Animal Behaviour 116 (2016) 61–74

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Chimpanzees coordinate in a snowdrift game

Alejandro Sánchez-Amaro [a, *], Shona Duguid [a], Josep Call [a, b], Michael Tomasello [a]

[a] Max Planck Institute for Evolutionary Anthropology, Developmental and Comparative Psychology, Leipzig, Germany
[b] School of Psychology and Neuroscience, University of St Andrews, St Andrews, U.K.

ARTICLE INFO

Article history:
Received 15 September 2015
Initial acceptance 13 October 2015
Final acceptance 11 March 2016

MS. number 15-00796R

Keywords:
chimpanzees
conflict
cooperation
coordination
decision making
snowdrift game

The snowdrift game is a model for studying social coordination in the context of competing interests. We presented pairs of chimpanzees, *Pan troglodytes*, with a situation in which they could either pull a weighted tray together or pull alone to obtain food. Ultimately chimpanzees should coordinate their actions because if no one pulled, they would both lose the reward. There were two experimental manipulations: the tray's weight (low or high weight condition) and the time to solve the dilemma before the rewards became inaccessible (40 s or 10 s). When the costs were high (i.e. high weight condition), chimpanzees waited longer to act. Cooperation tended to increase in frequency across sessions. The pulling effort invested in the task also became more skewed between subjects. The subjects also adjusted their behaviour by changing their pulling effort for different partners. These results demonstrate that chimpanzees can coordinate their actions in situations where there is a conflict of interest.

Social species need to coordinate with others to benefit from living in a group. However, in many cases individuals have competing interests. For instance, chimpanzees, *Pan troglodytes* (Boesch, 1994, 2002) and lions, *Panthera leo* (Scheel & Packer, 1991) are more successful when they hunt and defend their territories as a group; but individuals may be tempted to lag behind to avoid potential costs (e.g. risk of injury) and benefit from others' efforts (Gilby & Connor, 2010).

Previous experimental studies have found that when individuals need to work together to retrieve food chimpanzees can coordinate their actions (Chalmeau, 1994; Cronin, Bridget, van Leeuwen, Mundry, & Haun, 2013 Hirata & Fuwa, 2007; Melis, Hare, & Tomasello, 2006; Suchak, Eppley, Campbell, & de Waal, 2014). To a certain extent, chimpanzees can also coordinate their actions when there is an alternative (although lower-value) reward that can be obtained individually (Duguid, Wyman, Bullinger, Herfurth-Majstorovic, & Tomasello, 2014). Even when Melis, Hare, and Tomasello (2009) introduced a conflict of interest by presenting chimpanzee pairs with a choice between two cooperative tasks, one with equal payoffs (3–3) and other with unequal payoffs (5–1), pairs still cooperated in the majority of trials. In contrast, Bullinger, Melis, and Tomasello (2011) found that chimpanzees preferred to work alone to obtain the same amount of food. Their preference for solitary over social work, however, was reversed when the payoff of the social option was higher than the payoff of the solitary option. The subject's preference for the nonsocial option suggests that they did not take into account their partner's preference because the partner could not obtain the rewards by pulling alone.

In previous studies that did not offer subjects an alternative nonsocial option (but see Bullinger et al., 2011), subjects needed to cooperate with a partner to complete the task regardless of the payoff's distribution (Melis et al., 2009) or time constraints (Duguid et al., 2014). However, in some situations such as group hunting, initiating the action and investing energy in a cooperative act is not necessarily the best strategy from an individual's perspective as it is a costly and risky action (Gilby & Connor, 2010). Therefore, if a group member starts a hunt, others can benefit without actively participating and incurring the costs. However, if no one starts the hunt, they all lose the chance to get the prey. How can chimpanzees solve this dilemma? According to Boesch (2002), chimpanzees coordinate to take specific roles when initiating a hunt, providing a cooperative solution to the dilemma. However, chimpanzees may use other strategies when initiating the hunts. For instance Boesch (2002) reported that young chimpanzees tended to start the chase. This could be explained if we consider that young chimpanzees did not fully understand the contingencies of the hunting endeavour and therefore were willing to initiate it whereas more experienced

* Correspondence: A. Sánchez-Amaro, Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103, Leipzig, Germany.
E-mail address: alex_sanchez@eva.mpg.de (A. Sánchez-Amaro).

http://dx.doi.org/10.1016/j.anbehav.2016.03.030
0003-3472/

chimpanzees lagged behind (see Tomasello, 2009). Similarly, a study by Gilby et al. (2015) found evidence that some chimpanzees, described as 'impact-hunters', are willing to pay the extra costs to begin the hunt, letting others join in when the risks are lower. The dilemma faced by individuals in such situations is thus whether to initiate the action or not, given that if no-one initiates everyone loses out. In theory, each individual's preference ranking should be that (1) other begins, (2) I begin or (3) no-one begins. Despite the observational work of previous studies (Boesch, 2002; Gilby et al., 2015) there has been little experimental work studying how chimpanzees would behave in situations where a conflict of interest is present (but see Schneider, Melis, & Tomasello, 2012).

These types of interactions have been modelled by theorists in the snowdrift game (Doebeli & Hauer, 2005; Kun, Boza, & Scheuring, 2006; Sudgen, 1986). In the classic description of the snowdrift situation two cars become stranded on a highway that is covered with snow. The snow must be shovelled off the road before the drivers can return home. They could shovel the snow together and share the work, or alternatively, one driver could do it alone. Each driver would prefer that the other one do it. However, if one of them defects the other should shovel the snow, thus paying the costs to return home. So in the snowdrift dilemma, subjects have a common goal that can be achieved by either performing a cooperative act (either together or individually) or free riding. Of course, it is in the interest of each subject to defect and let the partner incur the cost but if neither pays the costs both lose. According to recent literature (Kun et al., 2006) chimpanzee hunting could be explained by applying the metaphor of the snowdrift game. Chimpanzees would prefer others to start the hunt unless no one else starts. In the latter case, as in the previous example, the chimpanzee would prefer to begin the hunt rather than let the monkey escape. So, unlike in the prisoner's dilemma (Axelrod & Hamilton, 1981; Maynard Smith, 1982) acting cooperatively can avoid the worst-case scenario as a cooperative act will always provide a benefit, even for the subject that carries out the costly action.

Besides agent-based model studies, the snowdrift game has been empirically applied to study human strategic behaviour (Duffy & Feltovich, 2002; 2006; Kümmerli et al., 2007; Rapoport & Chammah, 1966). Overall, these studies have found that humans cooperate more when they are faced with a snowdrift game in comparison to the prisoner's dilemma situation. However, as far as we know the snowdrift has not yet been used to study strategic decision making in nonhuman primates.

The aim of this study was to use the snowdrift model to investigate how chimpanzees solve a coordination task with a conflict of interest. We presented pairs of chimpanzees with a version of the snowdrift game in which they obtained food rewards by pulling a weighted tray towards them. They could either perform a cooperative act (pull the rope and do all the work or both pull and thus share the load) or one could free-ride while the other did the work. Importantly, chimpanzees were free to decide the amount of weight they pulled. Therefore, cooperation, defined by both individuals pulling during the same trial, could be skewed towards one subject depending on the efforts invested by each member of the dyad. In real-life situations, chimpanzees are able to vary their degree of investment by starting the chase, follow other individuals and join the chase or lag behind and reap the benefits from the hunt (Boesch, 2002; Gilby et al., 2015). For instance, in the case of hunting, chimpanzees could theoretically initiate the hunt but then let others do most of the work, although to our knowledge this has not been empirically demonstrated. Therefore subjects are not only faced with a binomial decision (either cooperate or free-ride) as in previous cooperative games (Chalmeau, 1994; Duguid et al., 2014; Hirata & Fuwa, 2007; Melis et al., 2006, 2009) but can adjust their actions by investing different amounts of effort (i.e. their speediness in chasing the monkey), allowing them to make precise decisions based on the physical contingencies and the partners' actions. In our task both subjects got the same amount of food as long as one individual pulled, so there was no need for cooperation. However, if neither pulled within a certain time frame both lost the food. This set-up reflects the payoffs of the two-person snowdrift game where the best strategy for a chimpanzee was to wait for the partner to pull and obtain the benefit (b) but pay the cost of the action if the partner did not pull ($b-c$) to avoid losing the rewards if no one pulls ($b = 0$). At the same time, if both partners pull simultaneously, that results in an intermediate cooperative strategy where costs are divided ($b-c/2$).

Importantly, although this set-up uses the same payoff matrix as behavioural economic experiments with adults, it differs from these studies in that chimpanzees in our task were not strangers and they were free to interact during the task. However, this set-up is more ecologically valid for chimpanzees because interactions with strangers are relatively rare and often aggressive; cooperation occurs between known group members (Boesch et al., 2008).

Our main interests were whether chimpanzees (1) would maximize their benefit (food − cost of pulling) by waiting for a partner to pull first, (2) would solve the task (get the food) by cooperating or free riding, or (3) change their strategies with different partners. We manipulated weight and time to approximate the contingencies of chimpanzee hunting: the apes had to overcome the costs to initiate the action (the weight that they have to move) while the prey was only available for a limited time (the time limits). If chimpanzees acted strategically, we expected them to wait longer to pull when the costs of pulling the tray were high (i.e. it was heavy) and for one individual to free-ride more often (understood as not pulling at all) while the other always pulled. In contrast, during low-weight trials we expected chimpanzees to pay less attention to their partners' actions and thus wait less to pull. We also expected chimpanzees to wait longer in long trials as they would have more opportunity to free-ride than in short trials. Our study consisted of two phases: all subjects completed the test with one partner first before partners were reshuffled for a second round. With this manipulation we could study the overall effect of experience and whether they were able to adjust their actions to the behaviour of their partners as they should consider not only the physical contingencies of the task (weight and time) but also their partners' decisions to maximize their rewards and coordinate their actions.

METHODS

Subjects

We tested seven female and five male captive chimpanzees (mean age = 23.4 ± 13.8, range 9–39 years) housed at the Wolfgang Köhler Primate Research Center in Leipzig Zoo, Germany (see Table A1). In phase 1 of the study all 12 made up six unique pairings. In phase 2, 10 of the 12 made up five new pairings. The experimental set-up required subjects to be in the same cage during testing. Consequently, we could only pair chimpanzees with a high degree of tolerance. Additionally, we paired them according to similar weight (as a proxy for strength).

The task required subjects to obtain out-of-reach food rewards (one 4 cm banana piece for each individual) by pulling on ropes to move a tray towards them (Fig. 1). Each subject had access to one of two ropes and the tray could be pulled with either one or both ropes. The weight of the tray (and thus the effort required to pull it in) could be adjusted by the experimenter. The weight (in kg) pulled by each individual was measured by two sets of scales that connected each of the ropes to the central weight. We recorded all measurements displayed on each of the scales for the duration of