

Research



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Children, but not chimpanzees, have facial correlates of determination

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Facial expressions have long been proposed to be important agents in forming and maintaining cooperative interactions in social groups. Human beings are inordinately cooperative when compared with their closest-living relatives, the great apes, and hence one might expect species differences in facial expressivity in contexts in which cooperation could be advantageous. Here, human children and chimpanzees were given an identical task designed to induce an element of frustration (it was impossible to solve). In children, but not chimpanzees, facial expressions associated with effort and determination positively correlated with persistence at the task. By contrast, bodily indicators of stress (self-directed behaviour) negatively correlated with task persistence in chimpanzees. Thus, children exhibited more behaviour as they persisted, and chimpanzees exhibited less. The facial expressions produced by children, could, therefore, function to solicit prosocial assistance from others.

1. Introduction

Human facial expressions have great similarity to those of other primates [1] and are produced using a highly conserved system of facial musculature [2]. Overall, physical similarity of the main facial expression configurations, however, may obscure important differences in how facial expression is actually used. Specifically, facial expressions have long been proposed as important agents in coordination and cooperation in social interaction [3–6], and so it is possible that facial expression differs between species depending on their tendency to cooperate. Humans exhibit a motivation for, and level of, cooperation in their social interactions that is unique among primate species [7], and so, in this context, we might expect human facial expressivity to exhibit some important differences from other primates.

Facial expressions are linked to internal emotional states, in the sense that they convey to others something about what the sender is feeling, thinking or is likely to do next [8]. The link between expression and emotion is not absolute [9], but in order for some level of honest communicative meaning to evolve, there must be an advantage to both sender and receiver [10]. Smiling, for example (and its counterpart in chimpanzees, the bared-teeth display), seems to act as an honest signal of benign intent and benefits both sender and receiver by increasing social contact and avoiding conflict [4,11]. Facial expressions that indicate potential weakness on the part of the sender, however, can be functional only for the sender if there is potential assistance from observers [12]. Otherwise, it could be disadvantageous for the sender, as others could withdraw investment or take advantage of the sender's weakened state.

Several studies have demonstrated that non-human primates, especially chimpanzees, cooperate with conspecifics [13], that individuals respond to distress in others [14] and that human empathy is rooted in socio-cognitive abilities present in other primates [15]. However, the extent to which humans help each other and live in large, cooperative societies is unique among primates [7,16]. Human helping can also be underpinned by conscious, goal-directed empathy, whereas

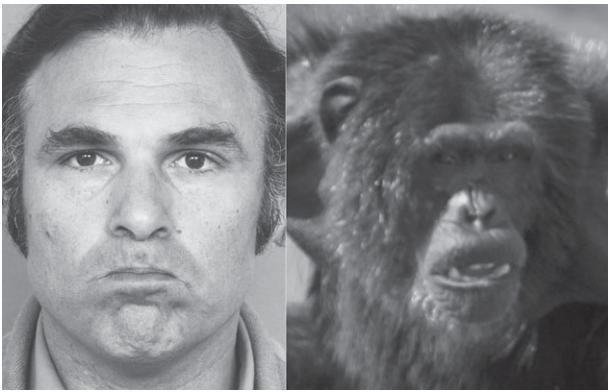


Figure 1. Human anger facial expression and chimpanzee bulging lip display, both composed of action unit 17 (chin raiser) and action unit 24 (lip presser). Human image from FACS manual [19] and chimpanzee image courtesy of Lisa Parr.

non-human primate cooperation could be explained by simpler (albeit closely related) phenomena [17]. Expressing weakness to others, therefore, could benefit humans more than other primates, by stimulating empathy and helping behaviour. In that case, we might see facial expressions that reflect difficulty reaching a goal (frustration, confusion, etc.) to a greater extent in humans than other primates. Such expressions could still stimulate helping in an indirect manner (mimicry of others' facial expressions is associated with empathy in humans [18]), but there is also the potential for goal-directed, helpful responses.

In this study, human children and chimpanzees were presented with a task that was impossible to solve, and thus designed to assess individual differences in persistence, frustration and determination. Facial action coding system (FACS) [19] and ChimpFACS [20] were used to systematically document facial movements produced throughout the task and to make explicit comparisons between the two species. We examined the full range of facial movements in both species, but focused the analysis on specific components of the human anger facial expression (AU17: chin raiser and AU24: lip presser) which are associated with determination [21] and may also signal effort and concentration. These movements have anatomically equivalent movements in the chimpanzee bulging lip face produced in aggressive contexts [22,23] (figure 1) which allowed us to make direct comparisons. Self-directed behaviour (SDB) was recorded as a measure of stress [24] (see the electronic supplementary material for descriptions and a video example).

2. Material and methods

(a) Participants

Participants were 32 children aged 3 (16 girls) and 33 children aged 6 (17 girls). Three 6 year olds had to be excluded from the analysis owing to experimenter errors. The children were tested in the Developmental and Comparative Psychology Department at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. Chimpanzees (34: 21 females; 7–25 years of age) were from the Ngamba Island chimpanzee sanctuary (Uganda).

(b) Design

All subjects participated in a task in which their persistence in trying to obtain a reward (that was suddenly impossible to get)

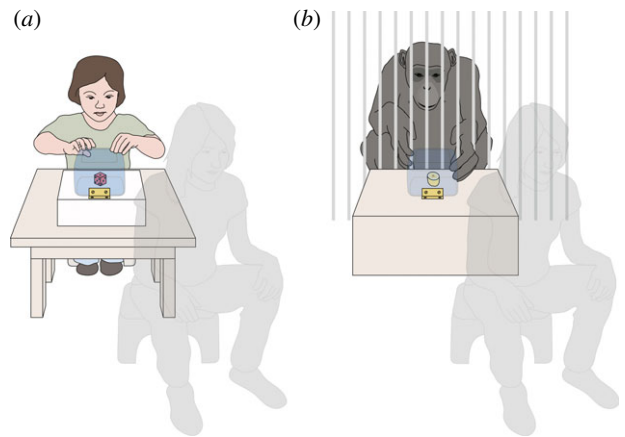


Figure 2. Experimental set-up for children (a) and chimpanzees (b). (Online version in colour.)

was examined (figure 2; [25]). In a pre-test, the subject was given a transparent box that contained a toy token (children) or a piece of banana (chimpanzee) and was shown how to open the box. In the test trial, the experimenter then locked the box (out of sight) and placed the locked box back in reach of the subject. After 2 min, the trial then ended.

(c) Coding

Each 2 min trial was coded for measures of persistence: the percentage of time the subject manipulated the box, the number of breaks taken (over 2 s) and the latency to the first break. Each trial was then coded using FACS or ChimpFACS (respectively) using point sampling (5 s intervals) to approximate the rates of facial movements. SDBs were coded in both species using continuous sampling, and transformed into rates. All FACS coding was conducted by certified coders, and coding agreement was obtained (see the electronic supplementary material for detailed explanations of coding and reliability assessment). Rate of AU17 (chin raiser) and AU24 (lip presser) was calculated, along with rates of total facial movement. (Note that other combinations of movement relevant to chimpanzee and/or human repertoires were also explored but there were no further relationships with task performance.)

3. Results

All variables were non-normally distributed, so non-parametric statistics were used throughout. Table 1 shows the relationship between the measures of task persistence and the behavioural variables for both species (the two children groups were similar in this respect and so were combined). In human children, the target movements negatively correlated with number of breaks from the task, and positively correlated with total time spent on the task, and latency to first break. Therefore, children who persisted most with the task (and did not give up easily) produced more of these facial movements. For the children, there were no significant correlations between measures of task persistence and overall facial movements or SDB. Chimpanzee SDB positively correlated with number of breaks from the task, but negatively correlated with total time spent on the task and latency to first break. Overall, therefore, chimpanzees who persisted least with the task, and gave up more easily, exhibited more SDB. There were no significant correlations between measures of task persistence and overall facial movement or target facial movements (see the electronic supplementary material).

Table 1. Relationship between measures of task persistence and the behavioural variables (Spearman's rho). Bonferroni-corrected from 0.05 as three tests were applied per behavioural variable.

task persistence	total facial movement	AU17 and AU24 facial movement	self-directed behaviour
<i>children</i>			
number of breaks	−0.159	−0.361*	0.018
time on task (%)	0.243	0.450*	−0.191
first break latency	−0.188	0.427*	−0.199
<i>chimpanzees</i>			
number of breaks	−0.119	−0.024	0.555*
time on task (%)	0.187	0.082	−0.516*
first break latency	0.133	0.188	−0.579*

*Significant at $p < 0.0167$.

4. Discussion

Children produced facial movements associated with effort and determination (components of anger facial expressions) at higher rates the more they persisted with an impossible task. Chimpanzees, by contrast, did not produce these facial movements in relation to task performance, despite having the capacity to produce identical movements, and having a (potentially) homologous facial expression to anger in their repertoire. No relationship between other facial movements and task performance was found in the chimpanzees, so it does not seem to be the case that the chimpanzees have a different form of facial expression that was missed. Instead, chimpanzees showed bodily indicators of stress (SDB) in relation to task persistence. Unlike the facial movements in children, however, SDBs are unlikely to signify determination or persistence, as chimpanzees produced more SDB when they engaged *less* with the task, and so were less determined to get the reward (possibly owing to finding it more stressful).

Whether these facial movements are associated with a subjective, emotional experience of effort/determination in children is unknown, but consideration of proximate correlates is not necessary to speculate on function. One reason that humans and chimpanzees differ in facial expressions in relation to a frustrating task might be that, as a more cooperative species [7], humans benefit more from communicating their weaknesses to others. By producing facial expressions that reflect the motivation to complete the task (or frustration in not being able to complete it), individuals could stimulate empathy in others [18] and receive support. By contrast, SDB may not convey the same kind of context-specific information and hence may not be suitable for eliciting helping behaviour in others. Whether SDBs are communicative to others (and in what sense), however, is unknown.

Because facial expression production is highly sensitive to the specific social context [26], the difference in experimental set-up between the two species (the experimenter was a conspecific for the humans, but heterospecific for the chimpanzees) might have played a role. While this is an important consideration, it seems unlikely to explain the differences for two reasons. First, although the setting was social in the sense that the experimenter was present, the experimenter was not interacting with the participant or reacting to their behaviour, but instead was turned away from the subject during the test. Second, in non-human primates, there is only limited evidence that the presence of an audience affects how facial expressions are produced to this level of subtlety [27].

In sum, this is the first explicit comparison of facial expression between humans and another primate species using systematic, anatomically based coding (FACS and ChimpFACS) and an equivalent experimental design. Such comparisons are necessary and important to understand how the similarities and differences in facial expression between humans and their closest-living relatives, the non-human great apes, have evolved.

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