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Manipulative repertoire of bonobos (*Pan paniscus*) in spontaneous feeding situation: the influence of food properties and context highlighted by new methodological approaches

Short title: Repertoire of food manipulation in zoo bonobos

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Abstract

In contrast to chimpanzees, the study of bonobos' manipulative abilities has been carried out in experimental contexts ~~essentially~~ related to tool use. The objective of the present study is to describe the richness of the manipulative repertoire of ~~zoo~~ bonobos, in a spontaneous feeding context including various physical substrates to gain a larger insight into our evolutionary past. In order to characterize the manipulative strategies spontaneously employed by bonobos, we performed a sequential analysis of manual postures during a complete feeding sequence. We analyzed the performance with an effectiveness score defined as the food intake (i.e, in number of mouthfuls) related to the manipulative effort (i.e, diversity and changes of manual postures) during the sequence. Our study describe a great variety of grasping postures and different strategies, used differently depending on the environmental context and the morphometric properties of food. Our results also show that the manipulative effort is higher for large foods and on substrates with less ~~stability. But~~ the effectiveness is not significantly lower for these items since the effort seems to be compensated by a greater number of mouthfuls. It appears that the strategy employed ~~involve~~ a trade-off between the complexity of the manipulation and the food intake obtained and would be linked to the cost-benefit balance. This study is the first to provide a broad description of the bonobo manipulative repertoire and allowed us to test and validate innovative analysis methods that are applicable to a large number of ethological studies.

Keywords: *Pan paniscus*, food manipulation, grasping posture, food properties, sequential analysis

Introduction

Grasping ability (i.e, "movements in which an object is seized and held securely partly or wholly within the hand" (Napier, 1956, p.902) or the foot) and more broadly manual dexterity (i.e, "the ability to make coordinated hand and finger movements to grasp and manipulate objects" (Makofske, 2011, p.1522)) in hominids has been an important subject of interest in evolutionary studies. ~~H~~human hand is traditionally considered as having a ~~unique~~ high degree of dexterity compared to other primates (Key et al., 2018; Marzke, 2013; Marzke et al., 1992), such as forceful precision grips between the pad of the thumb and the pads of the fingers and complex intra-manual precision manipulative movements (Kivell, 2015; Marzke, 1997, 2013; Marzke et al., 2015; Napier, 1960; Pouydebat et al., 2011). Morphological evidence ~~on~~ fossils shows that, in early hominids, the hand seems to have evolved a combination of ape-like features and human-like features (Feix et al., 2015; Kivell et al., 2011). Comparative behavioral studies of hand use in our closest living relatives, in zoo and free-ranging conditions, can then improve our understanding of the functional morphology of the earliest hominids (Bardo et al., 2017; Feix et al., 2015; Pouydebat et al., 2008, 2011; Susman, 1998). The first description of manual grips in primates were made in human and chimpanzees (*Pan troglodytes*), by Napier (1956, 1960), who distinguished two categories, power and precision grips. Since the pioneering work conducted by Napier, more diverse types of grasping postures and in-hand movements have been described in apes and humans (but see also in monkeys: e.g., capuchins (G. Byrne & Suomi, 1996; Truppa et al., 2019) and macaques (Macfarlane & Graziano, 2009; Pal et al., 2018)), including a wider range of manipulative behaviors compared to other mammals, both in zoo and in natural conditions (e.g., Bardo et al., 2017; Byrne et al., 2001; Christel, 1993; Christel et al., 1998; Crast et al. , 2009; Jones-Engel & Bard, 1996; Marzke & Wullstein, 1996; Neufuss et al., 2018; Pouydebat et al., 2011).

Tool use in particular is thought to have been a crucial adaptation during human evolution and the potential of tool use behavior in hominids has been central in functional studies of grasping (e.g., Bardo et al., 2017; Bardo et al., 2018; Osuna-Mascaró et al., 2020). Among great apes, chimpanzees (e.g., Boesch & Boesch, 1983, 1990; Goodall, 1964; Inoue-Nakamura & Matsuzawa, 1997; McGrew, 2010; Sanz & Morgan, 2013), gorillas (*Gorilla gorilla sp*.) (Breuer et al., 2005; Grueter et al., 2013; Kinani & Zimmerman, 2015; Wittiger & Sunderland-Groves, 2007) and orangutans (*Pongo sp*.) (Fox et al., 1999; Meulman & van Schaik, 2013; van Schaik et al., 1996) use tools in natural conditions, for social, feeding or hygienic (cleaning and protection) purposes. In free-ranging bonobos (*Pan paniscus*), it has only been observed in social (communication and play) and hygienic contexts (Furuichi et al., 2015; Hohmann & Fruth, 2003; Ingmanson, 1996; Kano, 1982; Nishida et al., 1999) but studies in zoos (Bardo et al., 2015, 2016; Boose et al., 2013; Takeshita & Walraven, 1996; Toth et al., 1993; Visalberghi et al., 1995) or semi free-ranging conditions (i.e, sanctuary) (Gruber et al., 2010; Neufuss et al., 2017) have shown their functional, behavioral and cognitive abilities to modify and use different kinds of tools to enhance food accessibility.

Studies about tool use have brought many clarifications on the ability of great apes to use precision grips close to those used by humans and have then questioned the idea that the human hand would be unique. But one limitation is that they often involve standardized objects of small size or of uniform shape, enabling cross-species or ~~studies~~ comparisons, therefore ~~giving a partial description of the whole species~~ manipulative repertoire. Furthermore, tool use is not the only interest of non-human primate manual abilities as the hand serves to explore and interact with the environment in its whole. Hand (and feet) skills in primates can be observed during more diverse grasping and manipulative behaviors, such as locomotion, feeding behavior and social interactions. Even if it is now known as insufficient

and unexclusive (as reviewed by Sussman, ~~Tab~~ Rasmussen, & Raven, 2013), one of the historical hypotheses on the origins of grasping abilities in primates focused on the selective pressures linked with food properties and the arboreal environment (Cartmill, 1974; Jones, 1916). Many studies showed the effect of food properties and arboreal substrate on grasping strategies, showing how much food difficult to extract (e.g., preys) and complex arboreal substrates (orientation, sizes) increase the use of the hand (MacKenzie & Iberall, 1994; Patel et al., 2015; Reghem et al., 2012; Toussaint et al., 2015). The link between the shape and/or the size of the object and the grasping postures used to manipulate it has already been considered in some studies in human and non-human primates, especially showing that precision grasping is preferentially chosen to manipulate small objects in all studied primates (e.g., Key et al., 2018; Pouydebat et al., 2009). Bonobos express arboreal and terrestrial feeding behaviors ~~but if~~ this environmental context has been well-studied in chimpanzees since 1960s (e.g., Jones-Engel & Bard, 1996; Marzke et al., 2015; Marzke & Wullstein, 1996; Pouydebat et al., 2011), few studies have investigated the foraging strategies, food processing skills and manipulation abilities in bonobos. Furthermore, they focused on precise experimental procedures with selected kind and size of food (Christel, 1993; Christel et al., 1998) which may have constrained the range of manipulative behavior observed. For a better understanding of the evolution of feeding strategies in primates, further research on manipulation in various feeding ~~context,~~ with and without tools, is needed as the ecological context could have a non-negligible influence on the manipulative strategies, particularly for this lesser known species.

The first aim of this study was to describe~~, document~~ and quantify the manipulative repertoire in spontaneous feeding situations, with and without tools, in zoo bonobos, with ~~all kind of food~~ they could encounter in different feeding context, both terrestrial and kind of

arboreal structures. Our hypothesis is that bonobos can use a much wider range of manipulative behaviors than the one described in a tool-use context because of a greater variety of shapes and sizes found in the consumed food than in experimental settings.

Secondly, we considered the manipulative sequence in its whole and the continuity of movement between the grasping postures by using a sequence analysis method, derived from molecular biology. By looking for the first time at the similarities/dissimilarities between the sequences, we expected to distinguish several manipulative patterns, characterized by a different prevalence of the grip categories between the patterns. We also expected the use of these patterns to vary according to the morphometric properties of the manipulated food as well as the physical substrate on which the individual manipulated an object (i.e, ~~terrestrial-like context like floor, and arboreal context such as the above ground artificial structure and ceiling grid).~~

The third aim of this study was to evaluate the performance of manipulation according to the item and the substrate. We built an “effectiveness score”, defined as the food intake related to the manipulative effort. Through this innovative methodological approach, we calculated this score from two manipulative parameters usually studied in the literature (Bardo et al., 2016, 2017): the number of distinct grasping postures used during a sequence and the number of posture changes during that sequence. We expected to observe an influence of both the morphometric parameters of manipulated objects (i.e, morphometric measures and hardness) and the substrate on the manipulative effort and effectiveness, as well as on the choice of manipulative strategies.

Methods

This research adhered to the legal requirements of France and all the experiments were carried out following the principles of laboratory animal care in accordance with the CNRS guidelines. It complies with the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates and followed the American Society of Primatologists Code of Best Practices for Field Primatology.

1. Subjects and housing

The study was conducted from January 27, 2020 to January 31, 2020 at the zoological park "la Vallée des singes" (France). This park houses a group of seventeen bonobos (i.e, Continuous Full Contact (group)) composed of nine adults (six females from 16- to 52-year old and three males from 15- to 23-year old), two subadults (one female and one male, both 10-year old) and six juveniles (four females from 3- to 7-year old and two males of 5- and 7-year old).

The bonobos were observed during the day in an indoor building where only two large cages, connected to each other (98m^2 each), were visible. They also have accessed to five smaller cages (from 16 to 24 m^2) and to a naturally vegetated outdoor island (0.7 ha) that was accessible to the group according to the weather. Many climbing structures, made of platforms, ladders and ropes, were settled in the cages.

At least two water taps were available *ad libitum* and the group was fed four times a day. Their food ration included mainly vegetables and one fruit (i.e, apple). It was completed by pellets, seeds, eggs, chicken necks and a homemade mix containing cereals, vitamins and vegetal oils. The food was distributed on the top of the cages (i.e, grid ceiling) or inside the cages, on the floor and the platforms. Daily enrichment was provided with tree branches (i.e, hazel or willow tree) and cooked rice placed inside tubes or wooden logs.

2. Data collection

2.1. Food morphometric properties

In order to evaluate the influence of food morphometric characteristics on the manipulative behavior, morphometric measurements ~~have been~~ taken on every kind of food manipulated by the bonobos of the group (Appendix 1). Vegetables were measured as distributed, in their whole or cut by the zookeepers before being distributed, so every category of shape and size has been measured and weighted separately. The aim of these measurements was to classify food items depending on their morphometric parameters. Every food item (mean ± SD = 4 ± 2 per category) was characterized by six quantitative values, except cooked rice contained in enrichments that is a particular case (not measurable in the same way) and treated separately in the analysis: length (cm), width (cm), height (cm), volume (cm^3), mass (gr) and hardness (N). We collected hardness data using a portable analog durometer (Force Dial™ FDN 50, Wagner Instruments). The durometer plunger was applied at several positions of each sample (mean ± SD = 2.0 ± 1.5 per sample) allowing us to calculate the average value (McGraw et al., 2014).

2.2. Video recording

One or several individuals were followed throughout a feeding session, balancing the distribution of records for each individual between observation days and periods of the day. The selection of focal subjects was made according to a daily list (based on the cumulative previous observation days) and visibility of individuals to the observer. One handheld camera (PANASONIC® HC-V380) was used to record the simultaneous movements of the ~~hand~~, feet and mouth. At the end of the feeding sessions and between the meals, the foraging behavior of additional individuals was recorded. The bonobos could also feed on enrichments, provided

between the meals, and were recorded using the all-occurrence sampling method (Altmann, 1974). The recordings were performed at 50 frames/sec.

2.3. Video scoring

2.3.1. Manipulative sequences

Video recordings were analyzed frame by frame with VLC Media Player (VideoLan, 2020), using the individual focal sampling method (Altmann, 1974). Videos were divided according to our definition of a "manipulative sequence", including contact, grasping and manipulation of the food items. It began with the first contact between an individual and an item (direct or through the use of a tool) and ended when the food was consumed in its whole (whole fruit/vegetable, bunch, branch previously sectioned (small fruit, bark, buds, etc.)) or abandoned before total consumption (partially or not consumed). A total of 3h30 of recorded sequences were analyzed. The parameters recorded during the sequence were the individual, the food consumed (categorized by species and by size, characterizing a "food item"), the substrate (ground, platform or grid), the manual/foot grip adopted, the hand(s)/foot used and the duration of each behavior. We recorded data with the frequencies technique (e.g., Hopkins, 1995).

2.3.2. Grasping postures

Every encountered grasping posture involving the hands or the feet was described and linked to the existing literature on human and apes (Bardo et al., 2016, 2017; Jones-Engel & Bard, 1996; Marzke et al., 2015; Marzke & Wullstein, 1996; Napier, 1956; Parry, 1966; Pouydebat et al., 2011). To name the grasping postures, we used the Marzke's typology of

~~grasp~~ and we divided them into five grip categories: Precision grips, Thumb lateral, Without thumb, Palm, and Other grips (see Tableau 2 for details).

2.3.3. Grip associations and compound grips

The grip associations included the cases of bimanual manipulation where the grasping posture of each hand was recorded and compiled. In the case of asymmetric coordinated bimanual hand movements, individuals had to hold or maintain the food or the enrichment with one hand and extract or pick up the food with the other hand. The hand used to extract the food was considered as dominant in some further analysis, based on previous studies about coordinated bimanual actions (Bardo et al., 2015; Hopkins, 1995; Meguerditchian et al., 2013).

We also included the compound grips (e.g., Jones & Fragaszy, 2020; Neufuss et al., 2018) with which several pieces of the same item were held. It could be used when the item broke during the manipulation and when two grips were used in the same time with only one hand.

3. Data analyses

3.1. Manipulative repertoire

In order to describe the manipulative repertoire of this captive group of bonobos, the maximum of grasping postures was observed. To assess the extent to which our observations maximized the number of possible postures, we plotted two accumulation curves of the number of grip associations as a function of the number of sequences or food items (Appendix 2a and b). Both curves plateaued, which meant that there was little benefit in carrying out

additional sampling to extend our evaluation of the manipulative repertoire (Colwell et al., 2004).

3.2. Food items classification

We observed 44 food items from 19 different plants or edible species (Appendix 1) during the video scoring. To classify them according to their morphometric characteristics (i.e, classification of 43 items, except for cooked rice) and simplify the analyses by decreasing the variability of food items properties, a Principal Component Analysis (PCA) and a Hierarchical Cluster Analysis (HCA) with Ward's method (*agnes* function of *Cluster* package; Maechler, 2013) were performed on the six morphometric variables (i.e, hardness, height, mass, volume, length and width). A pairwise comparison (see below for statistical details) was then carried out to investigate which variables were characterizing each cluster. The HCA analysis revealed two clusters describing item morphometric characteristics (Appendix 3). The six morphometric variables used for cluster discrimination differed significantly between the two clusters (Appendix 4). The first cluster (Cluster 1) corresponds to small, light and soft items and the second cluster (Cluster 2) corresponds to large, heavy and hard items. For further analyses, we assigned cooked rice to a third cluster (Cluster 0) as this item was uncountable and not measurable.

3.3. Sequences analysis and manipulative patterns

3.3.1. Optimal matching analysis

We also analyzed the sequences of manipulative behaviors by considering grip associations through their succession within a sequence. First of all, we calculated the pairwise dissimilarities between the sequences thanks to the optimal matching analysis (i.e, calculation

of the minimal number of modifications - substitutions, deletions, insertions - that one of the sequences must undergo to obtain another one) with the *seq.dist* function of the *TraMineR* package (Gabadinho et al., 2011). Derived from molecular biology, this method is usually used in social sciences to analyze time-ordered sequences of socio-economic states that individuals have experienced. It is particularly adapted to analyze categorical sequence data and retemporalize action by analyzing it as a process. To our knowledge, this method has only been used in our field by Borel et al., 2017, in which they described and quantified the sequential dynamic strategies of tool grip and manipulation of five human subjects during a tool-task. Here, we considered all the modifications of the sequences (i.e, substitutions, deletions and insertions) equally important. From the distances calculated between each pair of sequences, we performed a Hierarchical Cluster Analysis (HCA) with Ward's method, with the *agnes* function of the *Cluster* package (Maechler, 2013), in order to distinguish several manipulative patterns. We created an additional cluster containing the sequences without any manipulation (named "Manipulative pattern 0") (i.e, the item was grasped with the mouth and consumed directly), corresponding to a specific foraging strategy.

3.3.2. Grip ~~categories~~ proportions and manipulative patterns

The proportion of our five grip categories in a sequence was calculated as the number of grasping postures of the considered category divided by the number of distinct grasping postures used in the sequence. In bimanual manipulation, we only considered the action of the dominant hand (i.e, the hand extracting food) in this analyze. We performed multiple and pairwise comparisons to figure out if the manipulative patterns (obtained with the Optimal matching analysis) were characterized by some grip categories.

3.3.3. Manipulative patterns use according to the food item and the substrate

The aim was to determine the influence of the morphometric properties of the manipulated food items and the physical substrates on the manipulative patterns used by the individuals. After performing a multiple correspondence analysis (MCA) for visual evaluation of the link between the three variables (i.e, food item clusters, substrates and manipulative patterns), we considered all the possible modalities of the interaction between item clusters and substrates (see above). Because of the small or null samples in some modalities, we performed exact multinomial and binomial had hoc tests on the distribution between the manipulative patterns for every item-substrate modality, by comparing them to an homogeneous distribution (*multinom.test* and *binom.test* functions of *rstatix* package (Kassambara, 2020)). We then applied a Bonferroni correction on the p-values.

3.4. Handling score and manipulative effectiveness

In the literature, the manipulative performance during one task is evaluated using the number of manual posture changes (C), the number of distinct grasping postures used during a sequence (P) and the time needed to perform a task (Bardo et al., 2016, 2017; Neufuss et al., 2017). Unfortunately, the first variable (C) does not distinguish the sequences without manipulation (i.e, only using the mouth) from the ones involving only one grasping posture. The second variable (P) did not fit with our analysis as it did not include the repetitions of grasping postures in one manipulative sequence. We therefore created a handling score associating those two first parameters:

$$Handling\ score\ (HS) = P + C$$

The additive rather than multiplicative term is justified by the need to allow for the distinction of different sequences described above.

To evaluate the manipulative effectiveness (E), we created a second score, by comparing the handling score with the number of mouthfuls counted during the sequence. Effectiveness is here defined as the ratio of ingestion to the manipulative effort required for processing that food, but in no way has energetic implications:

$$Effectiveness\ (E) = \frac{N\ mouthful(s)}{P + C + 1}$$

For a mathematical purpose, we added the value of one to the handling score which was sometimes equal to zero.

We performed multiple and pairwise comparisons on the handling score on the one hand and effectiveness on the other hand, between the different item-substrate modalities (N=9).

3.5. Statistical analyses

All the multiple comparisons were performed using the Kruskal-Wallis test and for pairwise comparisons, we used the Wilcoxon rank sum test with Bonferroni continuity correction. All statistics were computed using the R 3.6.3 statistical environment (R Core Team 2020).

Results

1. Manipulative repertoire

1.1. Grasping postures

Manual or foot manipulations accounted for 83.5% of all sequences recorded (N=792; Table 1), and the remaining 16.5% are for the use of the mouth only. We found 22 distinct grasping postures including two new variants, never described for bonobos in the literature (Table 2). The thumb-middle grip (in the "precision grips" category) is a variant of the palmar thumb-index grip but involving the middle finger instead of the index. The dorsal scissor hold (in the "without thumb" category) is a variant of the palmar scissor hold, with the hand in supination and the fingers flexed. We detected a very restraint use of the feet (N=9/792) and with only two grasping postures (Table 3).

The most frequent grasping posture was the "lateral thumb-index grip" (N=325/792) and the second most frequent were the power grips (with thumb (N=158/792) and without thumb (N=49/792)). The use of branches as tools was observed in N=81/792 sequences.

1.2. Grip associations and compound grips

The whole repertoire included 28 distinct grip associations (bimanual manipulation or compound grips) and 21 single postures (Table 4). One of the grasping postures was never used ~~alone~~ (i.e, the "fifth finger probe" is always used in association with "power grips") and only 28 grip associations out of the 484 possible ones (N=22^2) were actually observed.

The number of distinct grip associations per sequence ranged from 1 to 8 (mean ± SEM=1.46 ± 0.04) and each individual used between 3 and 19 distinct associations ~~throughout this study~~ (mean± SEM=11.4 ± 1.16 or 23.3 ± 2.37% of the recorded grip associations). Branches were used as tools to reach food in about 10% of the sequences (Table 1). Sequences with tool use included 27 grip associations of which 8 (i.e, 16.5% of the recorded grip associations) are not found in sequences without tools.

2. Manipulative patterns

3.1. Sequences classification

From the overall non-interrupted sequences recorded (N=638, including N=48/49 grip associations), 120 distinct sequences varying from 1 to 17 successive grip associations were found. We extracted six patterns of sequences from the HCA analysis, of which only four were considered in our subsequent analyses (Appendix 5). The last two indeed contained only one or two sequences and were therefore too rare and particular to be considered as general patterns. The sequences in the four patterns we considered varied from 1 to 11 successive grip associations.

3.2. Grip categories proportions and manipulative patterns

Each pattern was distinguished by one or two dominant grip categories (Figure 1). Pattern 1 was associated with precision grips (PCG) (Kruskal-Wallis test: khi2=169.88, df=3, p<0.001; Pairwise Wilcoxon tests, p<0.001), pattern 2 with grips without the thumb (WT) (Kruskal-Wallis test: khi2=418.78, df=3, p<0.001; Pairwise Wilcoxon tests, p<0.001), pattern 3 with lateral thumb grips (TL) (Kruskal-Wallis test: khi2=401.52, df=3, p<0.001; Pairwise Wilcoxon tests, p<0.001), and finally pattern 4 was distinguished by two grip categories: palm grips (PMG) (Kruskal-Wallis test: khi2=254.25, df=3, p<0.001; Pairwise Wilcoxon tests, p<0.001) and grips not included in the previous categories (OG) (Kruskal-Wallis test: khi2= 125.74, df=3, p<0.001; Pairwise Wilcoxon tests, p<0.001).

4. Manipulative patterns and effectiveness for various food items and substrates

4.1. Manipulative pattern use according to the food item and the substrate

We compared the prevalence of every manipulative pattern within each modality of the interaction between the food item clusters (N=3) and the substrates (N=3) (Table 5, see also Appendix 6). Significant differences were found between the manipulative patterns used for all the items at the grid and on the platform (Exact multinomial tests, $p<0.05$ except for all the items on the ground)).

Pattern 0 (mouth manipulation) was significantly associated with small items on the platform (Binomial had hoc test, $p<0.001$) while pattern 1 (associated with PCG) was significantly associated with cooked rice (on the grid and the platform) (Binomial had hoc tests, $p<0.001$). Pattern 2 (associated with WT) was the least frequently used (N=64/766). It seemed to be prevalent for small items on all substrates (especially ground) but the difference is not significant. Pattern 3 (associated with TL) was predominant especially for small items (Binomial had hoc tests, $p<0.001$), except on the ground where it was well represented but the difference was not significant, and for large items on the grid (Binomial had hoc test, $p<0.001$) and the platform (Binomial had hoc test, $p<0.05$). Lastly, pattern 4 (associated with PMG and OG) was significantly associated with cooked rice on the platform (Binomial had hoc test, $p<0.001$). Grid manipulations (all items) were also well represented in this pattern 4 but the difference was not significant. Finally, cooked rice was more frequently manipulated using pattern 1 (at the grid) and 4 (at the grid and on platform), large items more frequently with pattern 3 (at the grid and on platform) and small items with pattern 0 (on platform) and pattern 3 (on all substrates).

4.2. Handling score and manipulative effectiveness according to the food items and the substrate

4.2.1. Handling score

Figure 2a shows how the handling score varies between item-substrate modalities (Kruskal-Wallis test: khi2=328.15, df=8, p<0.001). The large items manipulated at the grid required more manipulations than other items: the difference was significant when compared to the cooked rice at the grid (Wilcoxon test, p<0.05) and to the small items on the platform (Wilcoxon test, p<0.001) and on the ground (Wilcoxon test, p<0.001). Large items were more rarely manipulated on the ground (N=4 sequences) and on the platforms (N=8 sequences). On these substrates, the handling score differences between the large items and the others were not significant (i.e, no difference or too small class size), except for the large items on the platform that were significantly higher than the small items on the ground (Wilcoxon test, p<0.001).

Cooked rice, whatever the substrate, was the second item that involved more manipulations, especially compared to the small items on the platform (Wilcoxon test, p<0.001 for the three substrates) and on the ground (Wilcoxon test, p<0.001 for the three substrates). The handling score appeared higher at the grid than on the platform (Wilcoxon test, p<0.05) for this item.

Finally, the small items required less manipulations than the other items, except at the grid where the difference was not significant. The substrate had an important effect on the manipulation of these items as the handling score is higher at the grid compared to the ground (Wilcoxon test, p<0.001) and the platform (Wilcoxon test, p<0.001), and it is also higher on the ground compared to the platform (Wilcoxon test, p<0.001).

4.2.2. Effectiveness

The effectiveness was significantly different between some item-substrate modalities (Kruskal-Wallis test: khi2=254.94, df=8, p<0.001) (Figure 2b). The effectiveness was lower for

cooked rice whatever the substrate compared to the small items on the platform (Wilcoxon test, $p<0.001$ for the three substrates) and on the ground (Wilcoxon test, $p<0.001$, for the three substrates). A lower effectiveness was also observed on the platform compared to the grid (Wilcoxon test, $p<0.05$).

Manipulation of large items at the grid was less effective than the manipulation of the small items on the platform (Wilcoxon test, $p<0.05$) but there was no significant difference between the different substrates for the large items.

Finally, the manipulation of small items appeared significantly more effective than the one of cooked rice (except at the grid where the difference is not significant) and the one of large items on the grid (except at the grid and on the ground where the differences are not significant; Figure 2b). We also observed a difference in the manipulation of small items, being less effective at the grid versus platform (Wilcoxon test, $p<0.001$) and ground (Wilcoxon test, $p<0.001$), while effectiveness was lower on the ground than on the platform (Wilcoxon test, $p<0.001$).

Discussion

Our study provides the first description of the manipulative repertoire spontaneously used by zoo bonobos in a feeding context and by taking into account the diversity of manipulated food and physical environment. In addition, the use of two innovative methodologies (i.e, the sequential analysis by optimal matching and the effectiveness score) allowed us to study food manipulation as a dynamic process. Our main results validate our hypotheses by showing a large manipulative repertoire, including two newly described variants of grasping postures, and the existence of different manipulative strategies whose choice and effectiveness are dependent on the physical environmental context and the

morphometric characteristics of food items. The following discussion details the implications of our findings with regard to the evolution of manual abilities in hominoids and the behavioral flexibility, depending on the decision-making context, allowed by these manipulative abilities.

1. Manipulative repertoire

Despite the long-recognized importance of hand functionality in hominoid evolution (Almécija et al., 2015; Harrison & Rein, 2016; Kivell, 2015; Pouydebat et al., 2008), little is known of the manipulative repertoire of our closest relative, bonobos, both in natural conditions and in zoos. The aim of our study was therefore to provide a first description of the spontaneous repertoire used by bonobos in a feeding context, under zoo conditions. It includes a wide variety of grip categories, from precision to power grips, even if this species show morphological constraints of their hands, such as long fingers and short thumb, and the lack of a true flexor *policis longus* muscle (FPL) (Marzke & Wullstein, 1996; Susman, 1998; van Leeuwen et al., 2018). The ability of using precision grips, close to those used by humans, confirms the results of previous studies in bonobos for both tool use (Bardo et al., 2016) and grasping items (Christel, 1993; Christel et al., 1998). Our study supports the general capacities of great apes to manipulate items with a great variety of grasping postures since we have identified 22 distinct grasping postures as well as 49 grip associations and compound grips. Twenty grasping postures of the repertoire were already described in the literature on apes and humans (Bardo et al., 2016, 2017; Jones-Engel & Bard, 1996; Marzke et al., 2015; Marzke & Wullstein, 1996; Napier, 1956; Parry, 1966; Pouydebat et al., 2011), and we described two new variants (i.e, the “dorsal scissor hold” and the “thumb-middle grip”). We also observed a spontaneous use of tools (i.e, branches) to enhance the access to food, confirming the morphological and cognitive abilities of this species to use tools, as shown previously in zoo

and semi-free ranging conditions (Bardo et al., 2015, 2016; Boose et al., 2013; Takeshita & Walraven, 1996; Visalberghi et al., 1995). The existence of preferred grasping postures in bonobos is consistent with previous results in human and other great apes (e.g., Christel, 1993; Pouydebat et al., 2011; Bardo et al., 2016). In our study, the most frequent grasping posture is the "lateral thumb index grip", as also reported in the literature, whether it involves tools (Bardo et al., 2016) or to grasp small objects (Christel et al., 1998). The second preferred grasping postures used by the bonobos were the power grips involving the thumb and without the thumb. Therefore, this is the first report showing a high prevalence of the powerful postures used by bonobos coping with a wide range of food items (in size, shape and hardness), while powerful postures were not as frequent in previous studies focusing on tool use (Bardo et al., 2016) or small object manipulation (Christel et al., 1998). This result is also consistent with the manipulation of large objects in chimpanzees, in which the preferred grasping postures are the "power grips" (Pouydebat et al., 2011). This result highlights the importance of considering more the size and shape of handled objects in studies working on manipulation of food/objects/tools, in non-human primates as well as humans, to better understand the evolution of these behaviors (e.g., (Key et al., 2018; Pouydebat et al., 2009).

Finally, despite their marked differences in whether or not to use tools in natural conditions, chimpanzees and bonobos are very similar not only in their hand morphology (Diogo et al., 2017; Druelle et al., 2018), but also in their manipulative abilities. However, some differences appear when comparing our findings to the literature on apes, specifically the preference of human and chimpanzees for the "palmar thumb index" grip (including both "tip-to-tip" and "pad-to-pad") (Christel, 1993; Pouydebat et al., 2011). Nevertheless, the presence of this grip in the bonobo manipulative repertoire, as confirmed in our study, demonstrates the ability of bonobos to execute this opposable fingers grip. These observations suggest that

bonobos are not markedly different from chimpanzees in terms of cognitive and morphological constraints associated with food manipulation. This supports the hypothesis that the cognitive mechanisms underlying this flexibility of manipulative behaviors are shared by both species and would have already been present in their common ancestor, around 1 million years ago (Won & Hey, 2005). In an evolutionary context, research on tool use behavior of nonhuman primates has established crucial knowledge for theories of human evolution of language, brain and tool-using lifestyle (Greenfield, 1991; Parker & Gibson, 1979; Washburn, 1960) but all kind of manipulative skills are instructive. An extensive knowledge about manipulation in different ecological contexts is needed to improve our understanding of the development of foraging behaviors and ecological strategies through the evolution.

2. Manipulative strategies

Our results show that bonobos can use different manipulative ways to gain access to food. Our hypothesis was the existence of preferred manipulative strategies adapted to the morphometric properties of the food and the environmental context (i.e, substrate). This prediction was confirmed since some manipulative patterns were significantly more frequently used for one or several kinds of food, according to the substrate used for stabilizing the body during feeding. Together with the dominant grip categories assigned to each pattern, the results show a trend to manipulate cooked rice preferentially using “Palm grips” or “Other grips” (pattern 4) alone, or in association with “Precision grips” (pattern 1) when the substrate is more complex (i.e, at the grid). This can be explained by the fact that the individuals can reach the cooked rice contained in the enrichments by hitting the tube on the ground or on the platform (“Palm grips” category), by probing with their fingers (“Other grips” category) or by using a tool (“Precision grips” category and “V pocket grip” for storage (i.e, keeping a tool

in the hand or foot without using it)). The two last cases are bimanual manipulation as it requires to stabilize the enrichment with the other hand ("Palm grips" or "Other grips" categories).

The "Without-thumb grips" (pattern 2) and "Thumb-lateral grip" (pattern 3) are less specific to one kind of food or substrate. In contrast, manipulation with only the mouth (pattern 0) occurs almost exclusively with small items on the platform. This can be explained by the absence of dirt and sand on this substrate, allowing an easier grasping of the small items without foraging as suggested in the study of Christel et al. (1998) while grasping small objects on a cleaner floor required less time than on grassy/sandy ground.

Our result show that the chosen manipulative strategy can differ between the substrates for a same kind of item (i.e, cluster), depending on the substrate and confirming the necessity to consider the interaction between the two parameters. Furthermore, while some patterns are strongly associated with some modalities of item and substrate, we observed different manipulative strategies for a same item-substrate modality. The choice of one specific strategy by bonobos is supposed to enhance the access to the targeted food. When we looked at the manipulative effort (i.e, the complexity of manipulation) and the effectiveness (i.e, the food intake related to the manipulative effort) of the chosen strategy for every item-substrate modalities, we observed an association: the greater the manipulative effort, the lower the effectiveness. This rule was not strictly generalizable however, as the great number of manipulations for large items seemed to be compensated by a large number of mouthfuls ingested. This result suggests the existence of a trade-off between the manipulation effort and the food intake. It may be as efficient to process many small items (i.e, multiple lower effort) with many low intake ratios as few large items (i.e, higher effort) with a high intake ratio.

Furthermore, we did not observe any difference of effectiveness between the different substrates for the large items: this can be explained by the fact that the largest items do not pass through the bars of the grid without manipulation. During our observations, the large items were more rarely manipulated on the ground and on the platforms. In contrast, we observed a difference of effectiveness for small items where manipulation at the grid appears significantly less effective than on the platform and ground. Contrary to the large items, the complexity of manipulation imposed by the grid would not be compensated by the low number of mouthfuls. A lower effectiveness is also observed on the ground compared to the platform. This can be explained by the presence of dirt and sand inducing a greater number of manipulations to isolate the item. Finally, even if the grid makes manipulation more complex, it has a significant advantage related to the presence of the majority of the largest foods (79%). This link between the substrate choice and the position of the food has already been shown in other primates (*Microcebus murinus,* Toussaint et al., 2015). However, it remains significantly less effective than the manipulation of small items on the platform. Although it contains a majority of small items (75%), the platform has the advantage to present a support making manipulation simpler (stability and rarity of dirt and sand).

Our results highlight differences in manipulative strategies, and suggest the existence of a trade-off between manipulative complexity and quantity of food ingested. Furthermore, the variability observed in the choice of the manipulative pattern for each item and substrate, and the effectiveness of the chosen strategy could be linked to the individual decision-making process in bonobos. Indeed, primate foragers face daily challenges for which they have to regulate the balance between the costs and benefits for accessing the food (Garcia et al., 2021). As shown in research about primate decision-making, foraging decisions require the integration of multiple information, both ecological (food type and quantity, travelling

distance, temporal information, eventuality of predation) and social (presence and identity of congeners, including kinship and social status) (Garber et al., 2009; Rosati & Hare, 2012). Depending on the set of conditions, the foraging decisions can then differ for a same kind and amount of food, leading to divergent behavioral tactics and, in our study, to variable manipulative strategies. From the few studies available about decision-making process in bonobos, we know that compared to chimpanzees, they have a lower tolerance for risk in choices about food (Heilbronner et al., 2008), hypothetically linked to a less competitive and variable environment (Doran et al., 2002; Furuichi et al., 2015; Hohmann & Fruth, 2003) (but see also Koops, et al., 2015). But in the context of zoo, where the intragroup competition is high and the food is not *ad libitum* but regularly distributed, the interest of risky choices (i.e, carrying out a more complex manipulation is not always compensated by the quantity of ingested food and induces a higher risk of theft by congeners) could be enhanced. The individual parameters also are of critical importance in this decision process, as suggested by the inter-individual differences found in previous manipulative studies in zoo bonobos (Bardo et al., 2016) and chimpanzees (Pouydebat et al., 2011). Besides the physiological state of the individual such as its satiation level and energy status (see the risk-prone strategy in chimpanzees during periods of high diet quality; Gilby & Wrangham, 2007), age, sex and/or social status could induce different manipulative strategies for a same food item. Indeed, the manipulative behavior, as part of the whole foraging behavior, could be reinforced by social learning and/or operant conditioning and become more precise with growing age (Bouton, 2007). Sex and social status could also be important (Garber et al., 2009) while dominant females are less impacted by intra-group feeding competition and can spend more time manipulating food. This highlight the need, especially in complex social structures such as

bonobo communities, to incorporate not only the ecological context but also the individual and social parameters in a further study.

Conclusion

Food manipulative process is part of the foraging strategies adopted to enhance the access to food resources. In this context, knowing the differences and/or similitudes between humans and our closest living relatives, especially chimpanzees and bonobos, are of critical importance for our understanding of the evolutionary origins of hominid patterns of foraging strategies. In our study, we revealed a range of manipulative abilities in bonobos similar to that previously described in chimpanzees, from precision to power grips. Furthermore, we distinguished several manipulative strategies depending on the targeted food and the environmental context. But these two factors were not sufficient to explain the whole choice variability. This could be explained by the multifactorial aspect of individual making-decision process, relying on both ecological and social parameters and highlighting the need to frame these strategies within the whole ecological and social context. The comparison of our results with data on free-ranging bonobos in further studies would be of great value to improve our understanding of the mechanisms underlying bonobos manipulative strategies. Finally, the innovative methodologies used in this study, and applicable to any sequential behavioral data, enabled us to broaden our approach on the bonobo manipulative capacities to investigate a more complete dynamic process.

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Tables:

Table 1. Distribution and characteristics of the sample of manipulative sequences**.**

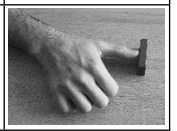
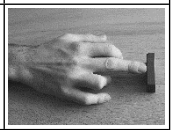
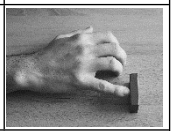
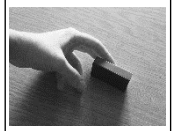
	N sequences	**Proportion of the sample (%)**	**ID**
Total	**792**	100	17
With manual/foot manipulation	661	83.46	17
With unimanual manipulation	615	77.65	17
With bimanual manipulation	115	14.52	12
With foot manipulation	9	1.14	4
With the mouth only	131	16.54	10
Without tool	711	89.77	17
With tool	81	10.23	6
Complete	769	97.10	17
Incomplete	23	2.90	NA

Table 2. Variability of grasping postures involving the hands: occurrence alone or in grip associations (number of sequences) and individuals using them alone or in grip associations.

Grip category†	Name in the literature	Reference(s)	Name	Description	Occurence in N sequences (/792)			Used by N individuals (/17)			Illustration
					Total	In unimanual manipulation	In grip associations	Total	In unimanual manipulation	In grip associations	
Precision grips (**PCG**)	Two-jaw chuck pad-to-pad/Two-jaw chuck tip-to-tip/Two-jaw chuck pad-to-pad side	Marzke and Wullstein 1996; Bardo et al. 2017	Palmar thumb-index grip	Item held between the distal phalanges of the thumb and the index finger.	**60**	59	1	**11**	11	1	
	None	None	Thumb-middle grip	Item held between the distal phalanges of the thumb and the middle finger.	**18**	18	0	**3**	3	0	
	Dynamic tripod grip	Wynn-Parry 1966	Dynamic tripod grip	Item held between radial side of third finger and thumb pulp, with index pulp on top of the item.	**10**	9	9	**3**	3	3	
Thumb lateral (**TL**)	Two-jaw chuck tip-to-side/Two-jaw chuck pad-to-side	Marzke and Wullstein 1996;	Lateral thumb-index grip	Item held between the thumb and side of the pad of the index finger.	**375**	325	54	**17**	17	7	

		Bardo et al. 2017									
Without thumb (**WT**)	Scissor held	Marzke et al. 2015	Palmar scissor hold	Item held between the index and middle fingers, with the hand in pronation.	**72**	71	4	**15**	15	4	
	None	None	Dorsal scissor hold	Item held between the flexed index and middle fingers, with the hand in supination,	**10**	10	0	**5**	5	0	
	Fingers hook	Marzke and Wullstein 1996	Fingers hook	Item enclosed by 2 or 3 flexed fingers.	**20**	15	6	**12**	11	5	
	Index finger hook		Index finger hook	Item enclosed by the flexed index.	**7**	4	3	**5**	3	2	
Palm grips (**PMG**)	Cup held	Marzke and Wullstein 1996	Cup hold	Item held with the palm of the supinated hand and the lightly flexed joined 4 fingers, except the thumb.	**6**	4	2	**3**	2	2	
			Cup hold with thumb	Item held with the palm of the supinated hand and the lightly flexed joined 4 fingers and with a	**2**	2	0	**2**	2	0	

				pressure applied by the opposed thumb.							
	Brush grasp	Bardo et al. 2017	Brush grasp	The 5 fingers are gathered along the item with the object end against the palm.	**9**	9	0	**8**	8	0	
	Power grip	Bardo et al. 2017	Power grip	Item held in opposition between the palm and flexed fingers, except the thumb.	**49**	32	18	**9**	9	2	
			Power grip with thumb	Item held in opposition between the palm and flexed fingers with a pressure applied by the opposed thumb.	**158**	138	69	**16**	16	12	
Other grips (**OG**)	V pocket	Marzke et al. 2015	V pocket	Item held in web between full thumb and index finger, other fingers are flexed but not in contact with the item.	**34**	28	7	**11**	10	3	

	Finger probe	Marzke and Wullstein 1996	Index finger probe	Item probed by the extented index finger.	**38**	13	26	**8**	2	7	
			Thumb probe	Item probed by the extented thumb.	**12**	2	10	**5**	1	4	
			Middle finger probe	Item probed by the extented middle finger.	**3**	3	0	**1**	1	0	
			Fifth finger probe	Item probed by the extended fifth finger.	**20**	0	20	**1**	0	1	
			Fingers contact	Item moved by the distal phalanges of 2 or 3 fingers.	**12**	11	1	**7**	6	1	
			Index finger contact	Item moved by the distal phalange of the index finger.	**43**	41	8	**8**	8	4	
			Middle finger contact	Item moved by the distal phalange of the middle finger.	**3**	3	0	**3**	3	0	
	Finger tips support	Bardo et al. 2017	Finger tips support	Item maintened by the tips of 4 or 5 fingers, but not held.	**34**	1	34	**2**	1	2	

Footnote: † PCG: contact between distal phalanges of the thumb and the index finger, also called “precision grip” in Jones-Engels and Bard (1996), “Thumb-index grips” in Pouydebat et al. (2011) and “Category 1” in Bardo et al. (2016). This category also includes one grip that wasn’t previously described and called “Thumb-middle grip”. It is described in the same way as the “Two-jaw chuck pad-to-pad side” (Bardo et al., 2016) but involves the middle finger instead of the index.

TL: contact between the distal phalange of the thumb, the lateral side of the middle, proximal phalanges of the index finger and the item, also called “thumb lateral” in Pouydebat et al. (2011) and “Category 2” in Bardo et al. (2016).

WT: contact between one or several fingers, except the thumb, and the item, also called “without thumb” in Pouydebat et al. (2011) and “Category 3” in Bardo et al. (2016). We distinguished in this category the “dorsal scissor hold” from the “scissor hold” as the hand is systematically placed in supination and fingers 2 and 3 are always flexed, which is not the case in the dorsal scissor hold grip.

PMG: contact involving palm, the thumb and one or several part of other fingers and the item, involving the power grasping posture (Napier, 1956; Jones-Engels & Bard, 1996), and also called “palm grips” in Pouydebat et al. (2011) and “Category 4” in Bardo et al. (2016).

OG: contact types which fell outside the above categories, called “other grips” in Jones-Engels and Bard (1996) and “Category 5” in Bardo et al. (2016). In our study, it mostly involves non-prehensile postures (i.e., “Finger probe” and “Finger tips substrate”) (Napier, 1956).

Table 3. Variability of grasping postures involving the feet (F): occurrence alone or in grip associations (number of sequences) and individuals using them alone or in grip associations.

Grip category	Name	Description	Occurence in N sequences (/792)			Used by N individuals (/17)		
			Total	Used alone	In grip associations	Total	Used alone	In grip associations
Palm grips (**PMG**)	Power grip with thumb (F)	Item held in opposition between the palm and flexed fingers with a pressure applied by the opposed thumb.	**9**	9	0	**4**	4	0
Other grips (**OG**)	V pocket (F)	Item held in web between full thumb and index finger, other fingers are flexed but not in contact with the item.	**1**	1	0	**1**	1	0

Table 4. Variability of grip associations involving the grasping postures used alone and the associations in bimanual manipulation or compound grips: occurrence (number of sequences) and individuals using them.

Grip association	Occurence in N sequences (/792)	Used by N individuals (/17)
Brush grasp	9	8
Cup hold	4	2
Cup hold + Power grip with thumb	2	2
Cup hold with thumb	2	2
Dorsal scissor hold	10	5
Dynamic tripod grip	9	3
Dynamic tripod grip + Dynamic tripod grip	1	1
Dynamic tripod grip + V pocket	1	1
Fifth finger probe + Power grip	17	1
Fifth finger probe + Power grip with thumb	20	1
Finger tips support	1	1
Finger tips support + Lateral thumb-index grip	33	1
Finger tips support + Power grip with thumb	1	1
Finger tips support + V pocket	1	1
Fingers contact	11	6
Fingers contact + Index finger contact	1	1
Fingers hook	15	11
Fingers hook + pi	1	1
Fingers hook + Power grip with thumb	5	4
Index finger contact	41	8
Index finger contact + Index finger contact	7	4
Index finger hook	4	3
Index finger hook + ind	2	1
Index finger hook + Power grip with thumb	3	2
Index finger probe	13	2
Index finger probe + Dynamic tripod grip	4	2
Index finger probe + Lateral thumb-index grip	1	1
Index finger probe + Power grip with thumb	18	4
Index finger probe + V pocket	2	1
Lateral thumb-index grip	325	17
Lateral thumb-index grip + Lateral thumb-index grip	2	2
Lateral thumb-index grip + Thumb probe	1	1
Middle finger contact	3	3
Middle finger probe	3	1
Palmar scissor hold	71	15
Palmar scissor hold + Power grip with thumb	4	4

Palmar thumb-index grip	59	11
Power grip	32	10
Power grip + Power grip with thumb	1	1
Power grip with thumb	138	16
Power grip with thumb + Dynamic tripod grip	2	1
Power grip with thumb + Lateral thumb-index grip	20	6
Power grip with thumb + Power grip with thumb	5	3
Power grip with thumb + Thumb probe	6	3
Power grip with thumb + V pocket	4	3
Thumb probe	2	1
Thumb probe + Dynamic tripod grip	4	2
Thumb-middle grip	18	3
V pocket	28	10

Table 5. Detailed pattern distribution in each item-substrate modality (Exact multinomial and binomial had hoc tests: number in red are significantly higher than a homogeneous distribution, number in blue are significantly lower, p<0.05)

Item-support modality	Multinomial test	Pattern 0	Pattern 1	Pattern 2	Pattern 3	Pattern 4	Total
0-grille	p<0,001	1	48	0	7	12	68
0-plateforme	p<0,001	0	44	2	3	38	87
0-sol	ns	0	3	2	1	1	7
1-grille	p<0,001	0	13	13	40	10	76
1-plateforme	p<0,001	128	14	12	140	1	295
1-sol	ns	1	56	29	89	1	176
2-grille	p<0,001	1	4	5	21	14	45
2-plateforme	p<0,05	0	0	1	5	2	8
2-sol	ns	0	1	0	3	0	4
Total		131	183	64	309	79	766

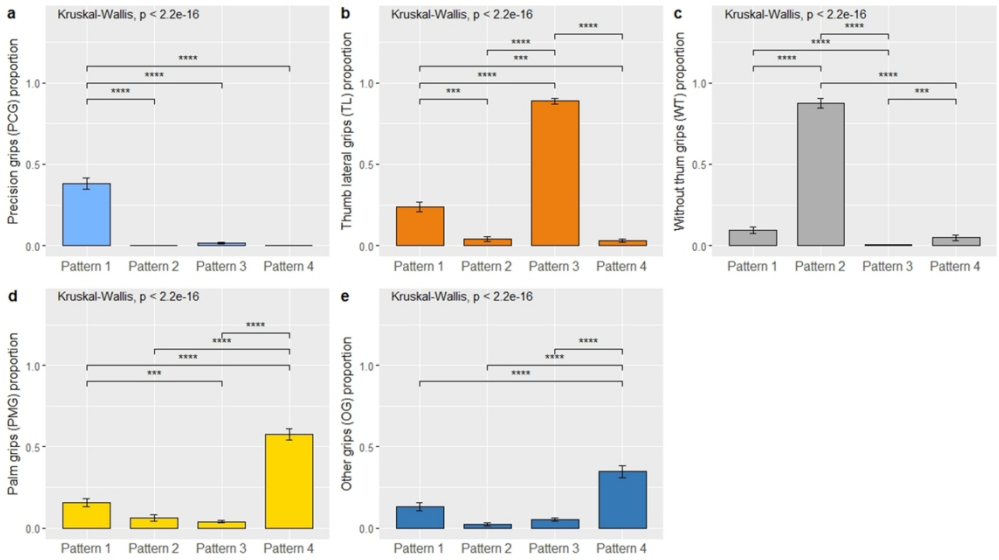
Figure legends:

Figure 1. Barplots presenting the means of every grip category proportions in the sequences of each manipulative pattern. (Wilcoxon rank sum test with Bonferroni continuity correction, ***: $p < 0.001$, ****: $p < 0.0001$. Error bars represent standard error of the mean (SEM)) (Npattern1=183 sequences, Npattern2=64 sequences, Npattern3=309 sequences, Npattern4=79 sequences)

Figure 2. Boxplot representing the handling score (a) and the effectiveness (b) of the sequences in each of the item-substrate modalities (Wilcoxon rank sum test with Bonferroni continuity; modalities that share a letter within and between substrate types do not differ significantly, on average, from each other: $p<0.05$). Bold horizontal bars represent median values.

Research highlights

- Our study provides the first description of the large manipulative repertoire spontaneously used by zoo bonobos in a feeding context.
- It also shows the existence of different manipulative strategies whose choice and effectiveness are dependent on the physical environmental context and the morphometric characteristics of food items.
- The application of these innovative methodologies on data from free-ranging bonobos in further studies would be of great value to improve our understanding of the mechanisms underlying bonobos manipulative strategies.



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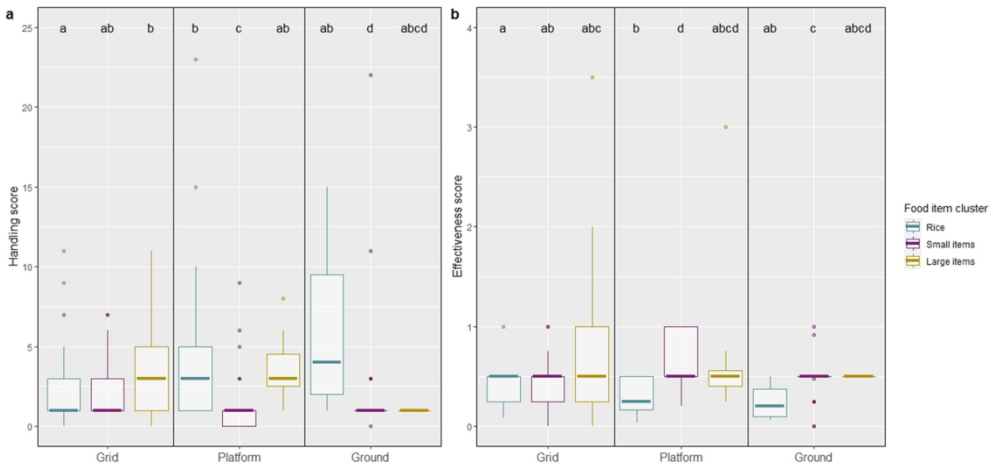

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180x83mm (300 x 300 DPI)

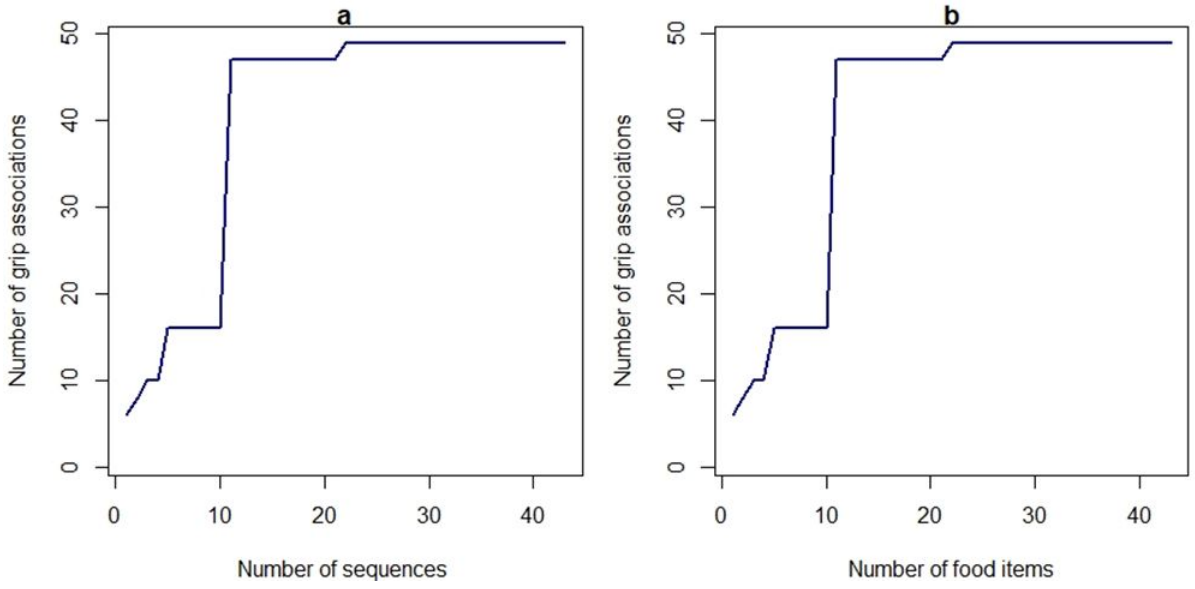
Supporting information

Appendix 1. Morphometric measurements (6 variables) of the 43 food items handled by the bonobos of the group in the scored videos. The categories (from cat 1 to cat 6) correspond to the decreasing cutting sizes of food distributed by the zookeepers.

Item	N samples	Mass (gr)		Hardness (N)		Length (cm)		Width (cm)		Height (cm)		Volume (cm3)	
		Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Black radish Cat2	3	27,0	3,6	10,5	0,8	6,0	0,0	5,5	0,0	1,0	0,0	33,0	0,0
Broccoli Cat1	3	42,0	6,1	23,5	0,6	14,5	0,3	6,0	0,0	5,0	0,3	435,0	30,9
Broccoli Cat2	3	18,0	2,5	20,5	0,5	6,0	0,3	6,0	0,0	5,0	0,0	180,0	8,7
Broccoli Cat3	6	3,0	0,6	0,0	0,0	2,5	0,3	2,0	0,4	1,5	0,0	7,5	2,6
Cake	3	110,0	3,0	0,0	0,0	15,0	0,0	4,0	0,0	4,0	0,0	240,0	0,0
Carrot Cat2	5	53,0	12,7	37,5	0,9	10,5	0,6	4,0	0,5	3,5	0,4	147,0	33,3
Carrot Cat3	2	41,0	1,0	31,0	1,2	17,5	2,0	3,5	0,0	2,0	0,0	122,5	14,0
Carrot Cat4	3	22,0	2,5	31,0	1,2	14,0	0,0	2,0	0,4	2,0	0,0	56,0	8,1
Carrot Cat5	2	11,0	5,0	31,0	1,2	6,0	0,0	2,5	0,7	2,5	0,0	37,5	7,5
Cauliflower Cat1	3	122,0	5,3	14,0	0,4	13,0	1,5	8,0	0,7	4,0	0,5	416,0	54,6
Cauliflower Cat2	3	78,0	4,0	26,0	0,6	17,0	1,2	8,5	1,1	2,0	0,3	289,0	54,6
Cauliflower Cat3	4	50,0	9,5	14,0	0,4	7,0	0,4	6,0	0,6	3,0	0,4	126,0	36,4
Cauliflower Cat4	3	17,0	4,0	8,5	0,5	6,0	0,3	3,0	0,7	1,5	0,0	27,0	6,2
Cauliflower Cat5	2	10,0	1,0	26,0	0,6	4,0	0,0	3,0	0,0	1,0	0,0	12,0	0,0
Cauliflower Cat6	9	2,0	0,6	0,0	0,0	2,0	0,3	2,0	0,3	1,0	0,1	4,0	1,8
Celery Cat1	2	63,0	12,0	14,5	1,0	14,0	0,0	6,0	0,0	6,0	0,5	504,0	42,0
Celery Cat2	7	19,0	2,6	14,5	1,0	21,5	1,7	6,5	1,4	1,0	0,0	139,8	35,1
Celery Cat3	3	9,0	1,5	14,5	1,0	7,0	0,0	1,5	0,0	1,5	0,0	15,8	0,0
Celery Cat4	5	2,0	0,0	0,0	0,0	13,5	0,7	6,0	0,8	0,5	0,0	40,5	7,2
Cucumber Cat1	3	32,0	1,0	11,5	0,4	11,0	0,0	3,0	0,4	2,0	0,0	66,0	6,4
Cucumber Cat3	4	21,0	3,0	11,5	0,4	7,0	1,1	3,0	0,5	2,0	0,2	42,0	14,1
Endive Cat3	1	11,0	NA	8,7	0,4	13,0	NA	5,5	NA	0,5	NA	35,8	NA
Endive Cat4	2	3,0	0,0	8,7	0,4	9,5	0,5	5,0	0,0	0,5	0,0	23,8	1,3
Green cabbage Cat1	3	167,0	11,5	34,5	0,4	19,5	0,0	9,5	1,3	6,0	0,9	1111,5	308,3
Green cabbage Cat2	5	34,0	2,9	26,0	0,9	24,0	0,9	19,0	0,7	0,5	0,0	228,0	16,3
Green cabbage Cat3	1	37,0	NA	34,5	0,4	7,5	NA	6,5	NA	6,0	NA	292,5	NA
Green cabbage Cat4	3	7,0	1,7	0,0	0,0	13,5	0,9	7,5	0,5	0,2	0,0	20,3	2,5

Green cabbage Cat5	5	1,0	0,0	0,0	0,0	6,0	0,5	3,5	0,4	0,2	0,0	4,2	0,6
Hazel bark	3	1,0	0,0	16,0	0,9	8,5	0,5	1,0	0,0	0,1	0,0	0,9	0,1
Hazel catkins	10	0,2	0,0	0,0	0,0	3,0	0,2	0,5	0,0	0,5	0,0	0,8	0,0
Leek Cat1	3	52,0	5,9	17,5	0,6	19,5	0,8	3,0	0,4	3,0	0,3	175,5	36,5
Leek Cat2	2	10,0	2,0	8,0	0,3	3,5	0,5	2,0	0,0	2,0	0,0	14,0	2,0
Leek Cat3	3	15,0	3,1	0,0	0,0	30,0	1,2	3,0	0,9	0,2	0,0	18,0	5,4
Leek Cat4	5	2,0	0,5	0,0	0,0	14,0	0,2	1,0	0,0	0,1	0,0	1,4	0,3
Lettuce Cat2	4	10,0	0,6	0,0	0,0	10,5	0,7	10,0	1,6	1,0	0,0	105,0	10,9
Lettuce Cat3	4	3,0	0,6	0,0	0,0	9,0	0,6	7,0	0,8	0,5	0,0	31,5	5,1
Oak leaf Cat4	7	1,5	0,1	0,0	0,0	7,0	0,7	5,0	1,0	0,1	0,0	3,5	0,8
Onion Cat2	2	20,0	1,0	15,0	0,0	8,0	0,0	3,5	0,7	2,0	1,0	56,0	36,0
Onion Cat3	3	4,0	1,2	5,5	0,0	6,0	0,0	2,0	0,0	0,5	0,0	6,0	0,0
Pepper Cat3	3	36,0	7,6	8,5	0,8	10,5	0,3	4,5	0,0	1,5	0,3	70,9	13,1
Pepper Cat4	4	14,0	1,6	8,5	0,8	8,5	1,2	4,0	0,7	1,0	0,2	34,0	9,1
Seeds	10	0,2	0,0	39,0	0,4	0,8	0,1	0,5	0,1	0,2	0,0	0,1	0,0
Zucchini Cat2	3	18,0	4,5	7,5	0,5	4,4	0,2	4,5	0,4	1,0	0,0	19,8	1,9

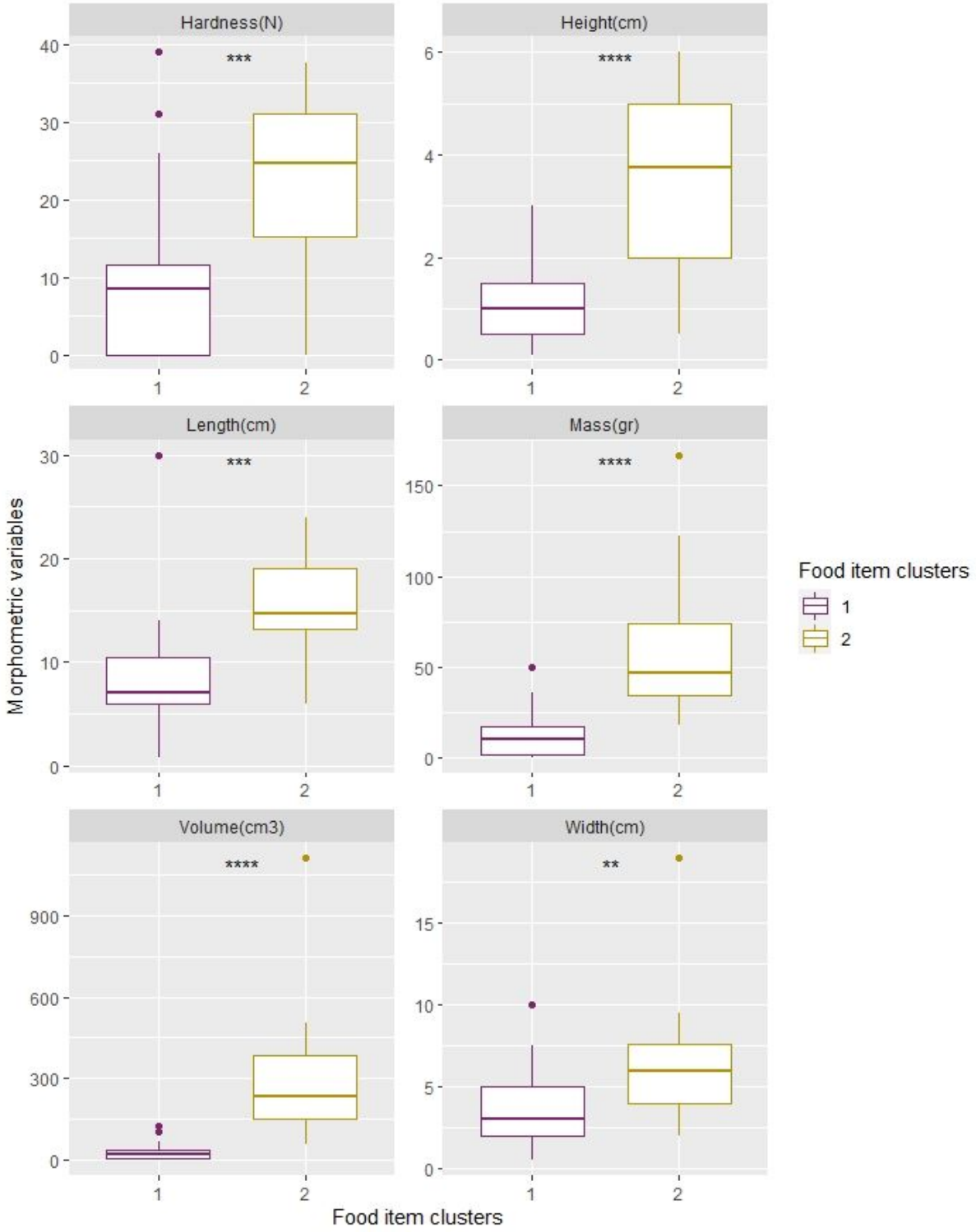
Appendix 2. Accumulation curves representing the cumulative number of grip associations observed as a function of the number of sequences (a) and number of food items (b). The 17 individuals of the group are represented in this sample (mean ± SEM=47 ± 5 sequences per individual; min=19; max=89).



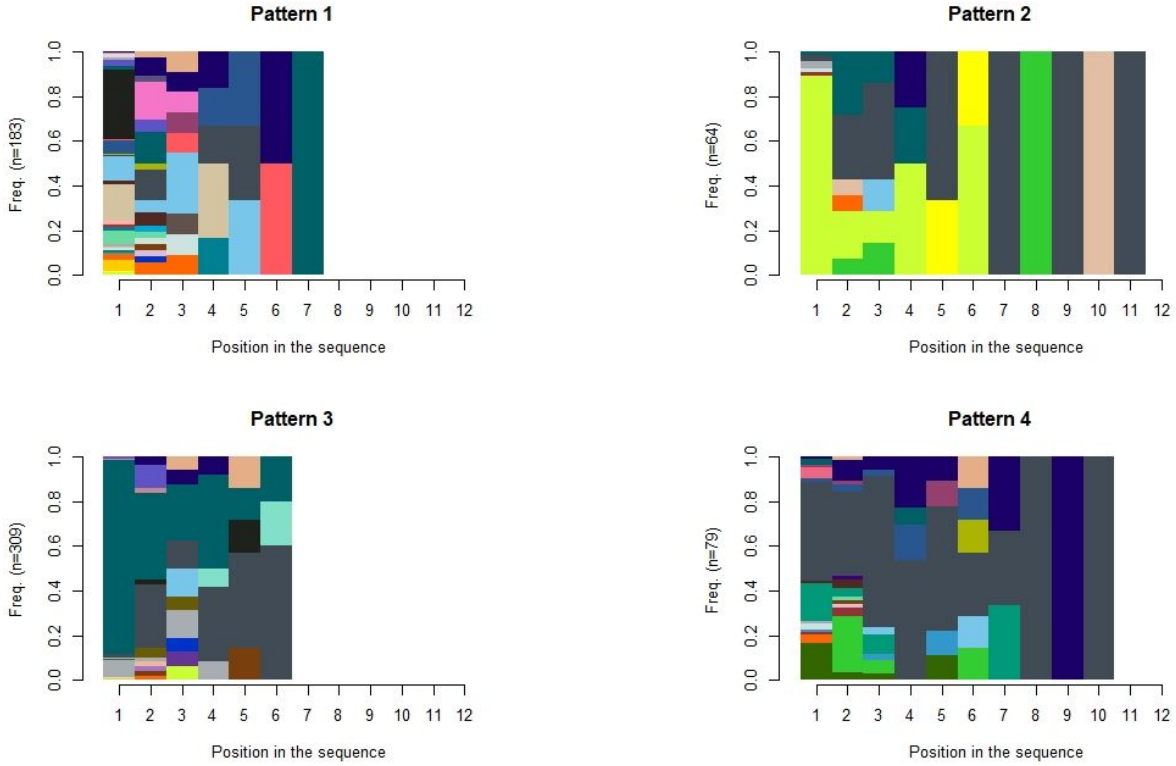
Appendix 3. Food item classification according to Hierarchical Cluster Analysis (HCA) and Ward's method. Three clusters are distinguished: Clusters 1 and 2 and Cluster 0, added for the special case of cooked rice.

Food item cluster	**Cluster 0**	**Cluster 1**	**Cluster 2**
Hardness (N) (mean ± SEM)	NA	8.7 ± 1.8	23.2 ± 2.8
Height (cm) (mean ± SEM)	NA	1.0 ± 0.2	3.6 ± 0.5
Length (cm) (mean ± SEM)	NA	8.2 ± 1.0	15.3 ± 1.4
Mass (gr) (mean ± SEM)	NA	11.8 ± 2.3	61.3 ± 11.7
Width (cm) (mean ± SEM)	NA	3.7 ± 0.4	6.6 ± 1.1
Volume (cm^3) (mean ± SEM)	NA	29.6 ± 5.7	309.8 ± 70.7
Food items	Cooked rice	Broccoli Cat3	Broccoli Cat1
		Black radish Cat2	Broccoli Cat2
		Carrot Cat5	Cake
		Cauliflower Cat3	Carrot Cat2
		Cauliflower Cat4	Carrot Cat3
		Cauliflower Cat5	Carrot Cat4
		Cauliflower Cat6	Cauliflower Cat1
		Celery stalk Cat3	Cauliflower Cat2
		Celery stalk Cat4	Celery stalk Cat1
		Cucumber Cat1	Celery stalk Cat2
		Cucumber Cat3	Green cabbage Cat1
		Endive Cat3	Green cabbage Cat2
		Endive Cat4	Green cabbage Cat3
		Green cabbage Cat4	Leek Cat1
		Green cabbage Cat5	
		Hazel bark	
		Hazel catkins	
		Leek Cat2	
		Leek Cat3	
		Leek Cat4	
		Lettuce salad Cat2	
		Lettuce salad Cat3	
		Oak leaf lettuce Cat4	
		Onion Cat2	
		Onion Cat3	
		Sweet pepper Cat3	
		Sweet pepper Cat4	
		Seeds	
		Zucchini Cat2	

Appendix 4. Box-plots presenting the 6 morphometric variables of the items in each of the clusters 1 (N=29) and 2 (N=14) obtained by Hierarchical Cluster Analysis (HCA) (Wilcoxon rank sum test with Bonferroni continuity correction, **: p<0.05, ***: p<0.001, ****: p<0.0001).



Appendix 5. Graphic presenting the frequencies of the different grip associations for each position in the sequences of the four manipulative patterns. The number of sequences in each pattern is indicated, in the y labels, by (n=x). Each color corresponds to a distinct grip association and is ranked, from bottom to top, in alphabetic order. For example, in the pattern 2, the grip association represented in light green in the first position of the sequences is the palmar scissor hold used alone and represents 90% of the first position in this pattern. The color distributions indicate different sequence structures between the patterns.



Appendix 6. Results of the two first axes of an MCA performed on three qualitative variables (i.e. the manipulative patterns, the food item clusters and the substrates) of 766 sequences. The first axis (horizontal) explained 62% and the second axe (vertical) explained (48%) of the total variance. The factorial plan is the same for the three projections and enables to visually notice some overlaps between the manipulative patterns and certain item clusters and substrates.