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RESEARCH ARTICLE

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Influence of food physical properties and environmental context on manipulative behaviors highlighted by new methodological approaches in zoo-housed bonobos (*Pan paniscus*)

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Abstract

Research on manipulative abilities in nonhuman primates, in the context of hominid evolution, has mostly focused on manual/pedal postures considered as static behaviors. While these behavioral repertoires highlighted the range of manipulative abilities in many species, manipulation is a dynamic process that mostly involves successive types of grips before reaching its goal. The present study aims to investigate the use of manual/pedal postures in zoo-housed bonobos in diverse dynamic food processing by using an innovative approach: the optimal matching analysis that compares sequences (*i.e.*, succession of grasping postures) with each other. To characterize the manipulative techniques spontaneously employed by bonobos, we performed this sequential analysis of manual/pedal postures during 766 complete feeding sequences of 17 individuals. We analyzed the effectiveness with a score defined by a partial proxy of food intake (i.e., the number of mouthfuls) linked to a handling score measuring both the diversity and changes of manual postures during each sequence. We identified four techniques, used differently depending on the physical substrate on which the individual performed food manipulation and the food physical properties. Our results showed that manipulative techniques were more complex (*i.e.*, higher handling score) for large foods and on substrates with lower stability. But the effectiveness score was not significantly lower for these items since manipulative complexity seemed to be compensated by a greater number of mouthfuls. It appeared that the techniques employed involved a trade-off between manipulative complexity and the amount of food ingested. This study allowed us to test and validate innovative analysis methods that are applicable to diverse ethological studies involving sequential events. Our results bring new data for a better

Abbreviations: HCA, hierarchical cluster analysis; MCA, multiple correspondence analysis; MFM, manipulative finger movements; OG, other grips; PCA, principal component analysis; PCG, precision grips; PMG, palm grips; SEM, standard error of the mean; TL, thumb lateral; WT, without thumb.

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understanding of the evolution of manual abilities in primates in association with different ecological contexts and both terrestrial and arboreal substrates and suggest that social and individual influences need to be explored further.

KEYWORDS
food manipulation, grasping posture, manipulative technique, sequential analysis

1 | INTRODUCTION

Food processing may require multiple and various abilities, ranging from powerful action to more precise manipulations. If human hand presents the highest level of dexterity compared with other primates (Key et al., 2018; Marzke et al., 1992; Marzke, 2013), with 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 et al., 2015; Marzke, 1997, 2013; Napier, 1960; Pouydebat et al., 2011), other species have shown their ability to process food in complex ways, using tools or not (*e.g*., Byrne et al., 2001). Comparative behavioral studies of hand use in our closest living relatives, in zoo and free-ranging conditions, can improve our understanding of the functional morphology in early hominins (*i.e*., *Homo sapiens* and their extinct relatives) as well as fossil apes (Bardo et al., 2017; Feix et al., 2015; Kivell et al., 2022; Pouydebat et al., 2008, 2011; Susman, 1998; Tbnooka & Matsuzawa, 1995). These studies continuously contribute to a better understanding of the evolution of manipulative behaviors that led to this extremely large manipulative flexibility in humans.

Complexity of food processing not only involves a large range of manual/pedal postures but also requires synchronization, stabilization, and ability to efficiently move the food without dropping it. Although dynamic hand movements have been described in human (*e.g*., Bullock & Dollar, 2011; Elliott & Connolly, 1984; Santello et al., 1998), only few studies have explored this ability in nonhuman primates (*e.g*., in chimpanzees: Crast et al., 2009; Marzke et al., 2015) but they did not consider the use and succession of manual/pedal postures. To our knowledge, the consideration of this detailed sequential use of manual/pedal grips has only been made in a context of tool-use (Bardo et al., 2016, 2017; Borel et al., 2017). Tool-use can be defined as "[…] the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just before use and is responsible for the proper and effective orientation of the tool" (Beck, 1980, p. 10). In this context, the *Pan* genus is of particular interest because the two species (chimpanzees and bonobos) present marked differences in whether or not to use tools in natural conditions (but see Hohmann & Fruth, 2003) despite the fact that chimpanzees and bonobos are very similar not only in their hand morphology (Diogo et al., 2017; Druelle et al., 2018; van Leeuwen et al., 2018) but also in their manipulative abilities. In bonobos, tool-use in a feeding context has only been observed in captive individuals (*i.e*., in sanctuaries, zoos, and laboratories) (Bardo et al., 2015, 2016; Boose et al., 2013; Gruber et al., 2010; Neufuss et al., 2017; Takeshita & Walraven, 1996; Toth et al., 1993; Visalberghi et al., 1995), while it has been described for hygienic and social purposes in free-ranging conditions (Furuichi et al., 2015; Hohmann & Fruth, 2003; Ingmanson, 1996; Kano, 1982; Nishida et al., 1999; Samuni et al., 2021). Yet, documentation about the dynamic techniques involving sequences of manual or pedal postures during food processing without tool in bonobos is lacking and necessary to complete our knowledge of bonobos manipulative abilities and to improve our understanding of the evolution of feeding strategies in primates. Furthermore, many studies have shown the effect of food properties and arboreal substrates on grasping techniques, demonstrating how much a food that is difficult to extract (*e.g*., preys or encapsulated foods) and a complex arboreal substrate (orientation and size of supporting branch) increase the complexity and diversity of the hand use (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 nonhuman primates (*e.g*., Key et al., 2018; Pouydebat et al., 2009) and are of critical importance to discriminate the causes of the origin of feeding manipulative behaviors in primates (Pouydebat & Bardo, 2019). The effect of the environmental context (arboreal *vs*. terrestrial) has also been well-studied in chimpanzees since 1960s (*e.g*., Jones-Engel & Bard, 1996; Marzke & Wullstein, 1996; Marzke et al., 2015; Pouydebat et al., 2011), but it has poorly been explored in the other *Pan* species, the bonobo.

Our previous study (Gérard et al., 2022) described for the first time the manipulative repertoire of a group of zoo-housed bonobos in a feeding context. To go further and consider any food manipulation as a dynamic and sequential process, the first objective of this new study was to identify and characterize the different manipulative techniques used by a group of zoo-housed bonobos to better understand the determinants and benefits of accessing food resources. We measured the similarities and differences between the manipulative sequences using an innovative method, the optimal matching analysis. Derived from molecular biology (Abbott & Tsay, 2000), this method is usually used in social sciences to analyze time-ordered sequences of socioeconomic 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 techniques of tool grip and manipulation of five human subjects during a tool-task. With this method, we expected to distinguish several manipulative techniques with preferential use of specific categories of manual postures (as identified in Gérard et al., 2022) in each of them. These different techniques are expected to be associated with the physical characteristics of the food (i.e., size, mass, and hardness) as well as the type of substrate (i.e., ceiling grid, ground, or platforms), as described for the preference of some grasping postures for small items (precision grips) and others for large items (palm grips) in *Pan* genus (Christel et al., 1998; Pouydebat et al., 2011).

The second objective was to evaluate the effectiveness of the food process according to manipulated food and substrate. To tackle this issue, we developed an innovative methodological approach in which we first calculated handling score using two parameters typically described in the literature to assess manual complexity (Bardo et al., 2016, 2017): the number of distinct manual postures used and the number of manual posture changes during a feeding sequence. Then we defined manipulative effectiveness as the number of mouthfuls per sequence related to this handling score. Based on previous studies in primates showing that a food difficult to extract and a complex substrate (*i.e.*, thin or suspended) increase the complexity and diversity of the hand use (MacKenzie & Iberall, 1994; Patel et al., 2015; Reghem et al., 2012; Toussaint et al., 2015), we expected to observe an influence of the physical parameters of the manipulated food and the substrate on the effectiveness, as well as on the choice of the manipulative technique used.

2 | 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 nonhuman Primates and conforms to Directive 2010/63/EU of the European Parliament and of the Council of September 22, 2010 on the protection of animals used for scientific purposes.

2.1 | Subjects and housing

The data were collected between January 27, 2020 and January 31, 2020 at the zoological park "la Vallée des singes" (France). The group was composed of 17 bonobos (i.e, Continuous Full Contact [group]) with 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 visible to the observer during the day in an indoor building with two large connected cages (98 m^2 each) containing climbing structures, made of platforms, ladders, and ropes (see Gérard et al., 2022 for more details). The ground was normal building floor with wood shavings and connected to outdoor areas, access to which was usually closed at this time of year because the temperature was too low.

The food ration was distributed four times a day on the top of the cages (i.e., ceiling grid) or inside the cages, either on the ground and the platforms, and included vegetables, apples, pellets, seeds, eggs, chicken necks, and a homemade mix containing cereals, vitamins and vegetal oils. All food items were provided in a same way on the top of the cages, on the platforms, or on the ground. Daily enrichment was composed of tree branches and tubes filled with cooked rice (Figure 1). Like food ration, they were distributed at different locations, and they were free to be displaced by the individuals.

2.2 | Data collection

2.2.1 | Food physical properties

To evaluate the influence of food physical characteristics on manipulative behaviors, physical measurements (i.e., size, mass, and hardness) were taken on every kind of food manipulated by the bonobos of the group (Supporting Information S1: Appendix 1). All the means were calculated with the standard error of the mean (SEM). Vegetables were measured just before being distributed, as whole items or cut pieces prepared by the zookeepers. One food item was defined as one cutting size of one food species (Supporting Information S1: Appendix 1). The aim of these measurements was to classify food items depending on their physical parameters. Every food item (mean ± SEM = 4 ± 0 samples per cutting size of each food species) was characterized by six quantitative values: length (cm), width (cm), height (cm), volume (cm^3) (*i.e.*, length*width*height), mass (gr) and hardness (N) (Supporting Information S1: Appendix 1). 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 ± SEM = 2.0 ± 0.3 measures per sample) allowing us to calculate the average value (McGraw et al., 2014). The measures were not applicable to cooked rice contained in enrichment devices (Figure 1) and we treated this food item separately in the analyses.

2.2.2 | Video recording and scoring

We used the same videos for the description of the manipulative repertoire in Gérard et al., 2022 (see the article for more details). One or several individuals were followed throughout a feeding session with one handheld camera (PANASONIC® HC-V380) to record the movements of the hands, feet, and mouth. The recordings were performed at 50 frames/s.

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" which began with the first contact between an individual and a food item and ended when the food was consumed in its entirety or abandoned before total consumption. A total of 3h30 of recorded sequences were analyzed (N = 792 sequences). The parameters recorded during the sequence were

FIGURE 1 Uni and bimanual manipulations of tubes filled with cooked rice (enrichment devices), at the ceiling grid (left) and on a platform (right) (©M. Anne).

the individual, the food consumed (categorized by species and by size, characterizing a "food item"), the substrate supporting the individual during manipulation (ground, platform, or ceiling grid), the manual/pedal grasping posture adopted, the hand(s)/feet used and the duration of each behavior.

2.2.3 | 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 & Wullstein, 1996; Marzke et al., 2015; Napier, 1956; Pouydebat et al., 2011; Wynn-Parry, 1966). To name the grasping postures, we used Marzke's grasping typology (Marzke et al., 2015; Marzke & Wullstein, 1996) and we divided them into six grip categories (see Gérard et al., 2022 for details):

- *Precision Grips* (PCG): contact between distal phalanges of the thumb and the index finger.
- *Thumb lateral* (TL): contact between the distal phalanx of the thumb, the lateral side of the middle, proximal phalanxes of the index finger and the item.
- *Without Thumb* (WT): contact between one or several fingers, except the thumb, and the item.
- *Palm Grips* (PMG): contact involving the palm, the thumb, and one or several part of other fingers and the item.
- *Manipulative Finger Movements* (MFM): contact types without real grasping (i.e., contact for moving or stabilizing the item and probe for sticking food to the finger) and involving the fingers (including the thumb) only.
- *Other grips* (OG): contact types which fell outside the above categories.

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 movements, individuals held or maintained the food or the enrichment device with one hand and extracted or picked up the food with the other hand. The hand used to extract the food was considered as dominant, based on previous studies about coordinated bimanual actions (Bardo et al., 2015; Hopkins, 1995; Meguerditchian et al., 2013) but both hands were considered later in the sequential analyses (see the optimal matching analysis below).

2.3 | Data analyses

2.3.1 | Food items classification

We observed 44 food items from 19 different plants or edible species (Supporting Information S1: Appendix 1) during the video scoring. To classify them according to their physical characteristics (i.e., classification of 43 items, the cooked rice being excluded) 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 the R package *Cluster*; Maechler, 2013) were performed on the six physical 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 physical characteristics (Supporting Information S1: Appendix 2). Each six physical variables used for cluster discrimination differed significantly between the two clusters (Supporting Information S1: Appendix

3). The first cluster (Cluster 1) corresponded to small, light, and soft items and the second cluster (Cluster 2) corresponded 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.

2.3.2 | Sequential analysis and manipulative techniques

Optimal matching analysis

We analyzed the sequences of manipulative behaviors by considering grasping postures used alone (unimanual or pedal manipulation) and grip associations (bimanual, annotated "left hand posture + right hand posture") through their succession within a sequence. Finally, the sequences could be composed of a succession of grasping postures used alone (manual or pedal) or a succession of several grip associations if the manipulation was only bimanual. It could also be composed of an alternance of grasping postures used alone and grip associations if the manipulation was alternatively uni and bimanual. A number was attributed to every grasping posture and grip association, so every manipulative sequence was a succession of numbers before analysis. First of all, we calculated the pairwise dissimilarities between the sequences using 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 R package *TraMineR* (Gabadinho et al., 2011). From the distances calculated between each pair of sequences, we performed a HCA with Ward's method, with the *agnes* function of the R package *Cluster* (Maechler, 2013), to distinguish several manipulative techniques. We added a supplementary technique containing the sequences without any manipulation (named "Manipulative technique 0") (i.e., the item was grasped with the mouth and consumed directly), corresponding to a specific foraging technique. Because it would require a larger amount of data and could be the topic of an entire study, we performed the analyses in this study at the group level and not at the individual level.

Grip category proportions and manipulative techniques

The proportion of the six 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. Because of their rare occurrence in the sequences (Gérard et al., 2022), the *manipulative finger movements* (MFM) and the *other grips* (OG) were considered as a unique category in the analyses. In bimanual manipulation, we only considered the action of the dominant hand (i.e., the hand extracting food) in this analysis. We compared the proportion of each grip category between the manipulative techniques to determine if these techniques (obtained with the Optimal matching analysis) were characterized by particular grip categories.

Use of manipulative techniques according to the food item and the substrate

To determine the influence of the physical properties of the manipulated food items and the physical substrates on the manipulative techniques used by the individuals, we considered all the possible modalities of the interaction between item clusters and substrates (see above). We assessed the link between manipulative techniques and item-substrate modalities by comparing the distribution of the manipulative techniques between the item-substrate modalities (N = 9 modalities, 3 item clusters, and 3 substrates) to a homogeneous distribution (see statistical method below).

2.3.3 | Handling score and manipulative effectiveness

In the literature, the manipulative effectiveness 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. Variable (C) in isolation also failed to distinguish sequences with the same length but containing only distinct postures or including a repetition of the same 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 and thus attributed an equal value to sequences of different length. We therefore created a new score representing the manipulative complexity and more representative of the variability of the sequences by combining the two variables:

$$\text{Handling score} = P + C.$$

Effectiveness is here defined as the ratio of ingestion to the manipulative score required for processing that food. For instance, if a food is handled with many changes of posture and several different postures but only provides one mouthful to the individual, this process will be less effective than the same number of manipulations on a food giving several mouthfuls. Effectiveness score has no direct energetic implications since it does not account for the nutrient composition of food:

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

For a mathematical purpose, we added the value of one to the denominator because the handling score (i.e., $P + C$) was sometimes equal to zero (for sequences involving the mouth only).

We compared the handling score and the effectiveness score between the different item-substrate modalities ($N = 9$) to determine whether the food access techniques were equally complex and effective according to the manipulated food and the environmental context.

2.3.4 | Statistical analyses

For the comparisons of every grip category proportions, handling score and effectiveness score, we performed multiple comparisons using the Kruskal–Wallis test and pairwise comparisons using the Wilcoxon rank sum test. Because of the small or null samples in some item-substrate modalities, we performed exact multinomial and binomial ad hoc tests on the distribution between the manipulative techniques for every item-substrate modality, by comparing them to an homogeneous distribution (*multinom.test* and *binom.test* functions of the R package *rstatix*, Kassambara, 2020). We then applied a Bonferroni correction on the *p* values. All statistics were computed using the R 3.6.3 statistical environment.

3 | RESULTS

3.1 | Classification of manipulative sequences

After a selection of the complete (*i.e.*, noninterrupted) sequences ($N = 769$), all the individuals of the group were represented in the data set (mean ± SEM = 45 ± 5 sequences per individual). From the sequences involving the hand(s) (N = 638 including $N = 115$ sequences with bimanual manipulation) and/or the foot (N = 9), 120 distinct sequences varying from 1 to 17 successive grip associations (*i.e.*, bimanual) or grasping postures used alone (unimanual or pedal) were found. The result of the optimal matching analysis associated with the HCA have enabled us to identify six clusters of sequences, of which only four were considered in our subsequent analyses. The last two indeed contained only one or two sequences and were therefore too rare to be considered as general techniques. The sequences in the four techniques we considered varied from 1 to 11 successive grip associations (*i.e.*, bimanual) or grasping postures used alone (unimanual). For instance, one sequence could eventually include only one manual or pedal grasping posture (for instance the lateral-thumb posture, only one grasping posture used alone) before the food was consumed, or be followed by other manipulations: a bimanual manipulation (grip association) like *power grip with thumb + lateral-thumb* or any other manual/pedal grasping postures or grip associations. The sequences included until 11 grasping postures or grip associations.

3.2 | Grip category proportions and manipulative techniques

Each technique was distinguished by one or two dominant grip categories (Figure 2). Technique 1 was associated with *precision grips* (PCG) (Kruskal–Wallis test: $\chi^2 = 169.88$, $df = 3$, $p < 0.001$; Pairwise Wilcoxon's tests, $p < 0.001$), technique 2 with *grips without the thumb* (WT) (Kruskal–Wallis test: $\chi^2 = 418.78$, $df = 3$, $p < 0.001$; Pairwise Wilcoxon's tests, $p < 0.001$), technique 3 with *thumb lateral grips* (TL) (Kruskal–Wallis test: $\chi^2 = 401.52$, $df = 3$, $p < 0.001$; Pairwise Wilcoxon's tests, $p < 0.001$), and finally technique 4 was distinguished by three grip categories: *palm grips* (PMG) (Kruskal–Wallis test: $\chi^2 = 254.25$, $df = 3$, $p < 0.001$; Pairwise Wilcoxon's tests, $p < 0.001$), *manipulative finger movements* (MFM) and *other grips* (OG) (Kruskal–Wallis test: $\chi^2 = 125.74$, $df = 3$, $p < 0.001$; Pairwise Wilcoxon's tests, $p < 0.001$).

3.3 | Manipulative techniques and effectiveness for various food items and substrates

3.3.1 | Manipulative techniques use according to the food item and the substrate

We compared the prevalence of every manipulative technique within each modality of the interaction between the food item clusters ($N = 3$) and the substrates ($N = 3$) (Table 1). Significant differences were found between the manipulative techniques used for all the items at the grid and on the platform (Exact multinomial tests, $p < 0.001$ except for the large items on the platform: $p = 0.036$ and all the items on the ground).

Technique 0 (mouth manipulation) was significantly associated with small items on the platform (Binomial ad hoc test, $p < 0.001$) while technique 1 (associated with PCG) was significantly associated with cooked rice (on the grid and the platform) (Binomial ad hoc tests, $p < 0.001$). Technique 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. Technique 3 (associated with TL) was predominant especially for small items (Binomial ad 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 ad hoc test, $p < 0.001$) and the platform (Binomial ad hoc test, $p < 0.010$). Technique 4 (associated with PMG, MFM and OG) was significantly associated with cooked rice on the platform (Binomial ad hoc test, $p < 0.001$). Grid manipulations (all items) were also well represented in this technique 4 (PMG, MFM, and OG) but the difference was not significant. Finally, cooked rice was more frequently manipulated using techniques 1 (at the grid) and 4 (at the grid and on platform), large items were more frequently manipulated with technique 3/TL (at the grid and on platform) and small items with technique 0/mouth (on platform) and technique 3/TL (on all substrates) (Table 1).

3.3.2 | Handling score and manipulative effectiveness according to the food items and the substrate

Handling score

Figure 3a shows how the handling score varied among item-substrate modalities (Kruskal–Wallis test: $\chi^2 = 328.15$, $df = 8$, $p < 0.001$). The large items manipulated at the grid required more manipulations than

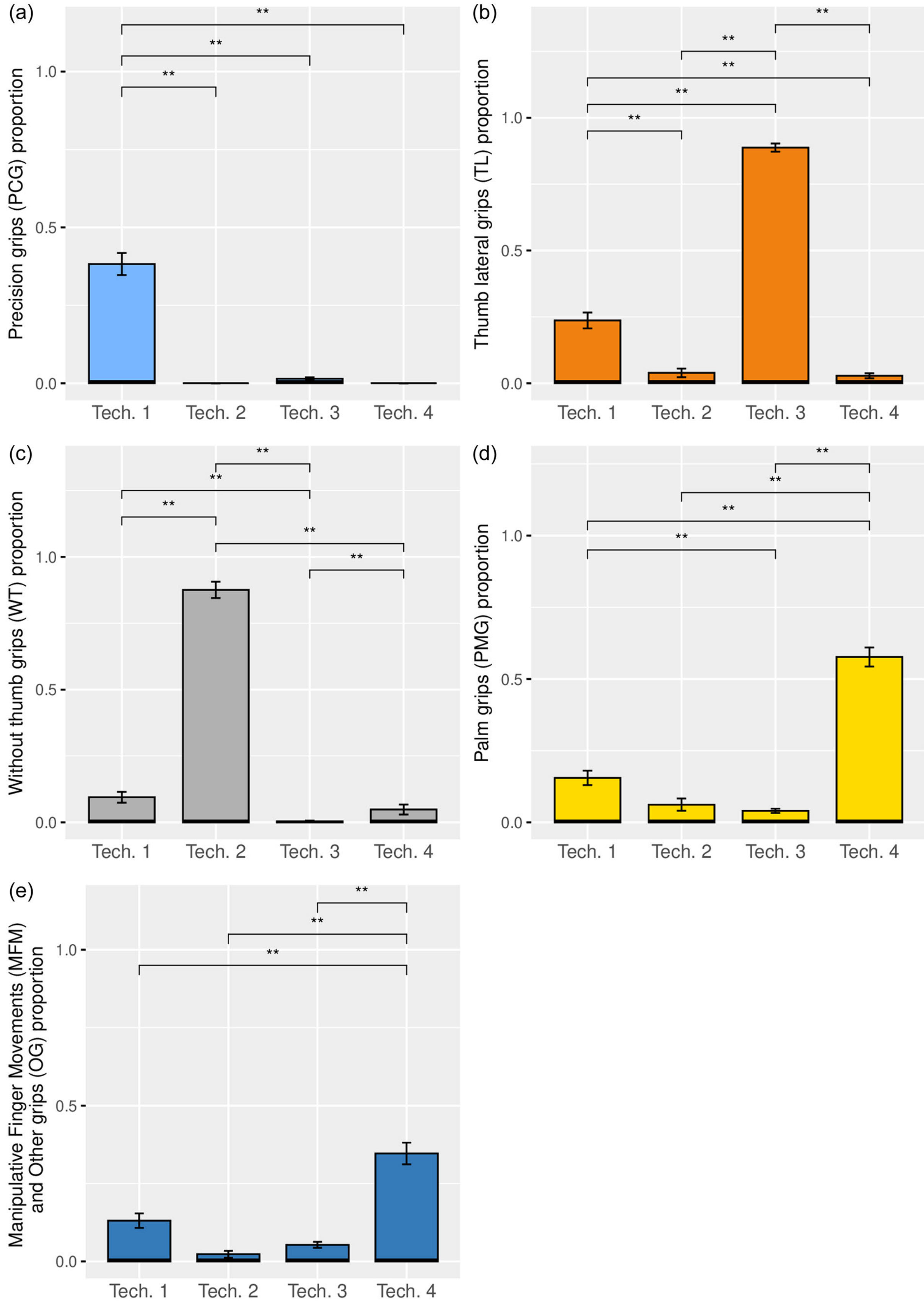

FIGURE 2 Barplots presenting the means of every grip category proportions (a: PCG; b: TL; c: WT; d: PMG; e: MFM) in the sequences of each manipulative technique (from 1 to 4). (Wilcoxon's rank sum test with Bonferroni continuity correction, $^{**}p < 0.001$. Error bars represent standard error of the mean (SEM)). (N technique 1 [PCG] = 183 sequences, N technique 2 [WT] = 64 sequences, N technique 3 [TL] = 309 sequences, N technique 4 [PMG, MFM and OG] = 79 sequences).

TABLE 1 Detailed distribution of the manipulative techniques in each item-substrate modality.

Item-substrate modality	Multinomial test	Technique 0 (mouth)	Technique 1 (PCG)	Technique 2 (WT)	Technique 3 (TL)	Technique 4 (PMG, MFM and OG)	Total
Rice-grid	$p < 0.001$	*1*	**48**	*0*	*7*	12	68
Rice-platform	$p < 0.001$	*0*	**44**	*2*	*3*	**38**	87
Rice-ground	ns	0	3	2	1	1	7
Small-grid	$p < 0.001$	*0*	13	13	**40**	10	76
Small-platform	$p < 0.001$	**128**	*14*	*12*	**140**	*1*	295
Small-ground	ns	1	56	29	89	1	176
Large-grid	$p < 0.001$	*1*	4	5	**21**	14	45
Large-platform	$p < 0.05$	0	0	1	**5**	2	8
Large-ground	ns	0	1	0	3	0	4
Total		131	183	64	309	79	766

Note: Exact multinomial and binomial ad hoc tests: number in bold are significantly higher than a homogeneous distribution, number in italic are significantly lower, $p < 0.05$.

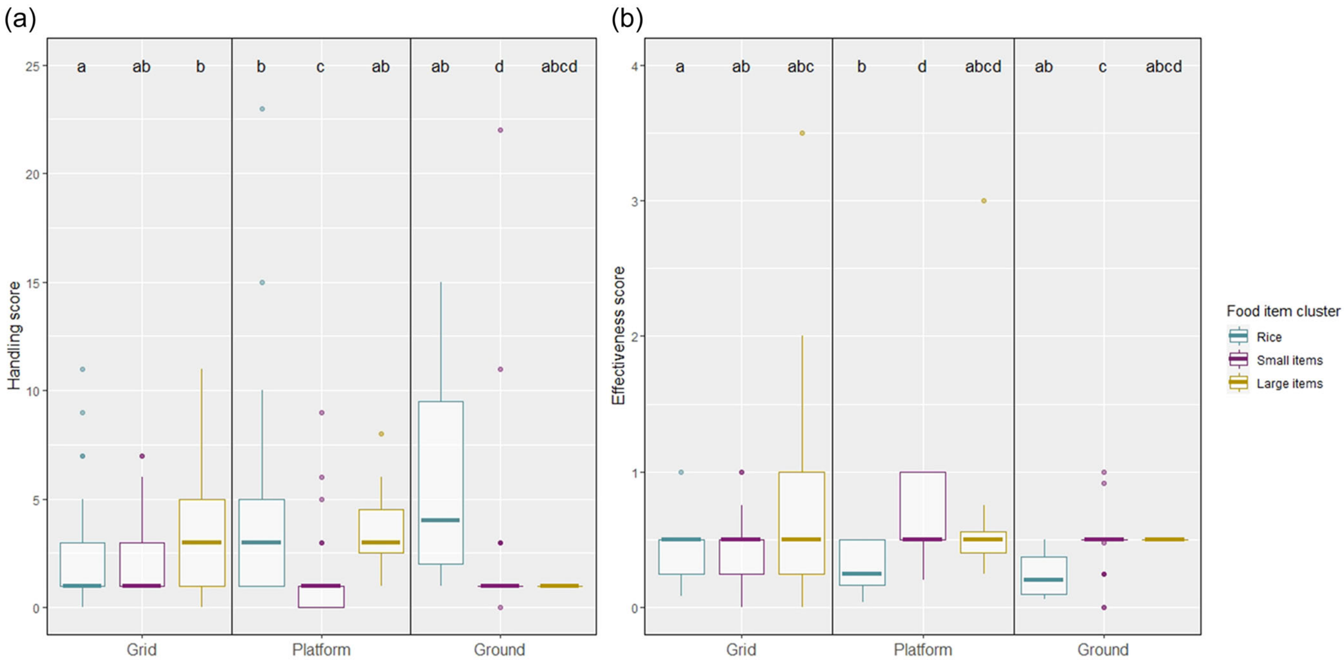

FIGURE 3 Boxplot representing the handling score (a) and the effectiveness (b) of the sequences in each of the item-substrate modalities (Wilcoxon rank sum test with Bonferroni continuity; modalities that share a letter within and between substrate types do not differ significantly, on average, from each other: $p < 0.05$). Bold horizontal bars represent median values.

other items: the difference was significant when compared with the cooked rice at the grid (Wilcoxon's test, $p = 0.034$), and to the small items on the platform (Wilcoxon's test, $p < 0.001$) and on the ground (Wilcoxon's test, $p < 0.001$). Large items were more rarely manipulated on the ground ($N = 4$ sequences/57 involving large items) and on the platforms (N = 8/57 sequences). On these two substrates, the differences of the handling score between the large items and the others were not significant (*i.e.*, no difference or too small class size). Only the handling score of the large items manipulated on the platform was significantly higher than for 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 with the small items on the platform (Wilcoxon's test, $p < 0.001$ for the three substrates) and on the ground (Wilcoxon's test, $p < 0.001$ for the three substrates). The handling score appeared lower at the grid than on the platform (Wilcoxon's test, $p = 0.014$) for this item (Figure 3a).

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

Manipulative effectiveness

The manipulative effectiveness was significantly different between some item-substrate modalities (Kruskal–Wallis test: $\chi^2 = 254.94$, $df = 8$, $p < 0.001$) (Figure 3b). The effectiveness was lower for cooked rice whatever the substrate compared with the small items on the platform (Wilcoxon's test, $p < 0.001$ for the three substrates) and on the ground (Wilcoxon's test, $p < 0.001$, for the three substrates). A lower effectiveness was also observed on the platform compared with the grid (Wilcoxon test, $p = 0.009$).

Manipulation of large items at the grid was less effective than the manipulation of the small items on the platform (Wilcoxon's test, $p = 0.005$) 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 manipulation of cooked rice (except at the grid where the difference is not significant) and also more effective than manipulation of large items on the grid (except at the grid and on the ground where the differences are not significant; Figure 3b). We also observed a difference in the manipulation of small items, being less effective at the grid versus platform (Wilcoxon's test, $p < 0.001$) and ground (Wilcoxon's test, $p < 0.001$), while effectiveness was lower on the ground than on the platform (Wilcoxon's test, $p < 0.001$).

4 | DISCUSSION

The use of innovative methodologies (*i.e*., the sequential analysis by optimal matching the handling score and the effectiveness score) allowed us to study food manipulation as a dynamic process in zoo-housed bonobos. Our results validate our hypotheses that the use and effectiveness of different manipulative techniques are dependent on the environmental context and the physical characteristics of food items. The following discussion details the implications of our findings with regard to the behavioral flexibility, depending on the decision-making context.

4.1 | Manipulative techniques

Our first hypothesis was that bonobos have different manipulative techniques adapted to the physical properties of the food and the environmental context (*i.e*., substrate). First, our results showed that bonobos could use different manipulative ways to gain access to food. The use of pedal grasping postures did not constitute a specific technique in this study and only occurred rarely but it was necessary to consider it in our analysis as an integral part of the manipulative process, in the same way as rare manual postures. Our hypothesis was confirmed since some manipulative techniques were significantly more frequently used for one or several kinds of food, according to the substrate used for stabilizing the body during feeding. Cooked rice was more frequently manipulated using technique 1/PCG (at the grid) and 4 (at the grid and on platform), large items were more frequently manipulated with technique 3/TL (at the grid and on platform) and small items with technique 0/mouth (on platform) and technique 3/TL (on all substrates).

The results showed a trend to manipulate cooked rice preferentially using *Palm grips*, *Manipulative Finger Movement* or *Other grips* (technique 4) used alone or in association with *Precision grips* (technique 1) when the substrate was 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 tubes by hitting it on the ground or on the platform (*Palm grips*), by probing with their fingers (*Manipulative Finger Movement*) or by using a tool (*Precision grips* and *Other grips* for storage, *i.e*., keeping a tool in the hand or foot without using it) (Figure 1). The two last cases are bimanual manipulation as it required to stabilize the tube with the other hand (*Palm grips* or *Other grips* categories).

The *Without thumb grips* (technique 2) and *Thumb lateral grips* (technique 3) were less specific to one kind of food or substrate. In contrast, manipulation with only the mouth (technique 0) occurred 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 as suggested in the study of Christel et al. (1998) in which grasping small objects on a cleaner ground required less time than on grassy/sandy ground.

Our result show that the manipulative technique can differ between the substrates for the 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 techniques were strongly associated with some modalities of item and substrate (*e.g*., technique 1/PCG for the rice manipulated at the grid for instance), we observed different manipulative techniques for the same item-substrate modality. This result is consistent with both the stability and variability showed in Borel et al. (2017) where the subjects modified their technique to find new solutions to perform a tool-task when experimental parameters were changed. These results show that in hominids, manipulative abilities are not only depending on the size and diversity of the repertoire but also on its flexibility of use and adaptability to different situations.

4.2 | A trade-off between complexity and gain

Our second hypothesis was that the physical parameters of the manipulated food and the substrate influence the handling score (*i.e*., the complexity of manipulation based on the number of distinct manual postures used and the number of manual posture changes during a feeding sequence) and the effectiveness (*i.e.*, the food intake related to the manipulative investment). We considered that a food that is complex to manipulate and requires many changes of manual postures could be less interesting than a food that requires few manipulations. Our results showed that 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 investment and the food intake, trade-off that could also relate to nutrient or energy intake, but we did not consider these parameters in this study. It may be as efficient to process many small items (*i.e.*, multiple lower investment) with many low intake ratios as to manipulate few large items (*i.e.*, higher investment) with a high intake ratio.

The lower effectiveness for the manipulation of the tubes containing cooked rice on the platforms compared with the grid can be explained by the fact that the individuals at the grid tended to stabilize the enrichment device rather than turning it and hitting it on a surface like on the platforms. The handling score was lower at the grid but the number of mouthfuls remained the same on the two substrates so the effectiveness was higher on the platforms. We did not observe any difference in effectiveness between the different substrates for the large items. This finding 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 (i.e., suspended body posture and passage of the food through the bars of the grid) would not be compensated by the low number of mouthfuls. This structure on the top of the cages and the distribution of large foods on it then appears to be an effective enrichment by extending the time spent for processing foods (Yamanashi & Hayashi, 2011). A lower effectiveness is also observed on the ground compared with 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%, Table 1). 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 substrate making manipulation simpler (stability and rarity of dirt and sand). 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).

This study didn't take into account the interindividual variability in the size of the mouthfuls. Our calculation of the effectiveness score could be biased by smaller mouthfuls, in juveniles for instance. But the precise classification of the food items, based on their size, is thought to limit that bias. Competition, with the presence of other individuals within immediate vicinity, could also induce variability in this score. These two limitations could participate to explain the variability of manipulative techniques observed in the same item-substrate modality.

4.3 | How to choose a manipulative technique?

The use of one specific technique by an individual bonobo is presumed to enhance the access to the targeted food. The variability observed in the choice of the manipulative technique for each item and substrate, and the effectiveness of the chosen technique 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 sources of information, both ecological (food type and quantity, traveling 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 techniques. From the few studies available about decision-making process in bonobos, we know that compared with 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-housing, where the intragroup competition is high and the food is available only when distributed, 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, and avoidance of risk could be enhanced. The individual parameters also are of critical importance in this decision process, as suggested by the interindividual differences found in previous manipulative studies in zoo-housed 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 choices in chimpanzees during periods of high diet quality; Gilby & Wrangham, 2007), age, sex, and/or social status could induce different manipulative techniques for a given food item. Moreover, 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). The experience of subject has also been shown to enhance consistency and accuracy of tool task in human (Borel et al., 2017). Further studies will need to incorporate not only the ecological context but also the individual and social parameters, as they seem to influence manipulative techniques.

5 | CONCLUSION

In this study, we identified several manipulative techniques depending on the manipulated food and the environmental context. Variability in manipulative techniques for a given food and substrate 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 techniques within the whole ecological and social context. 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 by investigating manipulation as a more complete dynamic process. Our results bring new information contributing to our understanding of the evolution of manual abilities in primates in association with different ecological contexts and both terrestrial and arboreal substrates.

AUTHOR CONTRIBUTIONS

Caroline Gérard: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); project administration (supporting); writing—original draft (lead); writing—review and editing (lead). **Ameline Bardo**: Conceptualization (supporting); methodology (supporting); supervision (equal); validation (equal); writing—original draft (equal); writing—review and editing (equal). **Jean Pascal Guéry**: Resources (lead). **Emmanuelle Pouydebat**: Conceptualization (supporting); funding acquisition (equal); supervision (supporting); writing—review and editing (supporting). **Victor Narat**: Conceptualization (equal); funding acquisition (equal); methodology (supporting); project administration (lead); supervision (equal); validation (equal); writing—original draft (equal); writing—review and editing (equal). **Bruno Simmen**: Conceptualization (equal); funding acquisition (equal); methodology (supporting); supervision (equal); validation (equal); writing—original draft (equal); writing—review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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