order to remove the sound cues associated with the arrival of the stag the tray in the stag box started at the midway point and the gummibears were now inside red plastic balls, released by E3 via tubes at the back of the box. Also, the auditory cue indicating the approaching removal of the stag was removed. The length of the barrier was extended so that there was no visual access to their partner until both were at stag. Finally, music was played during pre-test and test trials to disguise the sound of the stag arriving, the closing of the hare box doors and children's movements.

Procedure

The design and procedure was the same as the low risk game with the following modifications. First, some of the training trials were replaced with demonstrations by experimenters to reduce the number of trials. The pre-test structure was adjusted to more closely follow the procedure for the chimpanzees: children had blocks of up to three social or non-social practice pre-test trials before the actual pre-tests and were then presented with two sets of one social and one non-social pre-test. If they responded correctly to both trial types within either set they could go on to test. However, if children did not pass, they were given one more set of "instructed" pre-tests in which E1 indicated what the best solution to the trial was. In the social pre-test: "The gummibears are here. Come and pull with me." In the non-social pre-test: "I have to answer my phone. Stay at the chocopuffs until I get back." If they responded correctly to these trials they moved on to test (see ESM for full details).

Coding

Coding was identical to Experiment 1, except that communication was divided into two categories: (1) ***Attention-getters***: verbalisations that get their partner's attention but do not refer to objects or actions in the game (e.g. calling their partner's name); and (2) ***Content:*** verbalisations that referred to objects in the game (e.g. red balls, gummibears, chocopops, rope), or to actions in the game (e.g. pulling, running, looking for gummibears). Content communication was further subdivided into: *imperatives* (instructions for their partner to perform an action related to the game, e.g. “come, pull with me”); *informatives* (reports to their partner about objects in the game or players’ actions in the game, e.g. “the balls are there”). Each occurrence of communication was coded for the type of communication hierarchically: content communication and attention-getters in the same phase was coded as content. Within the content category imperatives were prioritised over informatives.

Reliability. A second coder, unaware of the hypotheses coded one randomly selected trial per condition per dyad (33% of total trials). Agreement on whether dyads acquired the stag was 100% (K =1.00); whether individuals went for stag 97% (K =0.94); communication at hare 94% (K =0.85); communication after leaving hare 92% (K =0.81); monitoring at hare was 95% (K =0.89); monitoring after leaving hare was 89% (K =0.74); type of communication 91% (K =0.84).

Results

As with the chimpanzees, we directly compared the behaviour of children in the low risk and high risk games (Exp. 1 and 2a).

Children continued to leave hare at a high rate in the high risk game, despite the changes in risk. Individuals left hare on 92.0 % trials in the no-barrier condition (low risk: 96.7%, high risk: 88.2%) and 92.8% trials in the barrier condition (low risk: 98.3%, high risk: 88.2%), with no effects of game, condition or order (χ^2=14.05, df=8, p=0.08, N=528). Again, this resulted in high levels of coordination: 89.4% trials in the no-barrier condition (low risk: 95.0%, high risk: 84.7%, see Figure 1) and 90.2% trials in the barrier condition (low risk: 96.7%, high risk: 84.7%; χ^2=12.87, df=8, p=0.12, N=264).

Children responded to the increased risk of coordination failure by increasing their verbal communication prior to leaving the hare in the high risk game (low risk: 5.8% individual trials; high risk: 26%; χ^2=24.70, df=1, p<0.01, N=528). Strikingly, if we consider communication in terms of whether at least one of the partners communicated while both were still at hare (i.e. trials in which partners communicated before either of them had made their decisions), communication occurred in 47.9% of trials in the high risk game compared to 4.2% of trials in the low risk game (main effect of game: (χ^2=60.50, *df*=1, *p*< .01, *N*=264, no effect of condition or order; see Figure 4). In the high risk game most pairs (87.5%) communicated prior to leaving hare on at least one out of six trials, compared to 15.0% in the low risk game.

Children were most likely to communicate after leaving the hare in the riskiest trials: barrier trials in the high risk game. However, this was specific to when the barrier condition came first such that the pairs had little experience cooperating with each other (3-way-interaction between game, condition and order: χ^2=6.74, *df*=1, *p*=0.01, *N*=488).

Analysis of the type of verbal communication indicates how children were using it to reduce risk. Content communication was generally more prevalent than attention-getters (at hare: 80.7% trials with content communication, after leaving hare: 89.4%) and did not differ between high and low risk games, phase or condition (χ^2=12.90 , *df*=8, *p*=0.12, *N*=271). However, when we looked more closely at the type of content communication we found that informatives (typically “the balls are there!”) were employed most frequently in pre-decision communication, particulalrly in the high risk game (68.7% of trials with content communication were informatives; in the low risk game only eight trials contained content communication and 50% of those were informatives. In contrast, imperatives (such as “Hurry up!”) were generally used after leaving hare in both games (low risk: 90.0% of trials with content communication after leaving hare were imperatives, and high risk: 68%; main effect of phase χ^2=29.96, *df*=1, *p*<0.01, *N*=235). Children were also more likely to use informatives in the high risk game and the barrier condition, consistent with the hypothesis that they are using informatives to reduce risk when coordination is more challenging (main effects of game: χ^2=8.02, *df*=1, *p*<0.01 and condition: χ^2=5.26, *df*=1, *p*=0.02).

There was no possibility of visually monitoring a partner in the barrier condition in the high risk game while at hare, and reduced possibility after leaving hare due to the extended barrier. Thus, we only compared monitoring in the no-barrier condition. The pattern of pre-decision visual monitoring of their partners reflected that found for verbal communication: increasing in the high risk game relative to the low risk game (low risk: 13.3% trials, high risk: 29.1%; (χ^2=6.52, *df*=1, *p*=0.01, *N*=264) and also decreasing across trials (χ^2=7.33, *df*=1, *p*=0.01). There was a decrease in post-decision visual monitoring in the high risk game (perhaps because it was unnecessary in addition to the verbal communication and pre-decision monitoring; low risk: 72.4% trials, high risk: 38.6% trials; χ^2=21.69, *df*= 1, *p*<0.01, *N*=243).

Discussion

Increasing the difficulty of coordination in the high risk game had no effect on children's ability to achieve successful coordination, with children coordinating in more than 90% of trials in both the high and low risk versions. What differed was how they achieved coordination: in high risk conditions they increased their frequency of communication and visual monitoring before taking the risk of going for the stag, with verbal communication replacing much visual monitoring. The verbal communication was appropriate to the situation, as children's pre-decision communication was predominantly informative (e.g. "The gummibears are here.") – ensuring mutual knowledge of the stag's presence - whilst their post-decision communication was predominantly imperative (e.g. "Quick!"). Together these differences suggest a coordination strategy different from the cognitively simpler strategies such as the leader-follower: actively establishing mutual knowledge between partners in order to mediate the risk associated with coordination.

General Discussion

By presenting children and chimpanzees with a comparative foraging task we are able to clearly demonstrate a divergence in the mechanisms underlying mutualistic cooperation in humans and chimpanzees. Under conditions of low risk chimpanzees and children were both highly successful with minimal communication. Under conditions of high risk, however, the two species used different strategies. When chimpanzees were confronted with a more challenging Stag Hunt scenario in which the potential losses were higher and there were less cues to the appearance of the stag and a partner's decision, they were much less successful at coordinating, suggesting that there are limits to their coordination strategy. Individuals occasionally communicated while waiting for a partner at stag, but not prior to leaving hare. In contrast, children's coordination success remained high in the high risk game, and there was a marked increase in communication preceding their decision to leave hare. Children adjusted their strategy by using communication to establish mutual knowledge of the presence of the stag (e.g. by informing their partner "the balls are here!") and thus reducing the risk associated with leaving the hare to coordinate.

In comparison to Brosnan et al. [10, 11] we found humans, in this case 4 year olds, to be highly effective coordinators. This difference may be in large part due to differences in methodology. As the main aims of the current paper and Bullinger et al. [16] were to examine if and how the two species coordinated their decisions in the context of a Stag Hunt game, it was essential that the participants were aware of the contingencies of the game, particularly that their rewards were dependent upon the decision of their partner. In Brosnan et al. participants were not informed of the game structure, nor could it be inferred from the physical affordances of the task, as in the present study. Therefor it is unclear to what extent the level of coordination in the Brosnan et al. studies is due to a lack of understanding of the pay-off structure.

Our results are consistent with what is already understand about children's abilities to coordinate their actions: from 18 months can coordinate very simple actions in a cooperative activity with an adult or peer [27] [28]. Here we have shown that 4 year-olds are able to coordinate decisions, as well as actions, to cooperate successfully with a peer in a more complex coordination problem.

We have also extended findings on the role of communication in children's coordination. In Wyman et al. [20] non-verbal pre-decision communication from an adult experimenter (eye contact) influenced their decision making in the Stag Hunt game. We show that by 4 years children are able to initiate appropriate communication to solve a coordination problem with a peer. Similarly, Warneken et al. [29] found that communication predicted correct choices in a collaborative planning task with 3 and 5 year olds.

Several experimental studies have shown that dyads of chimpanzees can coordinate their actions to acquire a reward (e.g. [12, 14, 30]). In addition to this, the results from Bullinger et al. [16] and the current study show that they can successfully coordinate their decisions to forsake a safe, low value reward to acquire a higher value reward, although this is more limited in the high risk game. The pattern of communication seen here also reflects that of previous findings: when required to coordinate their actions to cooperate with conspecifics little communication is reported, even when the task demanded negotiation of conflicting preferences [15]. There is also little evidence from the wild that chimpanzees coordinate their decisions prior to the start of a hunt, though there is some recent evidence that chimpanzees vocalize to coordinate joint travel [31]. Although these calls (‘travel hoos’) did occur prior to the onset of travel movement, these calls could be interpreted as requests for travel companions by individuals who have already decided to travel (since callers continue to travel even if the recruitment has been unsuccessful) and thus, as more similar to the post-decision attention-getters, rather than the pre-decision communication exhibited by the children.

The Interdependence Hypothesis of the evolution of human cooperation suggests that humans have unique cognitive skills for mutualistic cooperation, an important set of which concern cooperative communication, and further that the selective context for uniquely human skills of cooperation was social coordination in something like Stag Hunt foraging contexts [5, 32]. In the current studies these unique abilities did not manifest themselves in the low risk game: both chimpanzees and children were successful coordinators. However, when the costs of coordination failure increased and the information available about a partner’s decision were reduced, the strategies available to chimpanzees limited their ability to coordinate; but children simply began communicating to the partner to establish mutual knowledge. This pattern of results is thus consistent with the hypothesis that humans evolved unique skills of coordination and communication in the context of especially risky coordination problems.

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References

[1] Cooper, R., DeJong, D.V., Forsythe, R. & Ross, T.W. 1996 Cooperation without reputation: Experimental evidence from prisoner's dilemma games. *Games and Economic Behavior* **12**, 187-218. (doi:DOI 10.1006/game.1996.0013).

[2] Fehr, E. & Gächter, S. 2002 Altruistic Punishment in Humans. *Nature* **415**, 137-140.

[3] Ostrom, E. 1998 A behavioral approach to the rational choice theory of collective action. *American Political Science Review* **92**, 1-22. (doi:Doi 10.2307/2585925).

[4] Alvard, M. 2012 Human social ecology. (Chicago: University of Chicago Press. Forthcoming.

[5] Tomasello, M., Melis, A.P., Tennie, C., Wyman, E. & Herrmann, E. 2012 Two Key Steps in the Evolution of Human Cooperation The Interdependence Hypothesis. *Current Anthropology* **53**, 673-692. (doi:Doi 10.1086/668207).

[6] Skyrms, B. 2004 *The Stag Hunt and the Evolution of Social Structure* Cambridge, Cambridge University Press.

[7] Duffy, J. & Feltovich, N. 2002 Do actions speak louder than words? An experimental comparison of observation and cheap talk. *Games and Economic Behavior* **39**, 1-27. (doi:DOI 10.1006/game.2001.0892).

[8] Boesch, C. 1994 Cooperative Hunting in Wild Chimpanzees. *Animal Behaviour* **48**, 653-667. (doi:DOI 10.1006/anbe.1994.1285).

[9] Mitani, J.C.C. & Watts, D.P. 1999 Demographic Influences on the Hunting Behavior of Chimpanzees. *American Journal of Physical Anthropology* **109**, 439-454. (doi:10.1002/(SICI)1096-8644(199908)109:4<439::AID-AJPA2>3.0.CO;2-3).

[10] Brosnan, S.F., Parrish, A., Beran, M.J., Flemming, T., Heimbauer, L., Talbot, C.F., Lambeth, S.P., Schapiro, S.J. & Wilson, B.J. 2011 Responses to the Assurance Game in Monkeys, Apes, and Humans Using Equivalent Procedures. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 3442-3447. (doi:10.1073/pnas.1016269108).

[11] Brosnan, S.F., Wilson, B.J. & Beran, M.J. 2012 Old World Monkeys are More Similar to Humans Than New World Monkeys When Playing a Coordination Game. *Proceedings of the Royal Society of London B Biological Sciences* **279**, 1522-1530. (doi:10.1098/rspb.2011.1781).

[12] Chalmeau, R. 1994 Do Chimpanzees Cooperate in a Learning Task? *Primates* **35**, 385-392.

[13] Hirata, S. & Fuwa, K. 2007 Chimpanzees (*Pan troglodytes*) Learn to Act With Other Individuals in a Cooperative Task. *Primates* **48**, 13-21. (doi:10.1007/s10329-006-0022-1).

[14] Melis, A.P., Hare, B. & Tomasello, M. 2006 Engineering Cooperation in Chimpanzees: Tolerance Constraints on Cooperation. *Animal Behaviour* **72**, 275-286. (doi:10.1016/j.anbehav.2005.09.018).

[15] Melis, A.P., Hare, B. & Tomasello, M. 2009 Chimpanzees Coordinate in a Negotiation Game. *Evolution and Human Behavior* **30**, 381-392. (doi:10.1016/j.evolhumbehav.2009.05.003).

[16] Bullinger, A.F., Wyman, E., Melis, A.P. & Tomasello, M. 2011 Coordination of Chimpanzees (Pan troglodytes) in a Stag Hunt Game. *International Journal of Primatology* **32**, 1296-1310. (doi:DOI 10.1007/s10764-011-9546-3).

[17] King, A.J., Johnson, D.D. & Van Vugt, M. 2009 The origins and evolution of leadership. *Curr Biol* **19**, R911-916. (doi:10.1016/j.cub.2009.07.027).

[18] Schelling, T. 1960 *The Strategy of Conflict*. Cambridge, Harvard University Press.

[19] Lewis David, K. 1969 Convention: a philosophical study. (Harvard University Press, Cambridge, Mass.

[20] Wyman, E., Rakoczy, H. & Tomasello, M. 2013 Non-verbal communication enables children’s coordination in a “Stag Hunt” game. *European Journal of Developmental Psychology* **10**, 597-610.

[21] Byrt, T., Bishop, J. & Carlin, J.B. 1993 Bias, Prevalence and Kappa. *J Clin Epidemiol* **46**, 423-429.

[22] Baayen, R.H., Davidson, D.J. & Bates, D.M. 2008 Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language* **59**, 390-412. (doi:DOI 10.1016/j.jml.2007.12.005).

[23] Schmelz, M., Call, J. & Tomasello, M. 2011 Chimpanzees know that others make inferences. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 3077-3079. (doi:10.1073/pnas.1000469108).

[24] Gilby, I.C., Eberly, L.E., Pintea, L. & Pusey, A.E. 2006 Ecological and Social Influences on the Hunting Behaviour of Wild Chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour* **72**, 169-180. (doi:10.1016/j.anbehav.2006.01.013).

[25] Gilby, I.C. & Wrangham, R.W. 2007 Risk-Prone Hunting by Chimpanzees (*Pan troglodytes schweinfurthii*) Increases During Periods of High Diet Quality. *Behavioral Ecology and Sociobiology* **61**, 1771-1779. (doi:10.1007/s00265-007-0410-6).

[26] Watts, D.P. & Mitani, J.C.C. 2002 Hunting Behavior of Chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology* **23**, 1-28.

[27] Warneken, F., Chen, F. & Tomasello, M. 2006 Cooperative activities in young children and chimpanzees. *Child Dev* **77**, 640-663. (doi:10.1111/j.1467-8624.2006.00895.x).

[28] Brownell, C.A., Ramani, G.B. & Zerwas, S. 2006 Becoming a social partner with peers: cooperation and social understanding in one- and two-year-olds. *Child Dev* **77**, 803-821. (doi:10.1111/j.1467-8624.2006.00904.x).

[29] Warneken, F., Steinwender, J., Hamann, K. & Tomasello, M. 2014 Young children's planning in a collaborative problem-solving task. *Cognitive Development* **31**, 48-58.

[30] Schneider, A.C., Melis, A.P. & Tomasello, M. 2012 How chimpanzees solve collective action problems. *Proceedings of the Royal Society B-Biological Sciences* **279**, 4946-4954. (doi:DOI 10.1098/rspb.2012.1948).

[31] Gruber, T. & Zuberbuhler, K. 2013 Vocal Recruitment for Joint Travel in Wild Chimpanzees. *PloS one* **8**. (doi:ARTN e76073 DOI 10.1371/journal.pone.0076073).

[32] Tomasello, M. 2008 *Origins of Human Communication*. Cambridge, MA, MIT Press.

Figure 1: The set-up for the children (Exp. 1 and 2b). Both children start at their hare boxes (top left and right), and then stag reward (red balls) becomes available. The barrier (between the two children) is present only in the barrier condition.

Figure 2: Test trial set-up for the chimpanzees (Exp. 2a) in the no-barrier condition. Each individual has their own hare box (top left and right). The stag reward is then placed between the two cages.

Figure 3: The mean likelihood to successfully coordinate for chimpanzees (left) and children (right) in the low and high risk games with 95% confidence intervals.

Figure 4: The mean likelihood for communicate to occur before either partner left hare (upper panels), and after at least one partner has gone for the stag (lower panels) for chimpanzees (left panels) and children (right panels) in the low and high risk games (with 95% confidence intervals).