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PAPER

Do great apes use emotional expressions to infer desires?

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Abstract

Although apes understand others' goals and perceptions, little is known about their understanding of others' emotional expressions. We conducted three studies following the general paradigm of Repacholi and colleagues (1997, 1998). In Study 1, a human reacted emotionally to the hidden contents of two boxes, after which the ape was allowed to choose one of the boxes. Apes distinguished between two of the expressed emotions (happiness and disgust) by choosing appropriately. In Studies 2 and 3, a human reacted either positively or negatively to the hidden contents of two containers; then the ape saw him eating something. When given a choice, apes correctly chose the container to which the human had reacted negatively, based on the inference that the human had just eaten the food to which he had reacted positively – and so the other container still had food left in it. These findings suggest that great apes understand both the directedness and the valence of some human emotional expressions, and can use this understanding to infer desires.

Introduction

By four months of age, human infants discriminate between some facial expressions such as fear and happiness (Nelson, 1987). By 14 months of age, they understand that emotional signals have directedness (Repacholi, 1998). And by 18 months of age, infants have a non-egocentric understanding of the difference between their own desires and those expressed emotionally by others; that is, they understand what a person's emotional expression towards an object means about their desires towards that object (Repacholi & Gopnik, 1997).

From as early as Darwin (1872, 1998), researchers have noted similarities between the facial expressions of humans and nonhuman primates. Faces, and the eyes in particular, play an important role in the emotional signals of both humans and apes, and the way facial information is processed in those species is quite similar (see Parr, Winslow, Hopkins & de Waal, 2000; Parr, Dove & Hopkins, 1998). Similar patterns of emotional development can be observed in human and chimpanzee neonates in the first month of life, in that young chimpanzee infants, like human infants, engage in mutual eye gaze with their mothers or with other human adults when reared in a nursery (Bard, 1994; Bard, Platzman, Lester & Suomi, 1992). Behavioural observations also indicate that ape emotional expressions and human emotional expressions can play similar functional roles. For example, human infants use a pout face to solicit their mother's attention, and a similar facial expression can be found in infant chimpanzees for the same bonding functions (Blurton Jones, 1971; van Lawick-Goodall, 1968). Furthermore, chimpanzees exhibit silent bared-teeth displays and play faces that assist in social bonding and the maintenance of social groups. In humans, the same bonding function is served by smiling, which looks similar to those chimpanzee displays (van Hooff, 1967, 1972; Chevalier-Skolnikoff, 1973, 1982; Preuschoft & van Hooff, 1995; Burrows, Waller, Parr & Bonar, 2006; see Gaspar, 2006 for a review).

Nonhuman primates have also shown some ability to discriminate the emotional states of others. Parr, Hopkins & de Waal (1998) showed chimpanzees a photograph of an unfamiliar conspecific's facial expression as a sample. Subsequently, a pair of pictures was presented, one depicting the same facial expression and one with a new expression. Chimpanzees discriminated four of the five expressions from a neutral face at above chance levels. Chimpanzees failed to discriminate the relaxed-lip face from neutral faces, however, and Parr, Preuschoft & de Waal (2002) suggested that this was because both possess a neutral function in social contexts and so perhaps additional auditory or behavioural cues may play an important role in determining the meaning behind some kinds of facial expressions. Accordingly, when Parr (2001) presented three chimpanzees with emotional video scenes containing multimodal information, they were able spontaneously to match all scenes to emotional expressions.

Apes thus can differentiate the emotional expressions of other apes. However, it is unclear whether they understand that in some cases these emotional expressions reflect internal states (i.e. desires) directed referentially to outside entities. The aim of the current study, therefore, was to determine whether apes can determine what

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kinds of desires towards external referents (e.g. foods) are indicated by the emotional expressions of others. Our studies were based on studies on human infants. In one study (Repacholi, 1998), 14-month-old infants saw an adult approach two boxes, open each one in turn, and show an emotional expression according to the content of each box (either happiness or disgust). When handed both boxes afterwards, the infants were more likely to open the box to which the adult had responded with a happy expression. This preference indicates that the infants understood both the directedness and the valence of the emotional signals. Repacholi & Gopnik (1997) showed that 18-month-old infants, after viewing an adult's emotional responses to different food items, responded to that adult's ambiguous request gesture by handing over her preferred food item even when it did not match their own preference. They thus demonstrated that 18-month-old infants have begun to understand that desires are mental states underlying behaviour and action. Specifically, infants at this age – but not 14-month-olds – have a non-egocentric understanding of the differences between their own desires and those of others.

Because we wanted to investigate whether great apes also have this understanding of others' desires[1] as internal states that cause certain actions (such as requests in the case of the study by Repacholi & Gopnik, 1997), our studies were designed to be as similar as possible to infant studies. Our first study was based on Repacholi (1998). Apes were allowed to select one of two containers to receive its content after viewing a human's emotional response (happy, neutral, or disgust) to each of these containers. Our second and third studies were adaptations of Repacholi & Gopnik (1997). Apes viewed a human emotionally responding to two containers (both containing food the apes liked) in different ways (happy versus disgust) and then eating something. Apes were then allowed to select a container themselves, with success depending on their ability to infer that the human had eaten the food he had acted positively towards (thus leaving the other).

Study 1: understanding emotional expressions as referential

In this study we asked whether apes would select a box based on an experimenter's emotional reaction to its content. We presented apes with two conditions. In the Happy–Neutral condition, one box was baited with desirable food and provoked a happy emotion from the experimenter, whereas the other box was baited with an inedible object and provoked a neutral reaction from the experimenter. In the Happy–Disgust condition, one box was baited with food as before, but the other box was baited with a dead cockroach and provoked a disgusted emotion from the experimenter.

Method

Subjects

Seventeen chimpanzees (*Pan troglodytes*, 3–29 years), five bonobos (*Pan paniscus*, 7–21 years), five gorillas (*Gorilla gorilla*, 6–26 years) and five orangutans (*Pongo pygmaeus*, 6–31 years) (n = 32) participated in the studies. All species were socially housed in groups of at least five individuals in a zoo equipped with research facilities (Wolfgang Köhler Primate Research Center, Leipzig, Germany). All subjects were born in captivity and had interacted with human caretakers, as is common in captive animals, for their whole lives. In addition, most apes had participated in several previous studies of their cognitive abilities. Although some of the subjects had been nursery-raised for various amounts of time, by the time of testing all of the apes were housed with their conspecific social group and so no longer had intensive human contact other than for routine caretaking and testing. Each species had access to an indoor area (230 to 430 m^2) and an outdoor area (1680 to 4000 m^2), both observable by the Zoo's visitors. During testing, subjects were separated in enclosures adjacent to their group members, a procedure they were accustomed to. Subjects were not food-deprived, and water was available throughout all testing times. Test sessions took place in a familiar room of approximately 15 m^2.

Materials and setup

An experimenter (E) sat behind a table (100 × 40 × 50 cm) with a moveable platform on top. This table was placed on the human's side of a plexiglass panel with three holes (left, middle, right; diameter 5 cm) that served as a wall of the subject's room. Subjects sat behind this panel during the testing sessions and could indicate their choices by poking or reaching through one of the holes in the panel. Two identical opaque plastic boxes (15 × 15 × 15 cm) with lids (thin square plastic pieces, 20 × 20 cm) were placed on the platform (one left, one right) on the table. The type of object inside each of these boxes varied according to condition. An assistant baited the boxes in each trial, and during this time the subject's view was blocked with a plastic occluder (100 × 50 cm). All tests were videotaped.

Design

Subjects were tested in two different conditions. In both conditions, E opened both boxes in succession and reacted with different emotions. In the Happy–Neutral condition, E reacted to one of the boxes with a happy display; this box contained a grape. He reacted to the

[1] Note that the term desire used here could easily be exchanged for other terms that describe a person's attitude towards outside entities and therefore cause actions towards those entities according to that attitude (i.e. like the term 'preference').

Figure 1 *The emotional expressions shown by the experimenter: (a) 'happy' when finding a grape inside the box; (b) 'disgusted' when finding cockroaches inside the box; and (c) 'neutral' when finding bedding material inside the box. All expressions are pictured as seen by the subjects.*

other box with a neutral expression; this box contained some pieces of bedding material (wood shavings). In the Happy–Disgust condition, E reacted to the box containing a grape with the same happy expression, but the alternative box contained dead cockroaches and so E reacted with a disgusted expression. E's emotional expressions of happiness and disgust were based on the descriptions of Ekman & Friesen (1975), see Figure 1. For the neutral display E had his eyes open, mouth closed and all facial muscles relaxed. Happy and disgust facial expressions were accompanied by verbalizations to augment the amount of emotional information available for the subject. However, these additional emotional cues did not have specific content: E began with a condition-appropriate exclamation ('Oh!' for happy or 'Eww!' for disgust) followed by the same German word 'Nachtigall' ('nightingale') with a different intonational structure (a high-pitched tone of voice for happy and low-pitched tone of voice for disgust) for each of the two emotional expressions. No vocalization was given when E presented a neutral expression.

The side placements of the contents of the boxes as well as the box first opened by E were counterbalanced. Each subject received 9 trials per condition in each of two test sessions (on different days) in a randomized order, so that each subject received a total of 18 trials per condition. Each subject's choice was coded live.

Procedure

The first test session started with warm-up trials. In these trials, E removed the lids from the empty boxes and placed them in front of the boxes on his side of the table. As the subject was watching, he then put a grape in one of the two boxes and moved the platform within the subject's reach. This ensured that subjects knew the boxes could contain food and that they would receive the content of the box they chose. Once a subject chose correctly on 4 out of 5 trials, the warm-up period ended and the test period began. As the subjects had had previous experience with similar tasks, most finished this warm up within 5 trials.

To begin each test trial, E stood up, moved to the opposite corner of the testing area, and looked out of a window pretending to be busy. Once E had walked away, an assistant pulled the sliding platform away from the plexiglass panel and then occluded this window to ensure that the subject could not observe the hiding process. She then removed the lids from the boxes (starting with the left one), placed them in the middle of the table, and baited first the left box and then the right one with the appropriate object (grape, cockroaches or bedding material) according to condition. After this she replaced the lids (starting with the right one) and removed the occluder. At this point E returned to the test table, sat down, and called the subject's name. Once the subject was sitting in front of the plexiglass window and attending, E gazed at one box, lifted its lid, such that he but not the subject could see inside the box, and then looked into the box, giving the appropriate emotional expression. E then looked at the subject for two seconds while saying 'Nachtigall' with the appropriate emotional expression. After looking back at the contents of the box, still showing the appropriate emotional expression, for two seconds, he closed the lid and gave the other cue for the remaining box. The displays took the same amount of time for each box. All demonstrations were done with E's left hand for the left box and his right hand for the right box.

After E had finished giving the cues, he looked at the middle of the test table and moved the platform towards the plexiglass window within reach of the subject. The subject then indicated one of the boxes. When subjects chose the box associated with the 'Happy' emotional display, they were given the grape through the middle hole. If they chose the other box ('Neutral' or 'Disgust' depending on condition), they were shown the contents of the box. If subjects were not successful in locating the food for three trials in a row they were given a grape out of a bucket through the middle hole to keep them motivated.

All trials were videotaped, and a second independent person coded 25% of the choices for reliability. Reliability over both conditions and sessions (36 trials per subject, choice left or right) was perfect (Cohen's kappa = 1.00). As the assumptions for the use of parametric statistics were met, we used them throughout the study. All *p*-values reported are two-tailed.

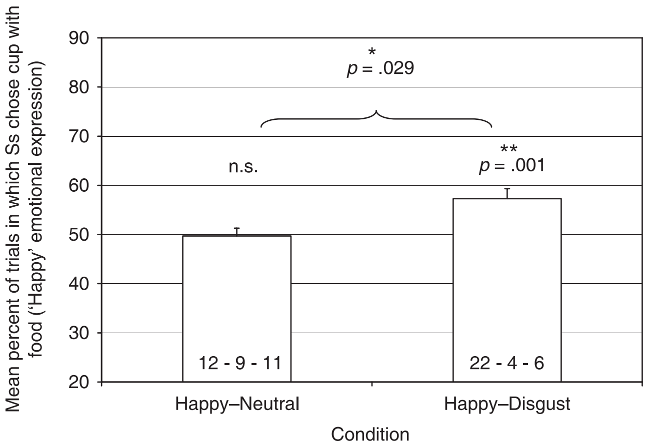

Figure 2 *Mean percentage (and SEM) of correct choices (food) in the two conditions tested in Study 1. Numbers within the bars represent the numbers of subjects that chose correctly in more than half of the trials (positive ranks) – half of the trials (ties) – fewer than half of the trials (negative ranks).*

Results

Overall, subjects chose the box reacted to with a happy expression in 57.3% of the trials in the Happy–Disgust condition and in 49.7% of the trials in the Happy–Neutral condition – see Figure 2 (note that the mean percentages of trials we report here are not directly comparable to the percentage of participants reported in Repacholi's, 1998, study). Each condition was analysed using a one sample *t*-test. Subjects as a group chose the box with food at above chance levels in the Happy–Disgust condition, $t(31) = 3.586$, $p = .001$, but not in the Happy–Neutral condition, $t(31) = .220$, $p = .827$. Two bonobos had individual results that were significantly above chance level in the Happy–Disgust condition ($p = .039$, binomial tests for both). However, no individual subject had significant results in the Happy–Neutral condition.

To check for species differences and to compare the subjects' performance in the two conditions and over the different test sessions (to test for learning effects), a repeated measures analysis of variance (ANOVA) was used with condition and test session as within-subjects factors, and species and age (covariate) as between-subjects factors. The difference between conditions was significant ($F(1, 28) = 5.307$, $p = .029$): subjects chose the 'happy' box more often in the Happy–Disgust condition than in the Happy–Neutral condition. There was no significant effect for session, $F(1, 27) = 1.362$, $p = .253$, and no positive correlation could be found between the proportion of correct subjects within each trial and the number of trials (Spearman correlations, Happy–Neutral: $r_{s(18)} = .085$, $p = .737$; Happy–Disgust: $r_{s(18)} = -.487$, $p = .041$), indicating no learning effects. There was also no effect of species, $F(3, 27) = 2.178$, $p = .114$, or age, $F(1, 27) = .018$, $p = .895$. There were no significant interactions.

Discussion

These results indicate that apes can use some emotional expressions provided by a human experimenter to locate hidden food. Although the physical actions associated with all emotional signals were identical, in the Happy–Disgust condition the apes selected the box to whose content E had reacted positively over an alternative to whose content E had reacted with disgust.[2] However, in the Happy–Neutral condition, in which E reacted to the content of one box with happy emotions and to the other one neutrally, the apes showed no preference. To be successful in this task, apes had to understand both the directedness and the valence of the human emotional expressions, and to use this information to infer his desires towards the hidden contents of the two boxes.

Apes' failure in the Happy–Neutral condition might be a result of their inability to distinguish between the happy and neutral emotional facial expressions. Perhaps this is similar to the findings of Parr *et al.* (1998), who showed that chimpanzees cannot discriminate two fairly similar expressions of conspecifics indicating similar emotional states. The difference between the happy expression and the disgusted expression is perhaps more extreme, as compared with the contrast between the happy and the neutral emotional expressions, and so perhaps this enabled them to be more successful at this discrimination. This interpretation suggests that apes distinguish between human emotional expressions when they are very distinct, but cannot distinguish expressions that are more similar.

Another possibility is that apes' success in the Happy–Disgust condition relies on some non-cognitive explanation. Thus, instead of a direct choice, the apes may have simply been avoiding the disgusted emotional expression, and thus 'chose' the box associated with the positive emotional display as being the only alternative. Or perhaps some kind of emotional contagion (affective resonance) played a role in the subjects' choice behaviour. If subjects successfully chose the positive display in the Happy–Disgust condition, it might be because the high-pitched emotional expression of E increased a positive arousal in the apes and the disgust expression induced some kind of lower or negative arousal – and again there was a bigger contrast in the Happy–Disgust condition. These interpretations would suggest that apes did not understand the emotional state of the human as stemming from his desires; rather, the human's emotional response generated some sort of involuntary positive or negative state in the apes. To attempt to rule out these less cognitive explanations, in Study 2 we set up a situation in which, to respond correctly, the ape had to choose the container to which the human reacted negatively.

[2] As this study was designed mainly to investigate whether apes would distinguish different emotional expressions (as in the original study on human infants), it was not our aim to clarify which exact meaning the apes attach to the emotional expressions presented. It is not clear whether the apes interpreted the negative emotional expression ('Disgust') in terms of the sophisticated form of disgust that some researchers propose might be uniquely human (e.g. Rozin, Haidt, McCauley & Imada, 1997), or whether they read this emotional expression 'simply' as a sign of distaste.

Study 2: Making inferences from referential emotional expressions

Study 1 showed that apes can distinguish a happy emotional expression from a disgusted emotional expression. Study 2 addressed whether the apes had succeeded in this study because they simply avoided the box associated with negative emotions or were aroused by the positive expression more in one condition than the other, or whether, in contrast, they truly understood the referential nature of E's emotional expressions of desire and disgust. In the current study, to respond correctly the ape had to choose the container to which the human reacted negatively. For this, we modified the food-request procedure used by Repacholi & Gopnik (1997): rather than handing the experimenter food, the apes selected a cup for themselves after watching the behaviour of the experimenter. In the key test, subjects knew that each of two cups contained a different food item, both of which were palatable. They then saw E react to the hidden contents of one cup with a happy expression and to the other with a disgust expression, and then eating something. To be successful, apes had to choose the cup whose contents E reacted to negatively, because that is the one whose contents he presumably did not like and so avoided.

Method

Subjects

All subjects from Study 1 participated in the current study, except for one male chimpanzee (5.1 years) who was not available during testing. Two additional chimpanzees (one female, 28.5 years, and one male, 8.5 years) who were not tested in Study 1 participated in Study 2.

Materials and setup

The same basic setup and materials from Study 1 were used. Instead of boxes, however, we used two round, white, opaque plastic cups (10 × 6 cm) that were placed upside down on the table to cover the food. Different kinds of food were put under these cups according to condition. The big occluder used in the first study was replaced by a smaller one (100 × 25 cm).

Design and procedure

The current study consisted of two familiarization conditions (1 and 2), followed by the key experimental condition. In each of two sessions (on different days),

Figure 3 *The emotional facial expressions shown by the experimenter in Study 2 as seen by the subjects: (a) happy and (b) disgusted.*

the subjects were presented with 4 trials from Familiarization 1, followed by 4 trials from Familiarization 2, and then 4 trials in the Experimental condition (in exactly this order, without breaks), such that each subject had a total of 8 trials of each condition. The emotional cues from the Happy–Disgust condition of Study 1 were used for Familiarization 2 and the Experimental condition (see Figure 3), with the same counterbalancing between and within trials (side of foods, side E started with) as in Study 1.

Familiarization 1. In Familiarization 1, we checked whether subjects could distinguish and remember the locations of two different food items and choose the remaining item after they saw the other one being removed. This kind of inference by exclusion was a prerequisite for successful performance in our experimental conditions. Following Call (2006), in all trials one of the two cups contained a grape and the other a slice of banana, both highly desirable foods for great apes. A research assistant took a grape and a piece of banana out of a bucket, called the subject by name, and held up the food, each in one of her hands, at eye level. She then placed those food items on the table: one in front of the hole on the left of the plexiglass window, and the other on the right. She then covered these items with the plastic cups, and subsequently blocked the subject's view with the occluder. She then removed one of the pieces of food, but lifted both cups in the process so that the apes could not determine where the food came from based solely on her actions (i.e. by hearing one cup being lifted). She then placed this piece of food in the centre of the table, in between the two cups, and removed the occluder so that the subject could see the piece of food. Once the ape saw the food, the assistant took it with her right hand, held it up for two seconds, and then put it away. She then pushed the table forwards so that the subject could make her choice. If subjects chose the cup with the remaining food they were given this food item. The experimenter (E) was present in the room during this test. The side each kind of food was placed on as well as the kind of food taken out of the cup were counterbalanced across trials.

Familiarization 2. In Familiarization 2, we added in the slightly more complex experimental choreography that would come in the Experimental condition, as well as the emotional cues, to make sure that subjects could still infer the location of the remaining food after E had removed one piece in the context of these added complexities.

Each trial began as in the Familiarization 1 trials, except that the assistant baited one cup with a piece of apple and the other one with a pellet (ape chow) of comparable size – both very palatable to apes. Crucially, the subjects watched the baiting process (while E was standing across the room pretending to be busy and therefore not attending). Once the assistant finished baiting the cups, she left the table and E sat facing the ape. He called the subject by name to attract her attention. Once the subject was sitting behind the window, E looked at one of the two cups, grasped this cup with his hands and then lifted it on the side facing him to see what was underneath. He then reacted emotionally to the food he saw underneath the cup: he reacted with a happy display if he found the apple, and with a disgusted display if he found the pellet (the displays were identical to those described in Study 1) – see Figure 3. After giving the first emotional cue, he replaced the first cup and performed the same series of actions on the remaining cup and gave the appropriate expression. While E looked under the cups, his hands blocked the subject's view so she could not see what was underneath the two cups during the demonstration.

After E finished giving the emotional cues for both cups, he put the occluder in front of the window, lifted the cups one by one, and placed the apple in the centre of the table. He then bent his head forwards, took the food with his right hand and started to eat the apple piece. While chewing the first half of it noisily with his mouth open he lifted his head and hand so that the subject could see him over the top edge of the occluder. He then continued eating the food. After he finished eating he removed the occluder and pushed the table into the subject's reach so that she could make her choice. If the subject chose the cup holding the pellet she was given the food. If she chose the empty cup, this cup was lifted so that the subject could see that there was no food under it. The side placement of the two types of food was counterbalanced between trials.

Note that subjects could be successful in this task without attending to the emotional cues. Because they knew where the two foods were, they only had to notice which was being eaten and choose the cup where the other food was hidden – just as in Familiarization 1.

Experimental. The design and procedure of the Experimental condition was similar to that used in Familiarization 2, with one important modification. After E had removed the food from one of the cups (from behind the occluder) – always the type associated with a happy display, as before – he placed it surreptitiously in his breast pocket. When he lifted his head he pretended to chew a food item making a chewing sound, but the subject could not see the particular kind of food he was 'eating'. Thus, subjects had to infer which cup still contained food based only on E's emotional displays. Once he finished the demonstration, E removed the occluder and pushed the platform towards the subject so she could choose. If subjects chose the cup still containing food, they received that food. If they chose the empty cup, this cup was lifted so that they could see it was empty. As in Familiarization 1, in all trials, one of the two cups contained a grape and the other one a slice of banana. E reacted positively to one kind of food for each subject in this condition. The side placement of the two types of food was counterbalanced between trials.

Scoring and reliability

We scored the cup selected by the subject. As in Study 1, an independent observer coded approximately 25% of the trials to check for reliability. Reliability for all three conditions including both sessions was perfect (Cohen's kappa = 1.00).

Results

Overall, subjects selected the cup with the remaining food in 63.3% of trials in Familiarization 1, in 78.4% of trials in Familiarization 2, and in 56.0% of trials in the Experimental condition (see Figure 4). Subjects chose correctly at above chance levels in Familiarization 1, $t(32) = 5.078$, $p < .001$, and Familiarization 2, $t(32) = 8.229$, $p < .001$, but failed to do so in the Experimental condition, $t(32) = 1.501$, $p = .143$. Several individual subjects performed above chance in Familiarization 2 (six chimpanzees, one bonobo and three orangutans; $p = .008$ for each individual), and in the Experimental condition (one bonobo and one orangutan; $p = .008$ for each individual), binominal tests. A repeated measures ANOVA with condition and test session as within-subjects factors, and species and age (covariate) as between-subjects factors revealed a significant species effect, $F(3, 28) = 3.389$, $p = .032$. Specifically, across all conditions gorillas performed significantly worse than chimpanzees, Mann–Whitney $U = 10.5$, $N_{gorillas} = 5$, $N_{chimpanzees} = 18$, $p = .006$, and orangutans, Mann–Whitney $U = 1.5$, $N_{gorillas} = 5$, $N_{orangutans} = 5$, $p = .024$. There was no effect of session, $F(1, 28) = .172$, $p = .681$, and no

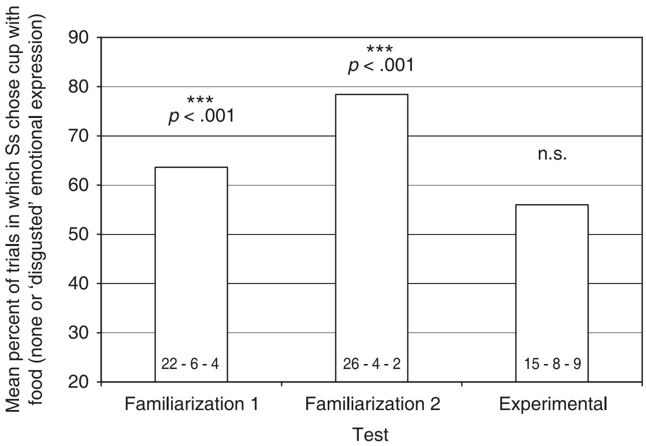

Figure 4 *Mean percentage (and SEM) of correct choices (food) in the three tests included in Study 2. Numbers within the bars represent the numbers of subjects that chose correctly in more than half of the trials (positive ranks) – half of the trials (ties) – fewer than half of the trials (negative ranks).*

positive correlation could be found between the proportion of correct subjects within each trial and the number of trials (Spearman correlations: Familiarization 1: $r_{s(8)} = .282$, $p = .498$; Familiarization 2: $r_{s(8)} = .216$, $p = .608$; Experimental: $r_{s(8)} = .133$, $p = .754$), indicating no learning effects. Furthermore, there was no effect of age or condition, all p's $\geq .461$, and no significant interactions.

Discussion

The great apes selected the cup with the remaining food item in Familiarization 1 and Familiarization 2, confirming that they could infer that if one piece of food was put away or eaten by E then the other (whose location they knew) should still be there. However, in the Experimental condition – when subjects could not see what specific type of food was being eaten by the experimenter and so had to rely solely on the emotional cues to know which piece was being eaten – they failed to choose the cup with the remaining food at above chance levels.

The apes' failure in the Experimental condition suggests that they might not have been able to use the emotional displays to infer which food was being eaten and which remained. Importantly, however, in this condition, as in the others, the subjects knew where each type of food had been hidden. It is thus possible that they were distracted by their own preference for a particular one of the foods, and indeed, in a subsequent food preference test, many individuals showed strong preferences (by choosing one kind of food in 79% of trials). That is to say, some apes may have perceived the experimenter's emotional displays and understood the link between these emotions and the experimenter's desires, but failed to use this information because it was inconsistent with their own preference for one of the foods – whose location they knew from the beginning. To address this possibility, in Study 3 we replicated the Experimental condition of Study 2 with one crucial change: the apes in this study could not see the initial hiding of the food items and so could not be influenced by their own preferences. The only cues they had were E's emotional expressions.

Study 3: Making inferences from referential emotional expressions II

This study replicated the Experimental condition of Study 2, but in this study the subjects did not see the baiting process and thus did not know the location of the different food items, thus ensuring that the subjects' own desires could not influence choices.

Method

Subjects

All subjects tested in Study 2 participated in this study.

Materials and setup

The same materials as in the Experimental condition of Study 2 were used in this study (using grapes and banana slices as food).

Design and procedure

We used the same procedure as in the Experimental condition of Study 2, and counterbalanced the side of the positively evaluated food item and the side E started to act on between trials. There were two modifications to the previous procedure: (1) before the assistant started a trial she always occluded the subject's view so that the subject could not see the hiding process; and (2) when she then held up the food before the baiting process she had both food pieces in her right hand so that the apes had no information about the side placement of the two types of food. She thus baited the cups as before but did so out of the subject's view. E then gave the emotional displays described previously (happy, disgust), pretended to eat a food that the subject could not identify, and then the subject chose. Each subject received 16 trials over two sessions (with eight trials each) on two different days.

Data were coded as in Study 2. Inter-observer reliability based on approximately 25% of the trials for both sessions scored by an independent observer was again perfect (Cohen's kappa = 1.00).

Results

Subjects chose the cup still containing food (i.e. the cup associated with the disgust display) on 56.1% of trials, which exceeds chance levels, $t(32) = 2.548$, $p = .016$, see Figure 5 (note that the mean percentages of trials we report here are not directly comparable to the percentage of

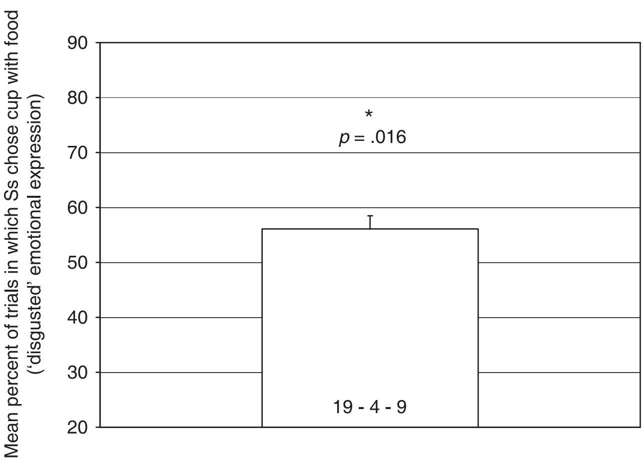

Figure 5 *Mean percentage (and SEM) of correct choices (food) in Study 3. Numbers within the bar represent the numbers of subjects that chose correctly in more than half of the trials (positive ranks) – half of the trials (ties) – fewer than half of the trials (negative ranks).*

participants reported in Repacholi & Gopnik's, 1997, study). A repeated measures ANOVA with test session as within-subjects factor, and species and age (covariate) as between-subjects factors revealed no evidence of improvement across the two sessions, $F(1, 28) = .137$, $p = .714$, and no positive correlation could be found between the proportion of correct subjects within each trial and the number of trials, Spearman correlation, $r_{s(16)} = .077$, $p = .776$, thus ruling out a learning explanation. Furthermore, there were no species differences in the subjects' performance, $F(3, 28) = .770$, $p = .521$, but there was an effect of age, $F(1, 28) = 5.162$, $p = .031$. Older subjects performed significantly better than younger ones, Pearson's $r = .346$, $p = .049$. Two subjects performed above chance as individuals: the oldest subject, a female orangutan ($p = .021$), and a female gorilla ($p = .004$), binominal tests. No significant interactions could be found.

Discussion

In this study, subjects selected the box still containing food at above chance levels. To do this, they had to understand how emotional expressions (i.e. disgust versus happiness) reflect personal desires towards things, and infer that E was more likely to eat the food item to which he had reacted positively. That is, the apes had to use E's emotional reactions to things to predict his behaviour, even in the absence of any other behavioural cues. This finding makes it likely that apes' failure in Study 2 occurred because their knowledge of which kind of food was hidden under which cup – and their own desires for certain of these food items – interfered. When the subjects' personal desires could not interfere with their choice, as in the current study, they successfully used the emotional information.

Importantly, simple non-cognitive explanations such as emotional contagion or avoiding negative valences – possibilities in Study 1 – would seem to be ruled out by the apes' successful performance in this study, as in this study successful performance required choosing the cup whose contents had been marked with a negative emotional expression.

General discussion

Collectively, the results of these studies indicate that great apes can use a human's emotional expression towards objects to predict his behaviour towards them. Thus, Study 1 found that apes interpreted a human's emotional expression as referring to a specific target and with a specific valence – much like 14- and 18-month-old human infants (Repacholi, 1998) – although they were able to do this only when the contrasting emotions were maximally distinct, as they were in the original study with human infants (i.e. happy versus disgust, not happy versus neutral). In Studies 2 and 3, apes showed that their success was not the result of some low-level, non-cognitive process such as emotional contagion or the avoidance of things associated with negative emotions. To succeed, they had to understand both the referential content of the emotional displays and the meaning behind emotional expressions. That is, given that the food associated with E's positive emotion was very likely the one he had taken and was currently eating, apes were able to select the cup associated with E's negative emotional reaction as the one in which food was most likely to be still available (in the case that they had no other knowledge of the food's location to distract them). The absence of learning effects also precludes the possibility that subjects learned to respond appropriately during testing. However, it is conceivable that individual subjects learned the associations between specific emotional expressions and certain patterns of behaviour over their ontogeny. Although subjects' age did not appear to be correlated with performance in the first study, the correlation of age and performance in Study 3 suggests that apes with longer human contact might show a more skillful understanding of the link between human emotions and human behaviour.

One key question raised by this research is what inference, if any, apes make about the mental states of the human experimenter. One possibility is that apes do not make any inference about mental states but use the emotional expressions to determine what reward to take. Positive and negative emotions would have been associated in the past with positive and negative rewards, respectively. Thus subjects could use this information to decide what to select. One problem with this explanation is that it cannot account for the data showing that subjects chose the reward that was paired with a negative emotion. In fact, these data suggest that apes at the very least understood the referential character of emotional expressions that represented the personal preferences of the human experimenter, not the absolute valence of the objects. Egyed, Király & Gergely (in preparation) showed that 18-month-old infants initially interpret referential emotional expressions as teaching them something about the person's individual attitudes towards objects ('person-centered interpretation'), not something about the valence of the objects. Only when the presented emotional cues were accompanied by the demonstrator's ostensive communication did the infants interpret the referential emotional expressions as teaching them something about the relevant object ('object-centered interpretation').

Having established that apes interpreted a human's emotional expression as referring to a specific target with a specific valence, the question remains whether apes are attributing desires to the human with regard to the objects. Our data do not allow us to answer this question. It may be that apes can use a human's emotional expression towards objects to predict his behaviour towards them but that they do not necessarily impute any mental states like desires. Note, however, that this same reasoning can be applied to the human studies (Repacholi, 1998; Repacholi & Gopnik, 1997) that motivated the current study. There is no reason to think that desires as opposed to preferences for action are underlying the behaviour of 14- and 18-month-old infants. From this point of view, the work with human infants and apes is equivalent. Furthermore, just like the original studies on human infants, our studies have two constraints that limit the generality of our results. First, we used only a small number of emotions. Whether similar results would have been obtained if other emotional expressions (e.g. sadness, anger) had been used is unclear. Second, since the setup involved a foraging context we are unable to say whether the apes' reasoning extends beyond the food contexts to other types of objects and situations (e.g. to attitudes towards specific conspecifics or specific locations within their enclosures). Thus, if human infants are attributed desires, there is no reason not to do the same with the apes.

It is true that the relatively low level of preference for the correct alternative makes us cautious regarding the robustness of apes' explicit understanding about the emotional expressions as indicators for the experimenters' desires. Perhaps focusing on desires is what helps children to obtain more robust results than the apes, especially for 18-month-old infants. However, it is conceivable that certain aspects of our procedure affected apes' performance negatively. The procedure of Study 3 in particular imposed a larger memory load on subjects than the procedure used with infants. More specifically, subjects did not see the content of the boxes and they had to remember the facial expression that had been associated with each box. In addition, subjects had to interpret the experimenter's eating-action. This action, which is functionally equivalent to the request gesture used in the original study, may have distracted the subjects' attention. Recall that apes had to decide which reward to choose after the eating-action had taken place, whereas children had to judge before the occurrence of that action (at the same time as the experimenter's request). Those procedural differences and the use of human emotional expressions to test ape responses might have contributed to the subjects' low level of performance.

Several intriguing questions remain unanswered. It is unclear which specific aspect of the human's emotional reaction drove the subjects' responses, as multiple facial and auditory cues were available. On the one hand, vocal intonation alone may be a more salient cue for apes than facial expression (as for human infants in social referencing tasks; Mumme, Fernald & Herrera, 1996). If so, they could have used tone of voice to infer emotional state in all three studies, ignoring the facial expressions entirely. On the other hand, evidence suggests that chimpanzees can discriminate facial expressions of conspecifics (Parr *et al.*, 1998) – although it is unclear whether they can likewise discriminate human facial expressions and whether apes' interpretation of emotional information is similar to that of humans. For example, we do not know if apes saw the displays presented to them as being of their own kind. If that had been the case, however, we should have found species differences because the human smiling facial expression used as our 'happy display' resembles a bonobo facial expression of pleasure, but it seems to be used to demonstrate submission or appeasement in chimpanzees (Parr *et al.*, 2002). This suggests that the apes did not see the displays as belonging to their own, but rather as belonging to humans' repertoire of emotional expressions. Again, this is consistent with the positive correlation of age and performance in Study 3.

Another interesting question that remains unanswered from our studies is whether great apes – like 18-month-old human infants – understand that different individuals can have different desires towards the same object. In contrast to the procedure of Repacholi & Gopnik (1997), the procedure we established in Study 3 ensured that the subjects were not able to observe the baiting process and therefore did not know which kind of food E desired when he reacted emotionally to the content of the cups. The apes' failure in the Experimental condition in Study 2, however, may suggest that apes have a more egocentric understanding of desires, possibly similar to that of 14-month-old human infants. When they previously observed the locations of the two kinds of food, their own desires appeared to preempt their understanding of others' desires. On the other hand, it is possible that in this study they understood the human's desires perfectly well, but their own desire interfered at the moment of choice in the sense that it was difficult for them to inhibit making a choice based on their own preferences. At the current time we are unable to choose between these alternatives.

Recent research has demonstrated that great apes understand a number of more concrete intentional states such as goals, perceptions and perceptual knowledge (Tomasello, Call & Hare, 2003; Tomasello & Carpenter, 2005). The findings of our current study suggest that great apes may also be sensitive to another component of theory of mind: desire attribution. This is not totally surprising, considering that other basic components of theory of mind such as goal and perception attribution have already been described in the great apes (Tomasello & Call, in press). Determining whether apes understand desires in a fully non-egocentric way and as a mental state rather than as a behavioural predisposition for certain actions is a task for future research.

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