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HUMAN NEURO-COGNITIVE DECODING ABILITIES AS A NEW CRITERION FOR HOMOLOGIZING PRIMATE COMMUNICATORY SIGNALS

ABSTRACT: Paleoanthropology can provide a lot of important information about body size, sexual dimorphism, locomotion, hand function, feeding ecology etc. of the last common ancestor of great apes and early hominids (LCA). But the fossils can reveal only limited information about LCA social organization or social behaviour. Reconstructions of the communicatory signals phylogeny are frequently based on observations of the living primates. This paper discusses a new type of evidence for homologizing human and primate facial displays. The proposed new approach uses human neuro-cognitive decoding abilities for the primate facial displays. There is an assumption that facial displays which will be interpreted more accurately than others, should be rather homological with some of human facial expressions. Results of the preliminary study involving recognition of chimpanzee facial expressions are evaluated with integration of the previous research.

KEY WORDS: Evolution – Behavioural homology – Decoding abilities – Facial expressions – Chimpanzee

INTRODUCTION

The concept of behavioural homology is widely used in the research on reconstruction of early hominids social behaviour and communication. Even paleoanthropology provides many important data about some types of behaviour of the last common ancestor of great apes and hominids (LCA) – as to body size, sexual dimorphism, locomotion, hand function, feeding ecology – but the fossils can reveal only limited information about LCA social organization, demographic characteristics or social behaviour (Potts 1987). For that reason many such interpretations have arisen from observations of the living primate species. In the further text the application of a new criterion for homologizing primate facial displays will be discussed.

HOMOLOGIZING PRIMATE FACIAL DISPLAYS

Facial expressions (or facial displays) constitute an important component of primate visual communication, especially in terrestrial Old World monkeys and apes – macaques, baboons and chimpanzees (Andrew 1964, Moynihan 1969, Redican 1982, Preuschoft *et al.* 1995). Facial signals pertain to the most stereotype behaviour in the whole primate order that is otherwise well-known for its behavioural flexibility (Preuschoft *et al.* 1995). Many researchers have asked the question whether basic primate facial expressions are homological with some human facial expressions (see *Table 1*). Van Hooff even suggested that facial expressions could offer the best example of interspecies behavioural comparison where the homology concept can be applied (van Hooff 1976).

TABLE 1. Classifying homology between human and chimpanzee facial expressions in previous research.

Basic chimpanzee facial expressions	Possible homologies in human facial expressions						
	no homology in human facial repertoire	human anger	human fear	human smile	human laughter	human sadness	begging
waa bark	Chevalier-Skolnikoff 1973, Redican 1982, Eibl-Eibesfeldt 1989	Jolly 1972					
scream face	Redican 1982, Preuschoft 2000	Jolly 1972, Chevalier-Skolnikoff 1973, Eibl-Eibesfeldt 1989					
glare	Chevalier-Skolnikoff 1973, Redican 1982, Preuschoft 2000	Jolly 1972					
silent bared teeth display				van Hooff 1967, 1972, 1976, Chevalier-Skolnikoff 1973, Preuschoft 1992, Schmidt 2001, Piteaun <i>et al.</i> 1976	Jolly 1972		
play face				Fairbanks 1977, van Hooff 1981, Preuschoft 2000			
silent open mouth display						van Hooff 1967, 1972, 1976, 1981, Chevalier-Skolnikoff 1973, Fairbanks 1977, Redican 1982, Eibl-Eibesfeldt 1989, Preuschoft 1992, Preuschoft 2000, Schmidt <i>et al.</i> 2001	
pout face	Redican 1982, Preuschoft 2000			Bolwig 1964			Jolly 1972, Eibl-Eibesfeldt 1989
whimper face	Redican 1982						Chevalier-Skolnikoff 1973, Eibl-Eibesfeldt 1989
cry face							Chevalier-Skolnikoff 1973, Eibl-Eibesfeldt 1989
hoot face	Jolly 1972, Eibl-Eibesfeldt 1989						

Preuschoft (1995) critically reviewed the methods commonly used for homologizing primate facial display. Relevance of six criteria is discussed in this study (Preuschoft 1995):

1. The stereotypy of facial displays (Lorenz 1950);
2. The similarity of individual facial components (Remane 1952, Wickler 1967);
3. The similarity of facial musculature (Tinbergen 1962, Atz 1970);
4. The existence of intermediate displays (Remane 1952);
5. The presence of the display in a large number of related species (Remane 1952, Wickler 1961);
6. The association of the display with the same motivation complex (Boerends 1958, Atz 1970, Hinde, Tinbergen 1958, Tinbergen 1959).

Finally she affirmed only three relevant criteria for assessing homology of human and primate facial expressions – 1. the stereotypy of facial displays, 2. the similarity of individual facial components and, in a lesser extent, 3. the similarity of facial musculature. In the third criterion Preuschoft pointed out the fact that "new" uniquely human facial muscles could be developed from older structures during the process of differentiation of the facial musculature (Preuschoft 1992: 126).

We can see quite large incongruity in the assessment of homology of individual chimpanzee and human facial expressions studied by researchers in *Table 1*. Silent bared teeth display (or grimace) and play face (or relaxed open mouth face) seem to be the most discussed chimpanzee facial displays in this way. Quite large agreement occurs among researchers in considering play face as a possible homology for human laughter (Darwin 1872, Kohts 1935, Foley 1935, Yerkes 1943, Blurton Jones 1969, Jolly 1972, Chevalier-Skolnikoff 1973, Pitcairn Eibl-Eibesfeldt 1976, van Hooff 1967, 1972, 1981, Redican 1982, Eibl-Eibesfeldt 1989, Preuschoft 1992, 2000, Preuschoft, van Hooff 1995, Schmidt, Cohn 2001). In contrast, Redican and Pitcairn assessed silent bared teeth display as a homology of human fear (Redican 1982, Pitcairn, Eibl-Eibesfeldt 1976), Jolly as a homology of human sadness (Jolly 1972) and other scholars considered bared teeth as a homology of human smile (van Hooff 1967, 1972, 1976, 1981, Chevalier-Skolnikoff 1973, Fairbanks 1977, Redican, 1982, Eibl-Eibesfeldt 1989, Preuschoft 1992, 2000, Schmidt, Cohn 2001). Also in homologizing other chimpanzee facial displays there seems to be more than one opinion stream. Then, another criterion would be helpful for new assessment of homology of human and primate facial signals.

DISCUSSING A NEW CRITERION FOR THE ASSESSMENT OF HOMOLOGY

This paper proposes a new type of evidence for homology of human and primate facial displays using human neuro-

cognitive decoding abilities for these signals. There is an assumption that facial displays, which will be interpreted more accurately than others, should be rather homological with some of human facial expressions. This criterion is connected with Preuschoft's criterion number two – similarity of individual facial components, but it does not mean detailed comparisons of particular facial components and their positions or construction of facial ethograms. In contrast, the proposed criterion is based on the human ability to recognize facial changes and their meaning as one complex, as we are used to do in everyday social interaction.

Foley's study from the year 1935 constitutes one of the rare attempts for testing human decoding abilities for chimpanzee facial expressions (Foley 1935). Unfortunately, due to its age and former state of knowledge, this research proved several crucial limitations. First, Foley used six photos of a five-year-old chimpanzee male that was raised by human keepers from early childhood (photos by Ladygina Khots 1935). Maybe for that reason, two of the six photos represented different facial configuration than that commonly observed in common chimpanzee groups in wild nature or in captivity (Fig. 5 – anger, Fig. 2 – sadness, pp. 42). Second, 127 students who judged the photos were asked to choose 1 of 16 given options consisting of verbal expressions for human emotions¹. Some pairs of options were on the threshold of synonymy. Finally, Foley stated the following correct frequencies: 21% for neutral face, 21% for cry face, 18% for play face and 0% for hoot face.

MATERIAL

Sex composition of the population sample was directed by quota sampling to get regular proportion of males and females in the sample. Most of the respondents were students of the Czech Agricultural University between 16 and 28 years of age.

METHODS

Our present preliminary study does not correspond with the mentioned results of Foley (Trnka 2002, 2003). 100 respondents (M=50, F=50) judged 8 standardized drawings of chimpanzee facial displays (drawings by Chevalier-Skolnikoff 1973). We carried out a pilot study with the intention to verify our research implement (N=20 students – not involved in the main sample). There was a good idea

¹ Preuschoft pointed out to the risk of anthropomorphic confusion in the comparative research when using human verbal repertoire for chimpanzee facial expressions (Preuschoft 2000). It seems better to employ rather the verbal terms commonly used for animal behaviour whenever possible in this way (such as threat, playfulness, submission, etc).

TABLE 2. Correct frequencies in recognition of 8 chimpanzee facial expressions by students (Trnka 2003).

Chimpanzee facial expressions	Total correct frequency	Males correct frequency	Females correct frequency
glare	62.6	60.0	65.3
hoot face	44.4	44.0	44.9
whimper face	31.3	40.0	22.4
scream face	26.3	26.0	26.5
pout face	20.2	24.0	16.3
silent vertical bared teeth	18.2	18.0	18.4
silent horizontal bared teeth	11.1	12.0	10.2
waa bark	5.1	6.0	4.1

TABLE 3. Comparison of total correct frequencies in recognition of human and chimpanzee facial expressions (Trnka 2002).

	Total correct frequency for human facial expressions	Total correct frequency for chimpanzee facial expressions	Common total correct frequency
males	56.2	31.9	44.0
females	58.5	30.4	44.5
total	57.4	31.2	44.3

at the start of the study – the respondents were allowed to judge each facial expression with their own words. The pilot study revealed one very important information – in most cases the respondents were not able to determine many of the showed facial expressions. Therefore we changed the "open questions" to 5 given options for each facial expression. Decision time for each judged facial expression was unlimited.

CONCLUSIONS

We can see higher variance of correct frequencies than in Foley's study (see *Table 2*) that points out to the fact that people are able to recognize better at least some of the chimpanzee facial displays. However, total successfulness in recognition of chimpanzee facial expressions was lower than total successfulness in recognition of human facial expressions (respondents also judged human facial expressions – see *Table 3*). The threshold of random incidence is 20% in our questionnaire design with 5 given options, so we can conclude that 5 of 8 chimpanzee facial expressions were judged correctly with higher frequencies than the random occurrence.

Our preliminary study shows several interesting findings. The correct frequencies of whimper face (31%) and scream face (26%) indicate that these two facial expressions have homology in human facial repertoire. In relation to the

previous research, the whimper can be homologous with the human expression of sadness and the scream with the human expression of anger (see *Table 1*). Glare seems to be homologous with human anger of lower intensity – the second type without prominent demonstration of teeth (Chevalier-Skolnikoff 1973).

Hoot face was recognized by 44% of respondents. Surprisingly, this expression has not been connected with any human facial expression in the previous research. Descriptive analysis of mouth and lips changes indicates similarity with the human facial expression of high intensity surprise², despite chimpanzee hoot face does not prove changes in the upper part of the face (eyebrows raised high, horizontal wrinkles across the forehead, eyelids widely open).

Waa bark gained the lowest correct frequency (5%). It indicates the absence of phylogenetical connection with any of human facial expressions. The correct frequencies of both silent horizontal and silent vertical bared teeth faces, usually classified as a homology of human smile, lie

² Comparison of the mouth facial components in human surprise and chimpanzee hoot face: a. chimpanzee hoot face: mouth corners retracted horizontally forwards lips greatly extended and forms a big pursed appearance with an "o" opening; b. human surprise expression: jaws half opened, lips relaxed and forms medium appearance, teeth covered or partly visible.

under the threshold of random incidence. But the second mentioned display approaches to the threshold of random incidence, which makes assessment of this frequency considerably difficult (as in the case of pout face).

It follows from the above that the usage of the proposed criterion is limited only for evaluation whether individual facial expressions have homology in human facial repertoire or not. Nevertheless, progress in this research hypothesis can bring a new interesting view to the evolution of human visual communication in the future.

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REFERENCES

- ANDREW R., 1964: The display of the primates. In: J. Buettner-Janusch (Ed.): *Evolutionary and Genetic Biology of Primates*. Pp. 227–309. Academic Press, New York.
- ATZ J., 1970: The application of the idea of homology to behavior. In: I. Aronson, E. Tobach, D. Lehman, J. Rosenblatt (Eds.): *Development and Evolution of Behavior*. Pp. 53–74. Freeman, San Francisco.
- BLURTON JONES N., 1969: An ethological study of some aspects of social behaviour of children in nursery school. In: D. Morris (Ed.): *Primate Ethology*. Pp. 437–463. Garden City, Anchor.
- BOERENDS G., 1958: Comparative methods and the concept of homology in the study of behaviour. *Archiv of Niederland Zoology* 13: 401–417.
- BOLWIG N., 1964: Facial expression in primates with remarks on a parallel development in certain carnivores. *Behaviour* 22: 167–192.
- CHEVALIER-SKOLNIKOFF S., 1973: Facial expression of emotion in nonhuman primates. In: P. Ekman (Ed.): *Darwin and Facial Expression*. Pp. 11–90. Academic Press, New York.
- DARWIN C., 1872/1998: *The Expression of the Emotions in Man and Animals*. Oxford University Press, New York. 285 pp.
- EIBL-EIBESFELDT I., 1989: *Human Ethology*. Aldine de Gruyter, New York. 863 pp.
- FAIRBANKS L., 1977: Animal and human behavior: Guidelines for generalization across species. In: M. McGuire, L. Fairbanks (Ed.): *Ethological Psychiatry: Psychopathology in the Context of Evolutionary Biology*. Pp. 87–110. Grune and Stratton, New York.
- FOLEY J., 1935: Judgement of facial expression of emotion in the chimpanzee. *J. of Social Psychology* 6: 31–67.
- HINDE R., TINBERGEN N., 1958: The comparative study of species-specific behavior. In: G. Simpson, A. Roe (Eds.): *Behavior and Evolution*. Pp. 251–268. Yale University Press, New Haven.
- JOLLY A., 1972: *The Evolution of Primate Behavior*. New York, The Maxmillian Company. 397 pp.
- KOHTS N., 1935: *Infant Ape and Human Child: Instincts, Emotions, Play, Habits*. Moscow, Scientific Memoirs of the Museum Darwinianum. 596 pp.
- LORENZ K., 1950: The comparative method in studying innate behaviour patterns. *Symposium of Social Experimental Biology* 4: 221–268.
- MOYNIHAN M., 1969: Comparative aspects of communication in New World primates. In: D. Morris (Ed.): *Primate Ethology*. Pp. 306–342. Garden City, Anchor.
- PITCAIRN T., EIBL-EIBESFELDT I., 1976: Concerning the evolution of nonverbal communication in man. In: M. Hahn, E. Simmel (Ed.): *Communicative Behavior and Evolution*. Pp. 81–113. Academic Press, New York.
- POTTS R., 1987: Reconstruction of early hominid socioecology: A critique of primate models. In: W. Kinzey (Ed.): *The Evolution of Human Behavior: Primate Models*. Pp. 28–47. State University of New York Press, New York.
- PREUSCHOFT S., 1992: Laughter and smile in barbary macaques (*Macaca sylvanus*). *Ethology* 91: 220–236.
- PREUSCHOFT S., 2000: Primate faces and facial expressions. *Social Research* 67: 245–271.
- PREUSCHOFT S., VAN HOOFF J. A. R. A. M., 1995: Homologizing primate facial displays: a critical review of methods. *Folia Primatologica* 65: 121–137.
- REDICAN W., 1982: An evolutionary perspective on human facial displays. In: P. Ekman (Ed.): *Emotion in the Human Face*. Pp. 212–280. Cambridge University Press, New York.
- REMANE A., 1952: *Die Grundlagen des natürlichen Systems der vergleichenden Anatomie und der Phylogenetik*. Leipzig, Goent und Portig KG. 400 pp.
- SCHMIDT K., COHN J., 2001: Human facial expressions as adaptations: Evolutionary questions in facial expression research. *Yearbook of Phys. Anthropol.* 44: 3–24.
- TINBERGEN N., 1959: Comparative studies of the behaviour of gulls (*Laridae*): A progress report. *Behaviour* 15: 1–70.
- TINBERGEN N., 1962: The evolution of animal communication – A critical examination of methods. *Proceedings of the Zoological Society of London* 8: 1–6.
- TRNKA R., 2002: *Comparison of Facial Expressions in Humans and Chimpanzees*. Rarach, Prague. 25 pp.
- TRNKA R., 2003: Discrimination of chimpanzee facial expressions. In: J. Vignerová, J. Riedlová, P. Bláha (Eds.): *Anthropology and Society*. P. 197. Prague, Charles University Press.
- VAN HOOFF J. A. R. A. M., 1967: The facial displays of catarrhine monkeys and apes. In: D. Morris (Ed.): *Primate Ethology*. Pp. 9–88. Aldine, Chicago.
- VAN HOOFF J. A. R. A. M., 1972: Comparative approach to the phylogeny of laughter and smiling. In: R. A. Hinde (Ed.): *Non-verbal Communication*. Pp. 209–242. Oxford University Press, New York.
- VAN HOOFF J. A. R. A. M., 1976: The comparison of facial expression in man and higher primates. In: M. von Cranach (Ed.): *Methods of Inference from Animal to Human Behaviour*. Pp. 165–196. Aldine, Chicago.
- VAN HOOFF J. A. R. A. M., 1981: Facial expressions. In: D. McFarland (Ed.): *The Oxford Companion to Animal Behaviour*. Pp. 165–176. Oxford University Press, Oxford.

WICKLER W., 1961: Ökologie und Stammesgeschichte von Verhafnensweisen. *Forschung Zoologie* 13: 303–365.
WICKLER W., 1967: Vergleichende Verhaltensforschung und Phylogenetik. In: G. Heberer (Ed.): *Die Evolution der Organismen*. Pp. 420–508. Fischer, Stuttgart.

YERKES R. M., 1943: *Chimpanzees: A Laboratory Colony*. New Haven, Yale University Press. 321 pp.

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