

Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically

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Human cooperation is unparalleled in the animal world and rests on an altruistic concern for the welfare of genetically unrelated strangers. The evolutionary roots of human altruism, however, remain poorly understood. Recent evidence suggests a discontinuity between humans and other primates because individual chimpanzees do not spontaneously provide food to other group members, indicating a lack of concern for their welfare. Here, we demonstrate that common marmoset monkeys (*Callithrix jacchus*) do spontaneously provide food to nonreciprocating and genetically unrelated individuals, indicating that other-regarding preferences are not unique to humans and that their evolution did not require advanced cognitive abilities such as theory of mind. Because humans and marmosets are cooperative breeders and the only two primate taxa in which such unsolicited prosociality has been found, we conclude that these prosocial predispositions may emanate from cooperative breeding.

cooperative breeding | non-human primates | prosociality | helping | dictator game

Humans are a remarkably cooperative species (1–5). People frequently cooperate with genetically unrelated strangers, often in large groups, and with people they will never meet again (3, 6–9). These exceptional forms of cooperation, which have been amply documented by field observations and in formal experiments (3, 6), are based on a psychological predisposition known to economists as other-regarding preferences (3)—i.e., a concern for the welfare of others. Here, we will call this prosocial motivational predisposition unsolicited prosociality.

Chimpanzees also engage in cooperative behaviors in a variety of contexts, such as food sharing, hunting, territory patrols, and targeted helping, both in nature (10–12) and captivity (13–15). Nonetheless, three recent experiments that explicitly tested for unsolicited prosociality indicate the absence of this psychological predisposition in our closest living relatives (16–18). Instead, the cooperative and prosocial behaviors of chimpanzees, remarkable as they are, appear to be part of self-interested cooperation (19) and reciprocal exchanges (14) or to be solicited by the receiver (15). The presence of targeted helping might appear to provide evidence for unsolicited prosociality (15), but experimental tests necessarily involve signaling of need by the potential recipient and therefore do not allow us to decide unambiguously whether the help is truly spontaneous. Finally, if unsolicited prosociality were to characterize chimpanzees, it should at least be expressed in the closest social bond, that between mother and infant. However, even infant chimpanzees must beg to receive valuable food items from their mothers (20, 21), and in formal experiments, mothers did not even show unsolicited prosociality toward their immature offspring (17).

In sum, the most parsimonious conclusion to date is that chimpanzees lack unsolicited prosociality and that, therefore, this psychological predisposition represents a uniquely human adaptation. However, Silk *et al.* (16) proposed a second possible evolutionary scenario for the presence of other-regarding preferences in humans but not chimpanzees. According to this

scenario, unsolicited prosociality has appeared in our lineage after the split from the great apes but may also have arisen independently in other species, like cooperative breeders, that are characterized by strong mutual interdependence and high social tolerance.

The great majority of primates do not show food sharing, mutual interdependence, and high social tolerance involving all independent group members. The most prominent exceptions among non-human primates are callitrichid monkeys, which are cooperative breeders. Groups contain a breeding pair and a variable number of nonbreeding mature and immature helpers, usually offspring. They emit food calls when they encounter valued food items, share food (22), and engage in communal territory defense (23). In experiments, they solve problems cooperatively (24, 25) and reciprocate food donations in repeated encounters (26). As in chimpanzees, these behaviors could be based on expectations of reciprocation or responsiveness to solicitation; hence, they may not be based on unsolicited prosociality. Nonetheless, because callitrichid helpers also carry infants extensively, spontaneously provision them with food even in the absence of begging (27), and take turns in vigilance (23), the presence of unsolicited prosociality may be more likely in these cooperative breeders.

As the chimpanzee case indicates, the underlying motivational forces can only be revealed by controlled experiments and not by observations of spontaneous cooperation in natural environments. An experiment designed to evaluate the factors affecting reciprocal exchanges in a callitrichid monkey (*Saguinus oedipus*) revealed results suggestive of unsolicited prosociality (26). Here, we systematically assess the existence of unsolicited prosociality in another callitrichid monkey, the common marmoset (*Callithrix jacchus*).

The presence of unsolicited prosociality in chimpanzees has been examined using an experimental design in which a subject playing the donor role could give food to a recipient by choosing between two payoff distributions (16–18). These experiments show that chimpanzee donors did not differentiate between a payoff distribution in which both donor and recipient received a food item (1,1) and one resulting in a reward only for the donor (1,0). Neither was there any indication that donors differentiated between a payoff distribution that yielded a reward only for the recipient (0,1) and a distribution that provided neither player with a payoff (0,0). Cognitively, the choice between (0,1) and (0,0) is less demanding for the donor than a choice between (1,1) and (1,0) because it involves fewer food items that have to be considered simultaneously. Motivationally, however, choosing

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Fig. 1. Experimental setting. A donor, the marmoset on the right-hand side, has the choice between two trays representing the payoff distributions (0,1) (upper tray with a cricket in the left food bowl) or (0,0) (lower tray). The donor pulls the tray with the (0,1) payoff distribution, resulting in a payoff to the recipient on the left side but none to itself.

(0,1) against (0,0) is more difficult because the potential donor does not receive any food for itself regardless of its choice. In the present experiment (Fig. 1), a marmoset donor had a choice between the cognitively simple payoff distributions (0,1) and (0,0), presented on two different trays. We therefore tested for a strong version of unsolicited prosociality in which the relevant spontaneous prosocial tendency must outweigh possible “envy.”

Results

Marmoset donors pulled the (0,1) tray more often when a partner was present than in the control condition when the partner was absent [individual means; one-sample *t* test, two-tailed: $t(14) = 2.662$, $P = 0.019$; Fig. 2]. This result provides the first indication that common marmosets care about the payoff to others and actively work to provide them with food even when not receiving a payoff personally. However, this pattern of results was not found in all classes of animals. Although female and male breeders as well as male helpers all pulled the (0,1) tray preferentially when a potential recipient was present, the same was not the case for female helpers [one-way ANOVA for

differences in pulling the (0,1) tray in partner-present vs. partner-absent condition: $F(3,11) = 6.322$, $P = 0.009$; for post hoc comparisons, see Fig. 2]. When female helpers are excluded from the analysis, the difference between pulling the prosocial tray when the partner was present compared with when the partner was absent increased to 21.2%; this large difference is highly significant [one-sample *t* test, two-tailed: $t(9) = 5.082$, $P = 0.001$]. The partitioning of our subject pool into male and female helpers as well as male and female breeders was justified by an additional analysis using regression models and an information theoretic approach to model selection [see [supporting information \(SI\) Text](#) and [SI Tables 1 and 2](#)]. A lack of prosociality in female helpers is consistent with some naturalistic observations indicating that female helpers engage less in infant carrying (28–30).

Four possible alternative explanations could potentially account for the main findings mentioned above. First, animals may not have really understood the experimental set-up and pulled (0,1) to obtain food for themselves. Arguing against this possibility is that in the control condition of the experiment—i.e., when the partner was absent and the partition was in place—the animals pulled the (0,1) tray dramatically less often than during the pretest baseline in which they did have access to the recipient’s compartment [Fig. 3; one-sample *t* test, $t(14) = 8.11$, $P < 0.001$; see [Methods](#) for details]. Moreover, the animals’ prosociality did not decline during the tests (see [SI Text](#)). We nonetheless conducted two additional confirmatory tests. In the first, conducted 4–9 months after the last experiment, we retested the animals using the baseline condition. All animals but one instantaneously reached the baseline criterion again [Fig. 3; difference between pretest baseline and posttest baseline: $t(13) = 0.9$, $P = 0.365$], indicating that the animals still understood the consequences of their actions. This conclusion was corroborated by a second control test in which, in the absence of any partner, the partition was either in place or absent in alternating trials. This procedure has a high potential to create confusion and thus represents a particularly strong test of the animals’ understanding. Nonetheless, the marmosets pulled the (0,1) tray significantly more often when they had access to the other compartment [$t(13) = 4.6$, $P < 0.001$], suggesting that they

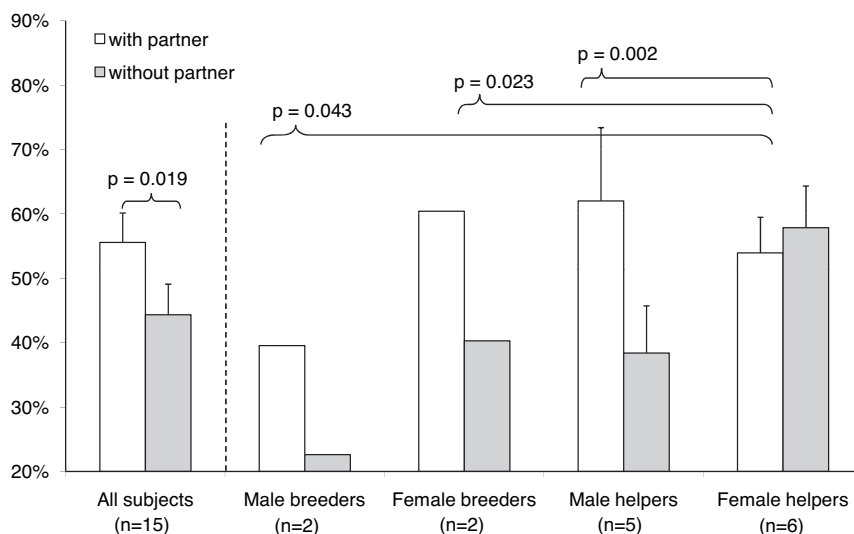


Fig. 2. Responses of the donors in the presence or absence of the recipient (mean + SEM; $n = 15$ individuals). The pair of bars on the left show that the proportion of prosocial choices (0,1) in all marmosets is significantly higher if the partner (recipient) is present than if the partner is absent (two-tailed *t* test: $P = 0.019$). The remaining bars on the right show the proportion of prosocial choices (0,1) in different classes of individuals. Post hoc comparisons show that female helpers are significantly different from each of the other three classes. For example, in female helpers, the difference in pulling the prosocial tray in the partner absent vs. the partner present condition is significantly different from the difference in male helpers (least significant difference, $P = 0.002$). In contrast, no significant differences are present between male breeders, female breeders, and male helpers.

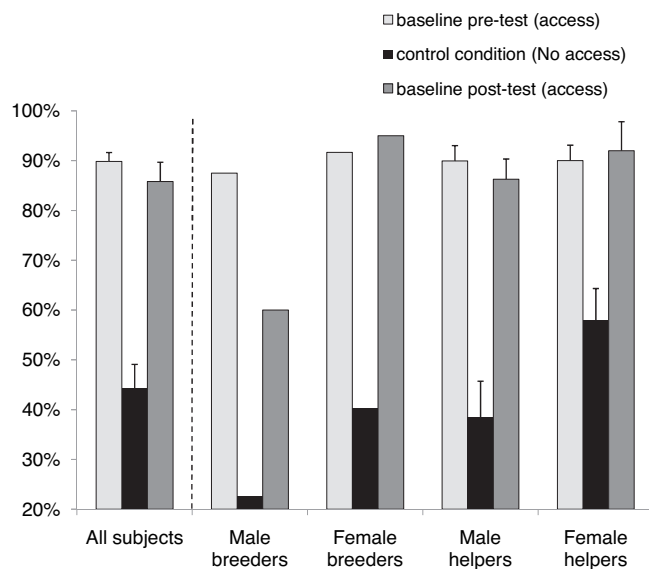


Fig. 3. Understanding of the experimental set-up. Shown are percentages (+SEM) of pulling the (0,1) tray in the pretest baseline (with access to the other compartment), the experimental control condition (no access to the other compartment), and the posttest baseline (with access to the other compartment) 4–9 months after the last session of experiment 1. In all three conditions, no partner was present. Only in the pretest and the posttest baseline did pulling the (0,1) tray provide food to the puller. Because animals pulled more frequently in these two conditions compared with the experimental control condition, they understood the apparatus.

had a subtle and lasting understanding of the experimental set-up.

A second alternative might be that the donors' behavior could have been driven by social facilitation—i.e., a general increase in arousal level and activity due to the mere presence of a partner (31). However, because social facilitation predicts a general increase in the rate of pulling when a partner is present, the presence of a partner should be associated with an increase in the rate of pulling both trays, regardless of the payoff distribution, so that the overall rate of pulling increases. In contrast to this prediction, the overall rate of pulling [i.e., pulling either (0,1) or (0,0)] did not depend significantly on the presence of the partner [one sample *t* test, two-tailed: $t(14) = 1.12, P = 0.25$]. Moreover, the three classes of animals (male breeders, female breeders, and male helpers) that significantly increased the pulling of the prosocial tray (0,1) when the partner was present also showed a significant decrease [$t(8) = -2.317, P = 0.049$] in choosing the asocial tray (0,0) when the partner was present, a finding that again directly contradicts the social facilitation hypothesis but is consistent with the existence of unsolicited prosociality. The female helpers, who did not exhibit unsolicited prosociality, pulled the (0,0) tray equally often with and without a partner [$t(5) = 0.486, P = 0.648$]. We can therefore reject social facilitation as an alternative explanation.

A third alternative is that the donors' (0,1) pulling was a response to solicitation by the recipient. However, begging by recipients, the most obvious form of solicitation, occurred in only 3% of all trials, and a single juvenile female was responsible for 55% of all begging. Therefore, begging was too rare to have caused the main result in Fig. 2. Potentially, attempts by the recipients to reach toward the tray before the donor pulled could also have been interpreted as begging by the donors. Unlike overt begging, reaching was common (41.9% of all trials). However, reaching by the recipients before pulling by the donors had no effect on the donors' pulling of the food-baited tray [$t(14) = -1.59, P = 0.135$; Fig. 4], confirming that the donors'

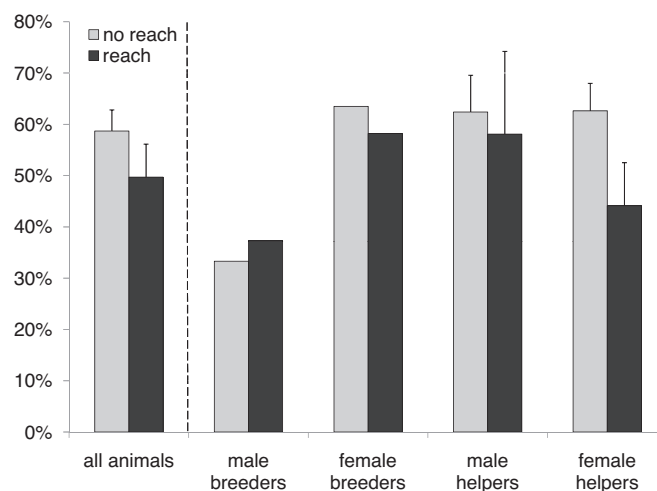


Fig. 4. Effect of recipients' reaching toward the trays on the donors' pulling behavior. Shown are percentages (+SEM) of pulling the (0,1) tray when pulling was preceded by the recipient's reaching toward the trays, as compared with trials in which recipients did not attempt to reach toward the trays. The donors did not provide the food more often if the recipients reached for the trays before the donor pulled the tray.

tendencies to pull the prosocial tray was not solicited by the recipients. This result also refutes alternative ways in which reaching by the recipients could have induced (0,1) pulling in the donors. For example, reaching could have increased the food's salience for the donor and thus induced it to reach toward the trays, hence producing a stimulus enhancement effect (32), or perhaps reaching is simply contagious in this species. Under either scenario, reaching would have increased the rate of (0,1) pulls among donors, which did not happen.

A fourth possibility is that the donors' behavior was driven by the expectation of reciprocation. By testing each dyad in only one direction, our design excluded reciprocity within the context of the experiment. Furthermore, the donor never begged for food after a prosocial choice, nor did the recipient ever share the food with the donor after the donor had chosen the prosocial tray. An expectation of delayed reciprocation after returning to their home cages is also unlikely because subjects were provisioned immediately upon returning to their cages, and not a single case of delayed reciprocity was observed and is in fact highly unlikely due to cognitive constraints (33, 34). Finally, if delayed reciprocity can falsely produce positive results in experiments testing for unsolicited prosociality, such an effect would have been most likely in chimpanzees, which are known for their capacity for delayed and calculated reciprocity (14). Because chimpanzees failed the prosociality test (16–18), whereas marmosets passed, this possibility is implausible.

Elimination of these four alternative explanations confirms that common marmosets display unsolicited prosociality, at least among the dyads tested here. However, because most of our dyads were related, it is possible that unsolicited prosociality is limited to relatives. To further explore this issue, we paired additional subjects with nonrelated partners in a second experiment, to gain a combined sample of 11 donor subjects (three male breeders, five female breeders, and three adult male helpers). These animals pulled the prosocial tray more often in the presence of the unrelated partner than when alone [mean 60.6% vs. 40.2%; two-tailed *t* test: $t(10) = 2.33, P = 0.042$; Fig. 5]. Thus, marmosets show equally strong unsolicited prosociality toward nonkin as toward kin. However, the unsolicited prosociality need not be indiscriminate because the nonkin in this experiment were actual or potential mates rather than same-sex

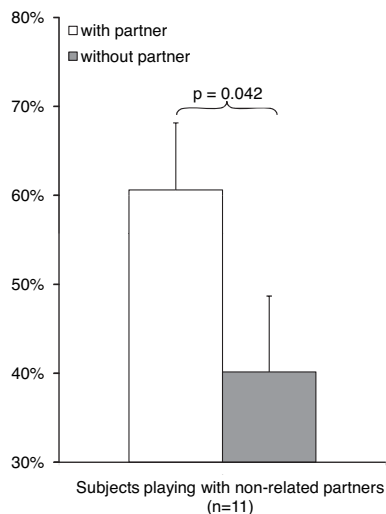


Fig. 5. Responses of donors in the presence or absence of a genetically unrelated recipient (mean + SEM; $n = 11$ individuals). Donors chose the prosocial tray significantly more often if a genetically unrelated recipient was present [two-tailed t test: $t(10) = 2.33$, $P = 0.042$], indicating that marmosets also show unsolicited prosociality toward nonkin.

strangers, which would probably be attacked (35). Yet, this prosociality is not merely kin favoritism because marmosets, just like other primates, recognize kin as shown by their ability to avoid inbreeding (36, 37) and differentiate between related and nonrelated extragroup individuals (38). Nonetheless, kin selection may well have played a role in the origin of unsolicited prosociality (39), which subsequently was extended to actual and prospective social partners (40).

Discussion

The presence of unsolicited prosociality in a non-human primate, the common marmoset, shows that the evolution of an altruistic concern for others does not depend on the presence of theory of mind, which has been proposed as a limiting factor in the evolution of altruism (16, 41) but is lacking in common marmosets (42). Neither does it critically depend on the presence of high general cognitive abilities, which are far lower in marmosets than apes (43). Instead, it may be that an external, contextual factor, rather than an internal, cognitive one, explains the presence of unsolicited prosociality in both marmosets and humans. Chimpanzees are among the most cooperative primates and nonetheless do not show unsolicited prosociality. Hence, unsolicited prosociality, if it occurs at all, should be very rare among primates, and their joint occurrence in humans and marmosets may reflect the joint occurrence of an uncommon contextual variable not found in other primates: cooperative breeding. Unsolicited prosociality may serve to optimize the functioning of cooperative breeding systems (4, 16). Humans are the only other primate besides callitrichids to have evolved features of cooperative breeding, such as infant care by grandmothers, older siblings, and fathers (4, 44, 45). Because only cooperatively breeding primates show such strong mutual interdependence (46), unsolicited prosociality in humans is likely to have arisen as our ancestors adopted extensive allomaternal care.

Recent proposals emphasize the role of shared intentionality as the crucial difference between the cognition of humans and other species (47). Shared intentionality is critically based on a motivation to altruistically share psychological states with others. However, why did such a motivation emerge in the human lineage but not in great apes? We hypothesize that unsolicited prosociality, which arose in the context of provisioning, carrying,

and sharing of food, was then generalized toward the sharing of information and psychological states, thus forming the basis for shared intentionality. Hence, adding unsolicited prosociality to the ape-like brain of our ancestors, which in contrast to marmosets already had some basic knowledge of psychological states (48), may have released a cascade of further developments toward shared intentionality and all its consequences: joint attention, language, instructed learning, and uniquely human forms of cooperation (49), as well as a fully developed theory of mind. In sum, the human sociocognitive package relies critically on the presence of unsolicited prosociality, which some have argued evolved in hominids because extensive allomaternal care arose sometime during our evolution (4).

Methods

Subjects. The experiment's subjects and their roles are listed in SI Table 3. In experiment 1, we tested 15 donors from two family groups. All animals played with fellow group members, which were all relatives except for the members of the breeding pair. We composed 57 dyads with 15 different donors and excluded reciprocation effects by testing dyads only in one direction. The test direction was chosen according to the main direction of spontaneous food sharing that occurs under natural conditions—i.e., from breeding parent to offspring, from male to female, and from older sibling to younger sibling.

In experiment 2, we tested 11 donors with unrelated recipients. The dyads were either members of bonded pairs (eight dyads) or unfamiliar different-sex individuals from different groups (three dyads) who encountered each other for the first time during the experiment. The subjects were housed in social groups containing breeding pairs with variable numbers of related helpers. Groups were in auditory and olfactory, but not visual, contact. For details on housing, see ref. 50.

Set-Up and Apparatus. The experimental cage contained two adjacent compartments (SI Fig. 6), one for the donor and one for the recipient, which were separated by a removable mesh partition. The apparatus was directly in front of this partition, and consisted of two trays, one above the other, placed in front of the two compartments.

The trays were longer on one side and could therefore only be pulled from the donor's compartment (SI Fig. 7). The trays contained two food bowls each. After the tray was pulled within reach, one food bowl was available to the donor, and the other was available to the recipient. If one tray was pulled, the other was automatically blocked, so that the animals had to make an exclusive choice in each trial.

Because the apparatus was directly in front of the door separating the two compartments, the donor could simultaneously see the apparatus and whether the mesh partition was in place. Thus, the experimental set-up was intuitive in that the donor immediately knew which of the three experimental conditions it was experiencing: (i) partner absent/door open (baseline condition); (ii) partner present/door closed (test condition); or (iii) partner absent/door closed (control condition).

Procedure. Before the test, the animals were subjected to a training phase to ensure that they understood the consequences of their choices. During this baseline condition, the animals were tested individually in the donor role and had access to both compartments of the experimental cage. One cricket was placed on the recipient side of either the upper or the lower tray, and hence the subjects could acquire the food by pulling the correct tray and then moving into the recipient compartment to collect the food. A trial always started with the experimenter showing the cricket to the animals and then baiting the corresponding tray behind a screen. The experimenter then removed the screen and, while turning away, pushed both trays simultaneously within

reach of the donor. A trial ended either when the test animal pulled one of the two trays or after 30 sec. Animals only entered the test after they had reached the baseline criterion of pulling the baited tray in at least 10 of 12 consecutive trials (83%) using a running frame (with the food either on the upper or lower tray). This pretest baseline condition ensures that the animals understood both the apparatus and the spatial conditions of the experiment, and this means that they knew that by pulling the (0,1) tray, food would be delivered to the other compartment.

In the experiments, the two compartments were separated by a wire mesh partition, and we tested whether marmosets would pull the tray containing food (0,1) to within their partners' reach. However, marmosets might simply prefer to pull the tray with food on it because they were previously trained to do so, and non-human primates in general cannot easily inhibit prepotent response tendencies (51). Therefore, we compared the behavior of the marmosets playing the donor role when a partner was present with a control condition in which the partner was absent.

Each dyad was tested in three sessions, usually on 3 subsequent days. The maximum interval between test sessions was 2 days. In sessions 1 and 3, both donor and recipient were present, whereas in control session 2, the donor was alone. This means that in session 2 the choice of the (0,1) tray did not indicate unsolicited prosociality because there was no partner that could benefit from this choice. In contrast, in sessions 1 and 3, when the partner was present, the choice of the (0,1) tray benefited the partner and thus the donor could express unsolicited prosociality. Therefore,

if the donors exhibited unsolicited prosociality, the (0,1) tray should have been chosen more often when the partner was present than when the partner was absent. During each session, we ran six test trials, each with one piece of food (dead crickets) placed in front of the recipient on either the upper or lower tray in an alternating fashion. Interspersed among these six test trials, the donors were presented with three motivation trials in which one piece of food was placed on their own side (see SI Table 4).

Data Coding. The response of the donor marmosets [i.e., pulling (0,1), pulling (0,0), or no pulling] was recorded directly during the experiment, and all trials were double-checked afterward by using the videotapes of the experimental sessions. Additionally, we coded the behavior of the recipients from videotapes to investigate whether the behavior of the recipients affected the donors' choices. Twenty percent of the trials were randomly selected and coded by a second, independent rater to assess the reliability of the ratings. The raters reached an agreement of 89.5% and an inter-rater reliability of 0.79 (Cohen's κ).

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