

Extra-linguistic cues in chimpanzees vocal communication

Chiara Zulberti¹, Joseph Mine², Gal Badihi³, Simon Townsend², Catherine Hobaiter³

¹Faculty of Life Sciences, Institute of Biology, Leipzig University, Leipzig, Germany

²Department of Comparative Language Science, University of Zürich, Zürich, Switzerland

³School of Psychology & Neuroscience, University of St Andrews, St Andrews, UK

chiara.zulberti@uni-leipzig.de

The linguistic faculty most likely evolved in face-to-face communication, a setting where speech interacts with other non-vocal stimuli like gestures, gaze, and facial expressions. These variety of corporeal signals and cues, often and henceforth referred to as extra-linguistic cues (ELCs), are known not only to naturally accompany speech production (Goldin-Meadow, 1999), but also to influence speech perception and comprehension (e.g., Holler et al., 2015; Kelly et al., 2009). While ELCs usage and function are broadly investigated in human systems, comparatively less is known about their evolutionary origins. Are ELCs a uniquely human phenomenon, or does this trait have its roots deep within the primate lineage? In other words, do other primates also engage in the use of similar cues during vocal production? In this study, we aimed to answer these questions by probing for structures comparable to ELCs in our closest living relative, the chimpanzee. Previous multimodal investigations in great apes have found that chimpanzees combine vocal and gestural signals (Hobaiter et al., 2017). However, alongside vocalisations and gestures, other body movements and visual behaviours that do not fulfil a strictly communicative function, might likewise carry information salient to the communicative interaction. A comprehensive analysis of the variety of these behaviours, i.e., cues, and their distribution across call types is currently missing. The present study aimed to fill this gap of knowledge, by systematically documenting the types of gestures, facial expressions, gaze orientation, body movements, and postures that co-occurred with the vocal repertoire of wild eastern chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. To this end, we observed the whole range of non-vocal behaviours deployed during vocal production in 12 individuals, and described a total of 36 morphologically distinct ELCs (see Tab.1) across nine call types. The vocalisations included in the analysis were barks, pants, pant hoots, soft hoos, grunts, pant grunts, pant barks, screams, and whimpers (Crockford et al., 2018; Slocombe & Zuberbühler, 2010). Moreover, to assess the patterns of interaction between ELCs and vocalisations and to identify above-chance co-occurrences of ELCs with specific call types, a collocation analysis was performed (Bossard et al., 2022). The analysis – which included both bigrams, formed by one call and one ELC, as well as n-grams combining one call with multiple (up to four) ELCs – returned 230 significant ELC-call combinations. In addition to documenting the chimpanzee ELC repertoire, we also constructed GLMMs to explore two possible functions of ELCs usage in the chimpanzee communication system. First, we tested whether levels of ELC production showed a significant correlation with the contextual ambiguity of calls. Second, we examined the role of potential aggressive escalation in promoting the use of such cues. While the former was confirmed, the data did not support the latter hypothesis. Overall, our results showed that ELCs are omnipresent throughout chimpanzee vocal production (with an average of 3.3 ELCs per vocal event) and conveyed through similar articulators to those deployed by humans. Moreover, ELCs seemed to combine with vocalisations in a flexible way, suggesting a combinatorial dimension of ELC usage in the chimpanzee communication system. Although the biological functions and communicative value of these combinations were not directly addressed by the study, hypothesis testing pointed to a potential role of ELCs in meaning refinement. Ultimately, the present investigation has two main implications. First, it suggests that the last common ancestor between humans and chimpanzees might have used ELC-like structures. Second, it represents the first crucial step for future studies delving into the meaning of vocal and visual combinations in the communicative system of chimpanzees.

Index Terms: visual and vocal production, animal communication, comparative linguistics

	ELC name	ELC description	
Action	copulate	copulating/initiating copulation with another individual	
	feed	grabbing food items and placing in mouth	
	groom	probing hair of other individual and extracting small particles, using one or both hands	
Brachiomaneal movement	groom self	probing one's own hair and extracting small particles, using one or both hands	
	arm reach	arm is extended straight towards another individual	
	arm wave	beckons, arm flings and other unspecified arm/hand movements	
	arms crossed	arms are placed in front of chest, crossed and grabbing on to each other	
	grab branch	hand or foot fingers are wrapped around a branch and move it, either once or repeatedly in back and forth motion	
	hit other	rapid, aggressive movement of hand or foot to make contact with body part of another individual	
	hold tree	hand or foot is grasping the trunk of a tree while the rest of the body is not touching the tree (no movement/shaking of the tree)	
	scratch self	loud scratching gesture of fingers against body surface	
	slap ground	palms of hands or feet are brought violently against the ground or an object to produce a smacking noise, sometimes repeatedly (includes drumming or stomping)	
	touch other	light contact of hands (palm or fingers) with body of another individuals (includes embrace)	
Body posture and movement	approach	movement in direction of another individual with 45 degree accuracy on either side, close range approximately <5m	
	climb	movement up, down or along the branch of a tree	
	crouch down	chest is brought closer to the ground, while hands and feet do not move	
	dangle	using hand or foot to dangle from a tree branch	
	extend body towards	chest, back or bottom is moved toward a specific individual but legs do not move	
	get up	transition from lying or sitting position to standing or walking	
	jump	rapid movement of the body briefly floating in air, both feet leave the ground/branch	
	lie down	resting position with chest or back touching the ground	
	present back	back and bottom orientation is shifted toward a specific individual by at least 90 degrees while vocalisation is produced	
	retract body	avoidant movement away from a specific individual, it can either involve only chest, back or bottom or the whole body	
	run	rapid quadrupedal movement with gallop-like appearance	
	sit	sitting with bottom touching ground, chest or back are not touching ground	
	sit up	transition from lying position to sitting position	
	stand	erect quadrupedal position without movement	
	turn body away	chest orientation is shifted away from specific individual by at least 90 degrees while vocalisation is produced	
	turn body towards	chest orientation is shifted towards a specific individual by at least 90 degrees during vocal production	
	walk	moving quadrupedally by more than 1 meter	
	Facial expressions	fear grin	lip corners are pulled back and teeth are showing, during aggressive or threatening contexts
		scream face	lip corners pulled back showing teeth, lips parted and mouth wide open
	Head orientation and gaze	gaze alternation	head orientation changes multiple (3+) times by more than 90 degrees
gaze upwards		head orientation is shifted towards the canopy/sky	
look away		head orientation is shifted away from a specific individual by at least 90 degrees during production of vocalisation	
look towards		head orientation is shifted toward a specific individual by at least 90 degrees while vocalisation is produced	

Table 1: *Repertoire of ELCs. The table reports the complete list of ELCs identified in the present study and their definitions, grouped by category*

References

- Bosshard, A. B., Leroux, M., Lester, N. A., Bickel, B., Stoll, S., & Townsend, S. W. (2022). From collocations to call-ocations: using linguistic methods to quantify animal call combinations. *Behavioral Ecology and Sociobiology*, 76(9), 122. <https://doi.org/10.1007/s00265-022-03224-3>
- Crockford, C., Gruber, T., & Zuberbühler, K. (2018). Chimpanzee quiet hoo variants differ according to context. *Royal Society Open Science*, 5(5), 172066. <https://doi.org/10.1098/rsos.172066>
- Goldin-Meadow, S. (1999). The role of gesture in communication and thinking. *Trends in Cognitive Sciences*, 3(11), 419–429. [https://doi.org/https://doi.org/10.1016/S1364-6613\(99\)01397-2](https://doi.org/https://doi.org/10.1016/S1364-6613(99)01397-2)
- Hobaiter, C., Byrne, R. W., & Zuberbühler, K. (2017). Wild chimpanzees' use of single and combined vocal and gestural signals. *Behavioral Ecology and Sociobiology*, 71(6), 96. <https://doi.org/10.1007/s00265-017-2325-1>
- Holler, J., Kokal, I., Toni, I., Hagoort, P., Kelly, S. D., & Özyürek, A. (2015). Eye'm talking to you: speakers' gaze direction modulates co-speech gesture processing in the right MTG. *Social Cognitive and Affective Neuroscience*, 10(2), 255–261. <https://doi.org/10.1093/scan/nsu047>
- Kelly, S. D., Özyürek, A., & Maris, E. (2009). Two Sides of the Same Coin: Speech and Gesture Mutually Interact to Enhance Comprehension. *Psychological Science*, 21(2), 260–267. <https://doi.org/10.1177/0956797609357327>
- Slocombe, K. E., & Zuberbühler, K. (2010). 16. Vocal Communication in Chimpanzees: . In E. V Lonsdorf, S. R. Ross, & T. Matsuzawa (Eds.), *The Mind of the Chimpanzee: Ecological and Experimental Perspectives* (pp. 192–207). University of Chicago Press. <https://doi.org/doi:10.7208/9780226492810-018>