Call combinations in bonobos and chimpanzees

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By combining morphemes or words into larger structures, humans can generate an infinite number of meaningful constructions. Despite growing evidence that animals have combinatorial capacities (Berthet et al., 2022), investigation into our closest living relatives, nonhuman apes, remains scarce (Crockford, 2019). Recent observational work (Bortolato et al., 2023; Girard-Buttoz et al., 2022; Leroux et al., 2022) is beginning to address this gap. Specifically, Leroux et al. (2022) studied the chimpanzees *Pan troglodytes* of the Sonso community, at the Budongo Conservation Field Station, Uganda, and identified 15 non-random vocal combinations (Leroux et al., 2022). Here, we followed up on these findings by investigating whether bonobos *Pan paniscus*, the closest living relatives of humans and chimpanzees, also combine calls in systematic ways. We further assessed whether this capacity differs from that of chimpanzees, using data from Leroux et al., 2022.

We conducted 150h of focal recording on 24 adult wild bonobos (14 females and 10 males) from 3 groups at the Kokolopori Bonobo Research Project, Democratic Republic of Congo (Surbeck et al., 2017). During 15-min continuous focal follows, we recorded every vocalization produced by the focal individuals and classified them as one of 10 call types of the bonobo vocal repertoire recently established by Wegdell et al (submitted). An inter-observer reliability test was

performed on 10% of the dataset, showing a good agreement between the coder and an external rater (305 calls, K=0.67). Following previous work on great apes (e.g., Leroux et al., 2022), we defined a call combination as two (or more) distinct call types emitted by one individual and separated by less than two seconds of silence.

We collected a total of 1174 utterances comprising 1 to 32 calls (mean=2.64 calls/utterance), and up to 17 call combinations (mean=0.68 combination/utterance). First, we found that the bonobos of Kokolopori vocalize on average 2.5 times more than the Sonso chimpanzees (8.53 vs 3.30 utterances/hour). To specifically investigate their combinatorial capacities, we focused on utterances comprising at least one call combination (N=373 utterances). We used collocation analysis, a method developed in computational linguistics, to detect non-random call combinations, specifically at the bigrammic (i.e., two calls) level (Bosshard et al., 2022). To analyze utterances longer than two calls, we decomposed them into bigrams: for instance, a combination ABC was processed as two separate bigrams AB and BC. A Multiple Distinctive Collocation Analysis (MDCA), showed that, similarly to chimpanzees, bonobos produce several non-random bigrams (N=17). Interestingly, bonobos produce non-random bigrams more frequently than chimpanzees, both in terms of production rate (3.90 vs 0.47 non-random call combinations/hour) but also as a proportion of their total vocal output (non-random bigrams represent 31.9% vs 15.1% of the total vocal production). Additionally, 7 (41%) of the bonobo non-random bigrams are unidirectional (e.g., we observe AB but not BA), suggesting that the order may be important, a finding that closely aligns with that of chimpanzees, where 46% of the non-random bigrams are also unidirectional. Finally, similarly to chimpanzees, male bonobos produce more single utterances than females (16.8 vs 9.3 utterances/hour), but males and females produce combinations at similar rates (4.0 vs 3.8 non-random bigrams/hour respectively). Overall, our results indicate that the vocal communication of bonobos from the Kokolopori population extensively relies on combinations. Moreover, they are more vocal and produce call combinations more frequently than the Sonso community of chimpanzees. We consider a number of social and ecological explanations for these differences. Further investigations should include an evaluation of the meaning of these combinations as well as a replication in other chimpanzee and bonobo communities to assess the more general nature of our findings. Overall, our study provides further tentative support for the hypothesis that the human combinatorial capacity is deeply rooted in the primate lineage.

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