

THE ONTOGENY OF BEHAVIOURAL RESPONSES TO PANT Hoots IN WILD CHIMPANZEES

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1. Introduction

Comparative researchers study the vocal systems of animal species to identify the presence or absence of traits shared with human language to explain its origins (Fitch & Zuberbühler, 2013). Traditionally, the vocal development of non-human primates, like their adult vocal communication, has been regarded as rather inflexible and hard-wired, which led to the idea that few parallels exist with the highly flexible and socially mediated acquisition of human language (Egnor & Hauser, 2004; Owren et al., 2011). However, limitations to this view include being largely based on studies conducted on monkey species, on alarm calls, and in artificial or captive settings (Seyfarth & Cheney, 1997; Snowdon, 2009). The development of pant hoots, complex vocal sequences used by wild chimpanzees as long-distance social calls (Fedurek et al., 2014; Marler & Hobbett, 1975; Mitani & Nishida, 1993), is largely unknown. Pant hoots are the most frequently used calls by adults and are flexibly used across most behavioural contexts (Marler & Tenaza, 1977). Chimpanzees either spontaneously produce pant hoots or respond vocally to others' pant hoots, sometimes by chorusing together. Given that this call is very rarely produced by immature individuals, one approach to determine if and how social factors mediate its ontogeny is to investigate how young receivers respond when exposed to others' pant hoots.

2. Methods

We collected data in the Sonso community (*Pan troglodytes schweinfurthii*) of the Budongo Forest, Uganda, from six infants (0–4 years; M:F, 4:2), seven juveniles (5–9 years; M:F; 4:3), all dependent on their mother, as well as from 25 mature individuals (M:F, 13:12). We used focal animal sampling as the main method of data collection (Altmann, 1974). We recorded the behavioural activity of the focal, information about pant hoots produced by the focal and by other group members, behavioural changes of the focal after being exposed to others' pant hoots, and continuous party composition. We used long-term data collected by field assistants to assess the gregariousness of individuals by measuring how frequently they were observed in a party while not being focal followed.

3. Results

Immature individuals spontaneously called 10 times less often than mature individuals but responded vocally only 2 times less often. The two most common behavioural responses to pant hoots were a head movement towards the call and vocal responses. When compared to mature chimpanzees, immature individuals produced both responses less often. More specifically, the older offspring, the male offspring, and the offspring of more gregarious mothers were more likely to move their head towards calls. The older male offspring, the older offspring of more gregarious mothers, and the offspring of more gregarious mothers in the presence of adult males were more likely to respond vocally. In addition, immature individuals were more likely to respond vocally when their mother also produced a vocal response. Finally, we observed that the male offspring of more gregarious mothers were exposed to more pant hoots overall.

4. Discussion

Our study shows that the ontogeny of vocal responses undergoes developmental changes, varies according to sex, and is socially mediated. The rather slow ontogeny of pant hoots is consistent with the idea that vocal usage and comprehension learning are less hard-wired in social calls. Our observations are also in line with the idea that the development of social skills tends to occur earlier in male great apes, likely as a result of different selection pressures. Higher levels of social and communicative exposure likely increase opportunities for immature individuals to learn appropriate responses. Chorusing between mother and offspring might function as a bonding signal or as auditory reinforcement. While a clear distinction between the development of human language and that of primate vocalisations exists, we demonstrated that chimpanzees' vocal ontogeny can be flexible and mediated by social factors, contrary to previous assumptions.

References

- Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, 49(3/4), 227–267.
- Egnor, S. E. R., & Hauser, M. D. (2004). A paradox in the evolution of primate vocal learning. *Trends in Neurosciences*, 27(11), 649–654.
- Fedurek, P., Donnellan, E., & Slocombe, K. E. (2014). Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. *Behavioral Ecology and Sociobiology*, 68(8), 1345–1355.
- Fitch, W. T., & Zuberbühler, K. (2013). Primate precursors to human language: Beyond discontinuity. In E. Altenmüller, S. Schmidt, & E. Zimmermann (Eds.), *Evolution of Emotional Communication* (pp. 26–48). Oxford University Press.
- Marler, P., & Hobbett, L. (1975). Individuality in a Long-Range Vocalization of Wild Chimpanzees. *Zeitschrift Für Tierpsychologie*, 38(1), 97–109.
- Marler, P., & Tenaza, R. (1977). Signalling behaviour of apes with special reference to vocalisations. In P. Marler, R. Tenaza, & T. A. Sebeok (Eds.), *How animals communicate* (pp. 965–1033). Indiana University Press, Bloomington.
- Mitani, J. C., & Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Animal Behaviour*, 45(4), 735–746.
- Owren, M. J., Amoss, R. T., & Rendall, D. (2011). Two organizing principles of vocal production: Implications for nonhuman and human primates. *American Journal of Primatology*, 73(6), 530–544.
- Seyfarth, R. M., & Cheney, D. L. (1997). Some general features of vocal development in nonhuman primates. In C. T. Snowdon & M. Hausberger (Eds.), *Social Influences on Vocal Development* (1st ed., pp. 249–273). Cambridge University Press.
- Snowdon, C. T. (2009). Plasticity of Communication in Nonhuman Primates. In M. Naguib, K. Zuberbuhler, N. S. Clayton, & V. M. Janik (Eds.), *Advances in the Study of Behavior* (Vol. 40, pp. 239–276). Elsevier.

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