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Sequence organization of mother–infant interactions in chimpanzees (*Pan troglodytes schweinfurthii*) in the wild

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Sequence organization is a fundamental feature of human communication, shaping our interactions. This organization underlies interactions with and without language, appears early in human development and is even hypothesized to precede language itself. However, remarkably little is known about the evolutionary origins of the sequence organization of interactions. Here, we investigated the sequence organization of mother–infant interactions in one of our closest living relatives, the chimpanzee (*Pan troglodytes*). We focused our study on two components of sequence organization: (i) adjacency pairs around turn transitions and (ii) flexibility on an interactional scale. In total, 361 communicative interactions containing 3647 signals and actions in 17 mother–infant dyads living in the Ngogo population, Uganda, were collected and analysed. The results showed that on a two-turn scale, a large proportion (42%) of turn transitions are non-randomly combined into potential adjacency pairs. Regarding flexibility, a conditional transition network revealed eight highly distinguished clusters of flexibly used units. With this consilience of methods, we show that, like humans, interactions of chimpanzees are sequentially organized, strengthening the hypothesis that sequence organization is indeed a fundamental feature of communication pre-dating the evolution of language.

1. Introduction

One fundamental feature of human interactions is that they are sequentially organized [1,2]. In this sequence organization, preceding turns set up a framework that shapes ‘valid’ responding turns [3,4]. For example, the question ‘Do you want to go for a walk?’ is setting up a framework for the answer: ‘Yes, I would love to’. Important to note is that while sequence organization limits potential responses, it does not predetermine them. In our previous example, the sentences *‘No, I am busy’*, ‘But it is raining outside’ or ‘Let me get my coat’ are all valid response options. Therefore, sequence organization balances between limitless flexibility where everything is possible and a pre-determined structure where A is always followed by B. This sequence organization appears across languages [5], including conversations in sign language [5,6] or in the proto-conversations of pre-verbal infants [7,8], making it a basic feature of human interaction. Additionally, it also appears in social interactions that are devoid of any language, such as joint actions [9–11] or a mix between signals and actions [12]. For example, the question ‘What are you reading?’ can be answered with a verbal response, a showing gesture, the action of passing the book over, or a combination of them. It has been suggested that sequence organization, together with other features characterizing human interactions—such as turn-taking, multimodality and intentionality—not only preceded language itself, but made the evolution of language possible in the first place [13]. As such, unravelling the evolutionary origins of these features is relevant for discovering and understanding the roots of human communication [14].

Here, we defined sequence organization as the structure of multiturn interactions involving multiple individuals, opposed to the organization of within-individual sequences, which is usually referred to as syntax [15,16] or, when related to object manipulation, action grammar [17,18]. The link between syntax, action grammar and sequence organization is an interesting topic detailed in other studies but falls outside the scope of this study [18–20]. One way of trying to investigate interactional skills of extinct hominins is the comparative approach, in which similarities and differences between humans and non-human animals, specifically non-human primates (hereafter primates), are examined [21,22]. Following this approach, a species-agnostic framework for the investigation of sequence organization is needed. Recently, Pika *et al*. [23,24] developed such a comparative framework by pinpointing and operationalizing four specific elements characteristic of human conversational turn-taking. As both sequence organization and turn-taking are inherently linked [4,25,26], two of the elements detailed in the comparative framework [23] describe essential components of sequence organization. Namely, (i) adjacency pairs— meaning the predictable and responsive nature of two consecutive turns produced by two individuals and (ii) flexibility of turn-taking organization—detailing the variation and interchangeability of different turns.

Previous comparative studies have explored aspects of sequence organization in primates qualitatively [3,27–30]. For example, Rossano [27] and Mondada & Meguerditchian [3] showed the existence of adjacency pair-like sequences in joint-travel initiations in captive bonobos and greeting interactions in baboons, respectively. Other studies have explored underlying processes and rules in behavioural sequences [31], such as tool use [18,32]. However, quantitative objective metrics of sequence organization of multiturn interactions that can be compared across species are still missing (but see [33]). Here, we want to address this gap by exploring and quantifying some interactional sequential capabilities of one of our closest living relatives, chimpanzees (*Pan troglodytes*), living in their natural environments. In humans, mother–infant interactions form a crucial platform, wherein the first stages of language acquisition occur [7,8,34], including the formation of its sequence organization [20]. Therefore, in this study, we focused on the communicative interactions between infants and mother chimpanzees over multiple contexts.

(a) Adjacency pairs

One simple but important structure of sequence organization in human interactions is the adjacency pair [4,25]. In its minimal form, an adjacency pair is defined as consisting of two consecutively produced turns by different participants that are relatively ordered such that the first part of the pair (the antecedent) initiates some exchange and sets up an expectation for which the second part (the consequent) is normatively responsive and conditionally relevant [4,28]. Examples of typical adjacency pairs in human interaction are greetings (e.g. 'Hello' → 'Hello'), or question–answer pairs [2]. These adjacency pairs underlie almost any conversation, and its structure seems to be a universal feature for language [4,5], but adjacency pairs also underlie joint actions [10,12]. Because adjacency pairs are directional, they can showcase an asymmetry in a conversation. This asymmetry can be caused by a difference in the status (e.g. teacher–student [35]), goals [12,36] or linguistic competence (e.g. infants [37]) of both interactants, or the setting in which the interaction takes place (e.g. a doctor's office [38]). For example, Terwilliger & Rossano [37] showed that in infant–caregiver interactions, infants produce relatively more responding second-pair parts compared to initiating first-pair parts, while it is the opposite for the caregiver.

For an utterance to be clearly definable as a second part of a pair, it needs to be shown that the consequent was responsive and contingent on the antecedent [39]. This aspect can be difficult to verify in interactions of non-linguistic species [40]. To bypass this problem, existing comparative studies have predominantly focused on specific signal-response pairs, which are characterized by distinct patterns of exchanges [3,27,40]. For instance, Rossano [27] investigated the requesting travel signals two bonobo infants deployed as first pair parts on which the mothers showed the contingent response of engagement in joint travel. However, by solely focusing on these signal-response pairs, studies limit themselves to a small part of all interactions. While these studies show that at least some interactions in primates contain adjacency pairs, they do not quantify the role of adjacency pairs in all social interactions.

One approach to establishing the distribution of potential adjacency pairs across all social interactions focuses on the predictable, non-random consecutive nature of adjacency pairs [41]. In human interaction, adjacency pairs often appear adjacent, even though they can be expanded on and recursively separated [2,4,5,26]. Potential adjacency pairs could then be identified by investigating if two signals or actions produced over two turns are non-randomly combined. This data-driven approach can be applied over a whole array of social interactions without limiting itself (i.e. focusing solely on specific signal-response pairs). While this method does not investigate the responsive and conditional relevant nature of the consequent on the antecedent or the cognitive mechanisms that drive the statistical adjacent relationships, it does provide useful candidates for future studies. Similar statistical approaches have been used to study syntactical structure in bird song [42–44] or call combinations in chimpanzees in the wild [45–47], but these studies focused on within-individual sequences and did not show the existence of adjacency pairs as they occured, by definition, between two individuals. By applying the same approach to multiturn interactions in chimpanzees, a crucial gap of knowledge could be filled, namely, whether adjacency pairs form a basic structure in the interactions of one of our closest living relatives [4,25].

(b) Flexibility

While adjacency pairs structure interactions on a small two-turn scale, humans still show a lot of flexibility in their interactions [25]. In this case, flexibility relates to the amount of variation and unpredictability seen in human interaction. Examples of this in human interactions are the interchangeability of words with close similarity in meaning (i.e. the synonymy of *hide* versus *conceal*, or *meadow* versus *pasture*, *paddock* and *field*), leading to more flexibility in expression [48,49]. However, this flexibility is not random and, on an interactional level, signals and actions organize themselves into clusters analogous to conversation topics where, within clusters, the exact order of signals and actions can be variable, but there is a limited set of 'appropriate' signals and actions that make up a cluster.

To investigate and visualize the organization of sequentially produced signals and actions, network analysis can be used [33,50–52]. Network analysis has been utilized to quantify other facets of non-human animal communication, such as syntax, across multiple species (e.g. nightingales, *Luscinia megarhynchos* [43]; chimpanzees [52]; humpback whales, *Megaptera novaeangliae* [53]; for reviews see [51,52]). One recent study by Mielke & Carvalho [33] used transition networks to investigate the flexibility of playing interactions in chimpanzees, providing evidence that these play sequences were organized in clusters or 'games' with high levels of flexibility within these game clusters. In this study, we use the same approach to investigate if multiturn interactions contain signals and actions that are globally structured in clusters.

(c) The present study

We introduced two components of sequence organization that form a basic feature of human interaction: Adjacency pairs and flexibility. While adjacency pair-like sequences in animal interactions have been studied quantatively (e.g. [27,54]) their role has not been quantified. Additionally, flexibility in sequence organization, defined as the organization of clusters of interchangeably used signals and actions, has so far not been investigated in multiturn interactions. The present study attempted to address this gap by analysing mother–infant interactions over multiple contexts of eastern chimpanzees (*Pan troglodytes schweinfurthii*) living in their natural environments. Specifically, we investigated the frequency and direction of potential adjacency pairs and the organization of these sequentially produced signals and actions into transition clusters. If these interactions are sequentially structured on an immediate two-turn scale, we expected to discover high frequencies of non-randomly combined consecutive units. In addition, if chimpanzee interactions are flexibly organized, we expected a network of multiple well-distinguished clusters. Additionally, by focusing on interactions between mother and infant chimpanzees, we investigated the influence of social role on sequence organization.

2. Methods

(a) Study site and subjects

This study focused on social interactions of eastern chimpanzees living in two communities of the Ngogo chimpanzee population, Kibale National Park, Uganda. Data were collected over two observation periods spanning from February 2021 to February 2023 (February 2021–September 2021 and August 2022–February 2023). The size of both communities varied, but by the end of the observation period in 2023, the two communities comprised 85 (west) and 110 (central-east) individuals respectively (Ngogo Chimpanzee Project 2023, unpublished data). The chimpanzees have been habituated to human presence since 1995, allowing full-day focal follows and the collection of high-quality video recordings from a distance of up to seven m. Our observations centered on 17 mother–infant dyads, with infant ages ranging from 4 to 62 months. This falls within the mean duration of the inter-birth interval for this population [55]. One mother gave birth to a second infant during the study period, resulting in two dyads involving the same mother (see electronic supplementary material, table S1 for an overview).

(b) Data collection

Full-day focal observations (07.30–18.30) of mother–infant dyads were conducted using continuous recording methods whenever visibility permitted [56,57]. The frequency of observations for each dyad was systematically tracked. When multiple dyads were available for observation, preference was given to those that had been sampled the least frequently. During focal follows, all interactions between infants and their mothers were documented with a special focus on the contexts of food sharing, grooming, joint travel and nursing. Interactions were defined as any exchange between at least two individuals, in which one individual initiated an interaction by producing a signal (facial expression, gesture, oro-facial sound or vocalization) or action, or a sequence of signals or actions, which could be responded to by a recipient with one signal or action, or a sequence of signals or actions. Contexts were defined by the presence of certain context-specific behaviours, which are detailed in the electronic supplementary material (table S2). In our analysis, we focused on the above mentioned contexts because they have been shown to be successful candidates to study frequently occurring communicative exchanges between mothers and infants [58–61]. Recordings were made using a high-definition digital camera (Sony AX100E 4K) paired with an external unidirectional microphone (Sony Shotgun Mod ECM-CG60). During 1295 observation hours, a total of 258 h of video footage was collected (mean ± s.d.: 15.2 ± 7.5 h per mother–infant dyad), comprising 2283 interactions.

(c) Video coding and analysis

For each mother–infant dyad, only those interactions were coded which fulfilled the following two criteria: (i) both interactants were visible throughout the interaction; and (ii) the interaction was complete, including both the beginning (initial use of an action or signal) and the end (neither interactant produced an action or signal for 30 s). This led to a total of 361 coded videos, totalling approximately 19 h of footage. Interactions were balanced for each combination of mother–infant dyad and context, to the extent permitted by the available data (i.e. grooming and nursing context 4–7 interactions per dyad; joint-travel context 7–8 interactions per dyad). However, due to a limited availability, all complete interactions with good visibility in the food-sharing context were coded (4–18 interactions per dyad for eight dyads). ELAN software (v. 6.2 [62]) was used for coding. As sequence organization in humans is not limited to language but appears in interactions devoid of language, we included all directed behaviours between two interactants in our analysis: Actions, which immediately achieve their apparent goal [63,64], and signals, which require a response from the recipient to achieve their goal [65]. Definitions of signals and actions were based on established ethograms of chimpanzee behaviour [65–71] supplemented with new behaviours where the literature was insufficient. A detailed ethogram can be found in the electronic supplementary material, table S3. The coding scheme was designed to explore all potential communication between mother and infant directed at each other. Any produced action or signal within the interaction was defined as one ‘unit’. Turns were defined as all consecutive units produced by the same individual, with turn transitions containing two consecutively produced units by two different individuals (for more information regarding the coding scheme and definitions, see [61]). Eighteen per cent of the videos were coded for accuracy by two observers and tested using Cohen’s kappa coefficient in EasyDIAg software package [72,73]. With a kappa coefficient of 0.66, the agreement was considered ‘good’ [74]. Due to the limited sample size, no control for dyad or age of the infant was made. This could influence the strength of bigrams or clusters, as specific dyads or age classes might have standardized ways of interacting. This approach also limits the interpretation of our results in regard to development. However, considerably more data would be necessary to control for dyad or age-specific effects in clustering patterns.

(d) Adjacency pairs

One statistical method to study adjacency pairs, prominently used in linguistics, is collocation analysis [41]. Collocation analysis has its foundation in corpus linguistics (for reviews see [41,75]), where it is used to analyse co-occurrences of two (or more) units in a large corpus. An important aspect of collocation analysis is that it contrasts the observed co-occurrence of two units with the expected probability co-occurrence based on the separate distribution of both units in the dataset. This process excludes the possibility that the observed co-occurrence was caused by random chance [41,76]. To be able to run a collocation analysis, we divided the dataset, containing all produced units, into bigrams of consecutive units that were produced across turn transitions. If a turn consisted of multiple units, we only considered the last unit in the first turn and the first unit in the responding turn. Additionally, to increase the likelihood that the second unit of the bigram was responsive on the first unit, we included the requirement that the two consecutive units had to occur within a temporal threshold, which was set at three seconds, based on a previous abrupt change point analysis [77,78] on the same dataset (for the actual graphical analysis, see [61]). This selection led to a total of 686 bigrams. To investigate the symmetry of mother–infant interactions, we categorized bigrams of the same units based on the direction of who produced the separate units (infant → mother or mother → infant). To test if the found results were not an artefact of the way we categorized the bigrams, one additional multiple distinctive collocation analysis (MDCA) was performed in which bigrams containing the same units were lumped together independent of the direction (e.g. rise (infant) → approach (mother) and rise (mother) → approach (infant) were lumped together to rise → approach). This additional model gave similar results and can be found in the electronic supplementary material, table S4. From this dataset, we calculated the exclusivity for each distinctive bigram using an MDCA in R [79,80]. The exclusivity of a bigram is expressed in a pbin value and relates to how often two units are combined in a bigram compared to how often you would expect to see this bigram if all observed units were combined randomly. Specifically, for each bigram, the binomial probability mass function was used to calculate its probability of occurrence, after which this probability was log-transformed into a pbin value for spacing. The final pbin values provide not only the degree of exclusivity of bigram, but also its direction, where more attracted bigrams receive larger positive numbers and more repulsed bigrams receive larger negative numbers. These pbin values correspond to p-estimation significance levels (i.e. $\text{abs(pbin)} > 1.3 = p < 0.05$; $\text{abs(pbin)} > 2 = p < 0.01$; $\text{abs(pbin)} > 3 = p < 0.001$) [76]. For a more detailed explanation of MDCA, see the electronic supplementary material. Additionally, we highlighted the strongest attracted or repulsed pairs within this dataset, defined as a bigram with a pbin value 2 s.d. away from the median.

(e) Flexibility

To investigate the flexibility in mother–infant interactions, we followed earlier work of Mielke & Carvalho [33]. For this analysis, the dataset containing all produced units over 361 interactions was used, where each interaction was analysed as a sequence of consecutively produced units. For the analysis, we considered all consecutive units produced by the same individual (within-turn) and by different individuals (across turns). For network analysis, the occurrence of rare units can inhibit establishing robust transition probabilities [33,81]. Therefore, an occurrence threshold was set at ten occurrences per unit. Units that failed to meet this threshold were initially combined with *a priori* established other units based on the similarity of the movement (e.g. raise arm and raise leg; electronic supplementary material, table S3). Units that still failed to reach the occurrence threshold after combining were considered 'NA' in the dataset. To check if this arbitrary threshold influenced the results, we performed the same analyses without the threshold, giving similar results.

To quantify and visualize the clustering of sequentially occurring units, we used a conditional transition network analysis, in which we calculated the conditional transitions for each pair of units. For example, the conditional transition A → B was the frequency of unit A as antecedent and B as consequent divided by the frequency of unit A as antecedent with any type of consequent (including unit B). In the network analysis, we only considered significant conditional transitions (significance level $\alpha = 0.05$) determined by comparing the observed conditional transition with conditional transitions from a thousand permutated datasets. For detailed information regarding calculating conditional transitions and their significance, see the electronic supplementary materials. Subsequently, a network was created in which all units appear as nodes, with edges representing transitions. To improve readability and biological relevance, only transitions that appeared at least five times in the dataset appear in the network [33]. To test whether there were distinct clusters of units in the network, we used the 'cluster_optimal' community detection algorithm in igraph, which maximizes modularity of clusters [82]. A modularity above 0.3 can be considered well-distinguished, meaning that units are more connected within clusters compared to between clusters. Finally, we labelled the clusters of the network based on the units they contain and our experience. The original dataset, as well as the used R code, can be found at OSF [83].

3. Results

The 361 coded interactions contained a total of 3647 units (1704 actions and 1943 signals). In total, there were 86 unique units (16 actions and 70 signals). A distribution of all units can be found in the electronic supplementary material (table S6). Interactions consisted of up to 67 units (mean ± s.d. = 10.13 ± 9.81) and up to 27 unique units (mean ± s.d. = 6.07 ± 3.45), distributed over up to 23 turns (mean ± s.d. = 4.21 ± 3.46). For more information about the distribution of signals and actions, see van Boekholt & Pika [61].

(a) Adjacency pairs

The collocation model revealed 686 bigrams consisting of 69 unique units, leading to a total of 336 unique bigrams. Out of these 336 bigrams, 140 were attracted (41.67%) and one was repulsed (0.30%) above chance level (absolute pbin value > 1.3, p-value < 0.05; 76). Almost all unique units (67/69 = 97.1%) were part of at least one attracted bigram (range: 0–19, average: 4.1 ± 3.8). Out of the 140 attracted bigrams, 64 (54.29%) occurred from mother to infant and 76 (45.71%) occurred from infant to mother. The one repulsed bigram occurred from mother to infant. Selecting bigrams with pbin values that were 2 s.d. away from the median of all bigrams in the dataset, the model revealed 11 (3.27%) strongly attracted bigrams and 1 (0.30%) strongly repulsed bigram (table 1). Out of these 12 bigrams, 8 (66.67%) occurred from mother to infant and 4 (33.33%) from infant to mother. From the 336 unique bigrams, 25 (7.44%) occurred in both directions (e.g. rise (infant) → approach (mother) & rise (mother) → approach (infant)).

(b) Flexibility

Over 361 interactions, mother and infant chimpanzees produced 86 unique units. However, after controlling for rare units, 48 unique units were used in the network analysis. These units formed a total of 3088 transitions. In total, 2006 transitions (65.0%) were part of the same turn, and 1082 transitions (35.0%) were produced across turns. The final network revealed which units follow each other above chance level. Out of 48 units, only 35 (72.91%) were involved in at least one transition that reached the significance threshold ($p \leq 0.05$). Units without any significant transitions can be found in the electronic supplementary material, table S7. The resulting network can be seen in figure 1, where different colours indicate the cluster membership, with each edge representing a significant transition. Edges that point to the node they originated from (loops) represent significant repetitions of the same unit, which could be either within or across turns.

The clustering algorithm revealed eight highly distinguished clusters (modularity = 0.91). Two clusters were related to food sharing contexts (blue and turquoise) and were split based on if the food was in the possessor's mouth (beg with mouth, extend hand, food share from mouth, giving, mouth stroke) or hand (food share from hand, touch food hold). Another cluster related to the grooming context (yellow) contained many of the tactile gestures (grab, grab hold, pull, touch, touch hold), but also some visual gestures (present, raise arm) and one oro-facial sound (lip-smacking). Closely attached to this grooming cluster was a cluster that was related to signals involved with the body manipulation in between grooming bouts (mint green: push, raspberry blow). A fifth cluster contained units displayed in the nursing context (red: grab nipple, full embrace, nursing, open arm) and units involved in ventral joint travel (climb ventral, joint travel ventral). This nursing cluster was closely connected to the grooming cluster and a sixth cluster that contained units related to joint travel (grass green: approach, climb dorsal, joint travel dorsal, leave, put ventral, rise). The seventh cluster consisted of signals that can function as 'attention grabbers' (pink: exaggerated loud scratch, leaf grooming, pout face, whimper) and was connected to the grooming, to the joint travel and to one of the food sharing clusters. The eighth cluster contained just one unit, which showed significant repetitional use and had less biological relevance as it was only produced by one individual (purple: hand-on-eye [84]). The units exaggerated loud scratch, present and rise were connected to the most clusters, with three to four connecting clusters.

Table 1. Overview of the attracted and repulsed bigrams for which the pbin value was 2 s.d. away from the median (median = 1.115, s.d. = 1.748).

first unit	*second unit*	*exclusivity (pbin value)*
nursing (infant)	grooming (mother)	18.440
rise (mother)	climb ventral (infant)	12.258
rise (mother)	climb dorsal (infant)	11.787
rise (mother)	joint-travel ventral (infant)	10.389
rise (mother)	joint-travel dorsal (infant)	7.493
climb dorsal (infant)	rise (mother)	7.195
full embrace (mother)	nursing (infant)	6.997
grooming (mother)	nursing (infant)	6.844
open arm (mother)	nursing (infant)	6.441
mouth stroke (infant)	giving (mother)	5.989
climb ventral (infant)	rise (mother)	4.744
rise (mother)	nursing (infant)	−3.112

4. Discussion

The aim of this study was to quantify aspects of sequence organization in social interactions between mother and infant chimpanzees living in a single population in the wild by focusing on the frequency of potential adjacency pairs and the organization of sequentially produced units into clusters. Using MDCA, we showed that a large portion of all turn transitions consisted of attracted bigrams, which almost exclusively occurred in one direction, highlighting that mother and infant chimpanzees initiate different bigrams. Regarding flexibility, the conditional transition network analysis revealed seven highly distinguished clusters of closely connected units that were present in most dyads and an eighth cluster consisting of an idiosyncratic gesture produced in repetition. Additionally, the transition network showed that only about three-quarters of the units in the expressed repertoire were part of significant transitions. In the following, we will discuss our results in more detail.

(a) Adjacency pairs

Our results showed that on a two-turn scale, a large portion of the analysed mother–infant interactions are organized in potential adjacency pairs in the form of attracted bigrams. Moreover, almost every unique unit produced was part of at least one attracted bigram, showcasing that, just as in human interaction, this adjacency structure forms a strong presence in chimpanzee interactions. A closer inspection demonstrated that there are strongly attracted bigrams appearing in all analysed behavioural contexts (e.g. *joint-travel*: rise → climb ventral; *nursing*: full embrace → nursing; *food sharing*: mouth stroke → giving; *grooming*: nursing → grooming).

Interestingly, these strongly attracted bigrams only appear as either a signal–action (e.g. open arm → nursing) or action–action pair (e.g. nursing → grooming) and never as a signal–signal or action–signal pair. The absence of signal–signal pairs illustrates the inherent importance of actions in mother–infant interactions. Moreover, the results revealed that, while chimpanzees might deploy a sequence of signals within their turn [61,85,86], the start of the responsive turn is often an action [87]. This aspect differs from human conversations, which are characterized by consisting of many signal–signal adjacency pairs [23,25]. However, adjacency pairs in humans are not limited to conversations and extend into other types of interactions, such as joint actions [9–11]. In its essence, these results show that, independent of the different types of adjacency pairs, chimpanzee interactions are structured along predictable bigrams, similar to what has been shown in human interactions.

The majority of attracted bigrams (92.56%) occurred only in one direction (e.g. raise arm → grooming only occurred from infant to mother and not from mother to infant), which highlights that mother–infant interactions are asymmetrical. This asymmetry did not arise through unbalanced production of the two parts of an adjacency pair (e.g. infant-initiated bigram n = 76; mother-initiated bigram n = 64) but rather showed that mothers and infants use similar units in different ways. Similarly, this asymmetry is also exhibited in human interactions between mothers and young infants (<2 years old: [34,88,89]). The observed asymmetry can partially be explained due to certain units being inherently unique to either infant or mother (e.g. nursing, climb dorsal for the infant, and put ventral, put dorsal for the mother), but can also be caused by both interactants trying to achieve different goals by having different behavioural needs (e.g. mothers' goal to protect her infant versus infants' goal to request food from the mother [90,91]).

Using collocation analysis, we have shown that mother–infant interactions contained many potential adjacency pairs. However, it does not provide evidence for the same number of actual adjacency pairs, as it does not investigate the responsive and conditional relevant nature of the consequent on the initiating antecedent. Moreover, there is no certainty that the produced consequent was also intended as a response by the responding individual, even though we increased this likelihood by only analysing responses falling within a temporal threshold. While in humans, most adjacency pairs occur consecutively, they can be expanded on and recursively separated [2,4,5,26]. In conclusion, the attracted bigrams identified by collocation analysis give

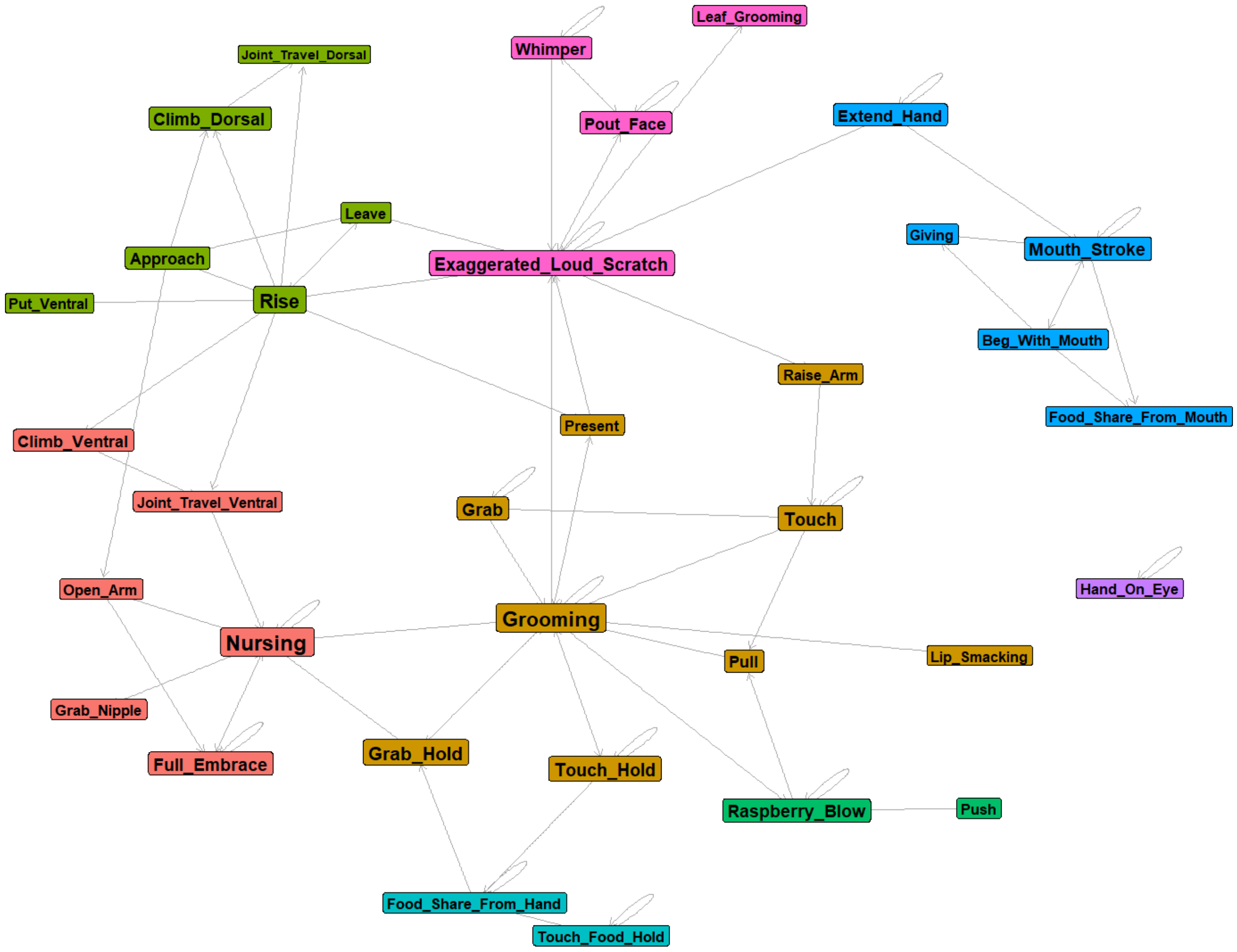

Figure 1. Network plot of weighted conditional transition probabilities between units used in mother–infant interactions. Units are nodes, significant transitions that occur at least five times are edges (directed), and colour indicates cluster membership. Edges that point to the node they originated from signify repetitions of the same unit. Units that are not part of any significant transitions are not displayed.

future studies a valid data-based starting point for further investigation of the role that adjacency pairs play in chimpanzee interactions.

(b) Flexibility

Our results showed that, similar to humans, mother–infant interactions of chimpanzees in the study community were organized into multiple well-distinguished clusters of interchangeable units. The conditional transition network analysis showed that a considerable part of the observed units did not have any significant transition (13/48 = 27.08%), highlighting that mothers and infants did not use their entire expressed repertoire of units in predictable repeated sequences. This could be because the predictable sequences in which these units are involved take place in behavioural contexts that were not studied here (e.g. play face in the playing context [92]). However, an alternate explanation could be that the infant still needs to learn how to communicate efficiently [93,94]. This would be similar to humans, where the size and flexibility of these clusters increase over ontogeny as infants develop more complex linguistic abilities [95,96]. While there is a lively debate concerning whether the production of some communicative signals is genetically fixed or involves some kind of learning (e.g. [97,98]), the usage of these signals in the right contexts and the forming of correct signal sequences requires learning [85,97,99]. However, this hypothesis could only be tested by comparing a transition network of adult chimpanzee interactions, which, as far as we are aware, does not yet exist.

Limiting the analysis to units that had significant transitions, the clustering algorithm found eight clusters. Most clusters could be related to one of the analysed behavioural contexts, raising the question of whether the production of certain signals and actions in chimpanzees is just driven by context instead of organized sequentially by preceding signals and actions. Based on the methods used, we cannot completely rule out this explanation. However, the analysis does provide some circumstantial evidence that there is another force driving unit production besides context. First, the network provided more clusters than analysed behavioural contexts with a high level of modularity. For example, both clusters related to food sharing were not connected with each other. Additionally, a large portion of all significant transitions occurs only in one direction (e.g. open arm to nursing), implying some order of units. If the production of units was solely dependent on the behavioural context, one would not expect an ordering effect. Moreover, the network contained one cluster we labelled ‘attention-grabbers’ that was not related to any of the behavioural contexts. The units in this cluster were well-connected, both within their own cluster and with other clusters, supporting the hypothesis that these attention-grabbing signals have the most flexible use in the form of elaboration or persistence, indicated by the occurrence of loops [100,101].

The well-distinguished clustering solution showed that mother–infant interactions in chimpanzees can be characterized by interaction topics, where a certain set of units is produced within a behavioural context. Other studies have shown the existence of highly context-specific units (e.g. [87,102,103]) and units that appear over multiple contexts in chimpanzee interactions (e.g. [87,100,104]). However, our results quantify that most units had a primary context in which they appeared most often, with a degree of flexibility or means-end dissociation [68,87].

(c) Limitations

The aim of this study was to explore two aspects of sequence organization in mother–infant interactions over multiple contexts in chimpanzees: Adjacency pairs and flexibility. Using data collected from individuals living in their natural environment comes with its own set of limitations. All data originated from two communities of one subspecies of chimpanzee. However, communication diversity and usage can differ across populations [68,105,106], and, therefore, generalizations should be made with caution [107]. Additionally, field conditions generally have lower visibility compared to captive environments, reducing the certainty that all signals and actions are visible in the recordings. However, by making a pre-selection, we ensured complete interactions with clear visibility, allowing coding the occurrence of individually produced signals and actions. Due to the used methodology requiring a large enough sample size to warrant robust results, no control for age or dyad was made. Therefore, we cannot make any conclusions about development and individual differences in sequence organization, which likely play a role as chimpanzees undergo multiple behavioural changes in the first few years of life [108,109]. While we analysed contexts known to be crucial candidates for communicative exchanges, we did not include all possible contexts (e.g. play or agonism). Future research could explore whether an expansion of the dataset to include more contexts, such as agonism or playing, will lead to an increase in the number of network clusters. Furthermore, the applied methodology focuses on the statistical relationships between consecutively occurring units and remains agnostic about the underlying cognitive mechanisms or drivers that could cause these statistical relationships. Additionally, there might be statistical relationships between non-adjacent units. Other studies have shown that some animal species are able to produce and comprehend non-adjacent relationships [110–113] for which other methodologies such as mutual information or second-order Markov chains could be used [18,113].

In conclusion, while limitations should be kept in mind, the presented methodology can be applied to quantify different aspects of sequence organization in interactions, allowing for cross-species comparisons. Additionally, these methods provide a data-driven starting point for future studies to qualitatively further investigate sequence organization in animal interactions.

5. Conclusion

In this study, collocation analysis and network analysis were applied to investigate the sequence organization of mother–infant interactions in chimpanzees. With this consilience of methods, we were able to quantify the sequence organization of mother–infant interactions on two different scales: predictable bigrams as potential adjacency pairs on a two-turn scale as well as clusters of flexibly used units on an interactional scale. Most of the strongly attracted bigrams in the collocation analysis also appeared in the network, highlighting how these methods complement each other.

The methods we present here are data-driven, have minimal assumptions and can be used to study interactions comparatively, as they eliminate the human-centric view often applied when studying non-human animal communication systems [114,115] (for a discussion of this see [116,117]). Additionally, because these methods do not rely on a *priori* selecting units based on intentionality criteria, cross-species comparisons, including humans, can be more easily conducted. Moreover, these results indicate that some form of sequence organization appears in the interactions of one of our closest relatives, the chimpanzees. These results strengthen the interaction engine hypothesis, which states that some interactional features evolved prior to modern language capacities [5,13]. Moreover, these results highlight the important role that behavioural context can play on interactions, in addition to meaning disambiguation [118], intentionality development [119] and turn-taking structure [61]. Future studies applying these methods on adult chimpanzee interactions could compare their results to our results exploring the role of ontogeny on sequence organization, while other comparative studies across the animal kingdom could compare the presented metrics to track the evolutionary origins of sequence organization.

The comparative field of animal communication has developed many methods to study and quantify patterns in individually produced sequences [33,43,45,50]. However, communication does not consist of individual sequences produced in a vacuum [26]. By studying whole multi-turn interactions across the animal kingdom, new light can be shed on the understudied aspect of sequence organization in animal communication, helping to uncover how language might have evolved.

Ethics. The present study was purely observational and non-invasive. All applicable national and/or institutional guidelines for the care and use of animals were followed. In accordance with the German Animal Welfare Act of 25 May 1998, Section V, Article 7, the study was classified as nonanimal experiment and did not require any approval from a relevant body. Our research adhered to the legal requirements of the state of Uganda and was approved by the Ugandan Wildlife Authority and the Ugandan National Council for Science and Technology. It followed the recommendations of the Animals (Scientific Procedures) Act 1986, as published by the government of the United Kingdom, and the principles of Ethical Treatment of Non-Human Primates, as stated by the American Society of Primatologists.

Data accessibility. The data associated with this research are available at OSF [83].

Supplementary material is available online [120].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. B.v.B.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; A.B.B.: conceptualization, formal analysis, writing—review and editing; S.P.: conceptualization, funding acquisition, supervision, writing— shaping of manuscript, review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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