Food Prehension and Manipulation in *Microcebus murinus* (Prosimii, Cheirogaleidae)

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Key Words

Primate · *Microcebus murinus* · Grasping · Repositioning · Evolution · Feeding

Abstract

Among primates, apes and monkeys are known to use their hands and to exhibit independent control of their fingers. In comparison, Prosimii are thought to have less digital individualization and to use their mouth more commonly for prehension. Unfortunately, prehension and manipulation studies in Prosimii have been conducted in conditions constraining the subject to grasp with the hand. Moreover, the effect of food size remains unexplored, even though it could affect the use of the hands versus the mouth. Thus, whether prosimians use the hand or the mouth to grasp and manipulate food items of different sizes in unconstrained conditions remains unclear. To address this question, we characterized the eating and manipulation patterns of *Microcebus murinus* in unconstrained conditions, using three food sizes. The results showed that *M. murinus* showed (i) an eating pattern similar to that of rodents, with smaller food items being grasped with the mouth, (ii) a greater tendency to use the hands for prehension of larger foods, and (iii) plasticity during food manipulation similar to that which has been observed in rodents. These results are discussed in the framework of grasping in mammals and are used to discuss the origins of prehension in primates.

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Introduction

Tetrapods employ three major modes of food grasping in terrestrial and arboreal environments: lingual, mouth and/or hand prehension [Iwaniuk and Whishaw, 2000; Schwenk, 2000]. Among primates, apes and numerous monkeys (in the subfamily Cercopithecinae and the genus *Cebus*) are known to use their hands for grasping food using various grip postures. Moreover, they are known to exhibit a degree

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of independent control of the fingers [Christel, 1993, 1994; Byrne et al., 2001; Frigaszy et al., 2004; Spinozzi et al., 2004; Macfarlane and Graziano, 2009; Pouydebat et al., 2009] and to manipulate tools [Boesch and Boesch, 1990; Van Schaik et al., 2003; Fragaszy et al., 2004; Pouydebat et al., 2005; Visalberghi et al., 2009]. In comparison, Prosimii (lemuriforms and loriforms) are thought to be less variable in grip posture, to show no digital individualization and to use the mouth for grasping more often [Bishop, 1964]. In order to grasp static foods, the lemuriforms appear to prefer to grasp with the mouth as shown both by observations in the wild [Petter, 1962] and studies on manual preference [Larson et al., 1989; Ward et al., 1990; Milliken et al., 1991a; Dodson et al., 1992; Ward and Hopkins, 1993; Ward, 1995; Leliveld et al., 2008; Nelson et al., 2009; Scheumann et al., 2011]. However, these studies on manual preference often adopted protocols forcing the subjects to take static food through a wire mesh or a slot with their hand. In contrast, in order to grasp mobile prey and during manipulation, the hand seems to be used spontaneously. For example, the specialized aye-aye (*Daubentonia madagascariensis*) is known to use the third finger to pry insects from holes in tree trunks or branches [Erickson, 1991, 1994; Milliken et al., 1991b; Erickson et al., 1998]. In addition, Galagidae and Cheirogaleidae catch insects with one or both hands [Bishop, 1964; Martin, 1972; Charles-Dominique, 1977; Hladik, 1979; Lemelin, 1996] as do several loriforms [Oates, 1984; Nekaris, 2005]. Finally, other studies have described variation in hand manipulative capacities in lemurs [Jolly, 1964; Sussman and Tattersall, 1976; Sussman, 1977; Torigoe, 1985; Schöneich, 1993].

However, even though several studies have analysed grasping and manipulative patterns in Prosimii, they were often conducted in conditions constraining the subject to grasp with the hand. Moreover, these studies did not test different sizes of food, although this could affect the use of the hand versus the mouth, raising the question of whether prosimians use the hand or the mouth to grasp and manipulate foods of different sizes in unconstrained conditions. To address this question, we quantified the grasping and manipulative patterns in the lemuriform *Microcebus murinus* in unconstrained conditions, using three sizes of static food. The small, arboreal, nocturnal *M. murinus* is one of the most distantly related primates to humans (fig. 1), and it is suggested that it represents the most ancient ancestral primate condition [Martin, 1972; Scheumann et al., 2011] and thus to possess a prehensile pattern which is phylogenetically conservative [Bishop 1964]. Therefore, this species is of particular interest in assessing the origins of grasping in primates. Our results are discussed with those obtained from other primates and mammals (rodents, carnivores, marsupials) and may contribute to the understanding of the origins and evolution of grasping and manipulation in primates.

Material and Methods

Animals and Husbandry

The mouse lemur *M. murinus* (Miller, 1777) is nocturnal and endemic to Madagascar. It is characterized by its small size (mass: 95.5 ± 15.7 g; snout-tail length: 24.5 ± 2.08 cm) and its quadrupedal arboreal locomotion along fine terminal branches [Napier and Napier, 1967].

Four adult males (2–3 years old) were housed individually in $100 \times 50 \times 30$ cm enclosures with branches and a wooden nest box (fig. 2). The cages were placed in a maintenance room recreating natural environmental conditions: (i) a 12-hour light/dark cycle, (ii) ambient tem-

Fig. 1. Primate phylogeny (based on Groves [2001]): Catarrhini [Christel et al., 1994; Pouydebat et al., 2008; MacFarlane et al., 2009], Platyrrhini (the capuchin is alone in using the precision grip among this group) [Fragaszy et al., 2004; Spinozzi et al., 2004; Pouydebat et al., 2009], Tarsiiformes [MacKinnon and MacKinnon, 1980; Niemitz, 1984; Lemelin, 1996], Lorisiformes [Bishop, 1964; Oates, 1985; Nekaris, 2005], and Lemuriformes [Bishop, 1964; Charles-Dominique, 1977; Lemelin, 1996; Lemelin and Jungers, 2007]. PG = Use of the precision grip (between index and thumb); WHG = use of the whole-hand grip (between all the fingers and the palm); m = some use of the mouth; M = considerable use of the mouth.

Fig. 2. Experimental set-up. **a** *M. murinus* on the platform, with front view (**b**), lateral and dorsal view (**c**) and ventral view (**d**). **e** Diagram of the Plexiglas enclosure used for the experience.

perature of 24–26°C and (iii) 55% relative humidity. The animals received fruits, insects and water ad libitum [Genin and Perret, 2003]. All data were obtained in unconstrained conditions. The daily recording sessions occurred at the beginning of the activity period of individuals in low light levels, lit by a dim red light (20 mW/cm², equivalent to 0.002 lx) not perceived by the animals yet allowing us to film using a digital camera at 50 Hz (Sony, ×40 Digital Zoom, Carl Zeiss, Vario Sonnar). During each session, a cube of apple was placed on a Plexiglas platform. Three sizes of food (size 1: 0.5 × 0.5 × 0.5 cm, size 2: 1 × 1 × 1 cm, size 3: 2 × 2 × 1.5 cm) were offered in different instances. The data were quantified from video recordings obtained with the camera filming three mirrors inclined at 45° allowing us to obtain simultaneous lateral, dorsal, ventral and frontal views (fig. 2). Each animal was food deprived for 24 h before filming. The weight of the animals was regularly controlled, and additional food was provided after filming to avoid any experimental effect on the mass of the animals. The research adhered to the legal requirements of the European Union.

Table 1. Abbreviations and definitions of the qualitative and quantitative variables analysed during food prehension and manipulation by *M. murinus*

Variables	Type of event	Definition
<i>Qualitative</i>		
1H	Grasp	One hand contact without mouth
2H	Grasp	Both hands contact without mouth
M	Grasp	Mouth contact alone
1HM	Grasp	One hand and mouth contact
2HM	Grasp	Both hands and mouth contact
<i>Quantitative</i>		
RepDGr	Food lift	Number of hand repositioning events during the grasp
RepAGr	Manipulation	Number of hand repositioning events after the grasp

Behavioural Analyses

A series of more than 25 feeding sessions was recorded for each individual. Seven variables were measured during prehension and manipulation events (table 1). The grasp and the lift of the food involved the following grip categories: one hand, both hands, mouth alone, and both mouth and hand(s). The hand manipulations were quantified using two variables: the number of hand repositionings on the food during the grasp (i.e. these manipulations adjusting the food position in order to grasp and lift it) and the number of hand repositionings after the grasp, during the initial chewing.

Statistical Analyses

First, the G test was used to test the effect of food size and individual on grasping strategies (one hand, both hands, mouth, one hand and mouth, both hands and mouth) [Sokal and Rohlf, 1995]. Second, the non-parametric Kruskal-Wallis (KW) test was used to explore the effect of food size and individual, on the number of hand repositionings during and after the grasp. Multiple comparisons were implemented using the `kruskalmc` function [Siegel and Castellan, 1988] of the `pgirmess` R package to specify which variable combinations showed significant differences. Statistical significance was set at 0.05.

Results

General Feeding Session

For the two larger food sizes, a complete feeding session included 6 successive phases (fig. 3): (1) the food was sniffed, (2) the mouth and the hand approached the food, or the mouth alone approached the food with the hand remaining on the substrate, (3) the food was grasped by one or two hands, by the mouth alone or by both, (4) during the grasp, the first sequence of hand repositioning occurred in order to seize the food correctly and lift it, (5) the food was lifted by both hands and mouth, the animal straightened the trunk, sat down or adopted a bipedal or tripodal posture, then (6) the second sequence of hand repositioning occurred during eating. When handling food items of smaller size, some differences were observed (fig. 4). There was no hand repositioning during the grasp, and the lift of the food always occurred with the mouth alone.

Fig. 3. Lateral view of food prehension and manipulation in *M. murinus* (intermediate food size): hand grip (**a**), mouth grip (**b**). T0 = First contact with the mouth or the hand. Black scale bar = 5 cm.

Prehension Strategies and Effect of the Food Size

Before a mouse lemur left the nest box, it always started by turning its head in the direction of the food, then jumped outside toward the food and advanced its head close to the food before grasping it. During the reaching phase, the forelimb advanced while pronated or semisupinated. The fingers were adducted and placed under the wrist. When the hand approached the food, the fingers showed a progressive opening until maximum abduction, followed by a gradual closure to the grasp. This classic biphasic grip (fig. 3) involved a flexion-extension of the metacarpophalangeal, interphalangeal and wrist joints, and an abduction-adduction of the fingers. The hand grasping itself involved a whole-hand grip by one or both hands. During the mouth grasping strategy (fig. 3, 4), the head advanced and the mouth displayed a maximal opening to seize the food. Finally, the grasping strategy concerning both hand(s) and mouth presented a combination of the two previous behaviours.

The statistical analyses showed an effect of food size on grasping strategies ($G = 46.30$, χ^2 d.f. = 8, $p < 0.001$) but no interindividual variability ($G = 9.78$, χ^2 d.f. = 12, $p = 0.64$). Indeed, all the individuals used only the mouth to grasp the small food (size 1), in contrast to the larger food samples (sizes 2 and 3) which involved use of the hand in a greater proportion in addition to several grip postures (table 2). No significant differences in grasping strategy between the intermediate and the large size food items were detected ($G = 5.84$, χ^2 d.f. = 8, $p = 0.66$). However, the grips involving one hand without the mouth represented 45% of the grip used for the inter-

Fig. 4. Lateral view of food prehension and manipulation in *M. murinus* (small food size). T0 = First contact with the mouth. White scale bar = 5 cm.

mediate food size (size 2) versus 75% for the large food size (size 3). Finally, the use of the mouth alone decreased with an increase in food size (small size: 100%, intermediate size: 35%, large size: 10%) and the bimanual grip was rarely used in comparison to the unimanual grip (table 2).

Repositioning Strategies

The hand and finger movements contributed to grasping the food firmly, lifting and manipulating it during eating. In the first sequence of hand repositioning (during gripping), the food was still in contact with the substrate (fig. 5). The hands were placed alternatively in pronation on the superior face of the food and in semisupina-

Fig. 5. Lateral view of a food repositioning in *M. murinus* (large food size): repositioning before the grasp (**a**) and repositioning after the grasp (**b**). T0 = Beginning of a food repositioning. Black scale bar = 5 cm.

Table 2. Proportions (%) of the different behavioural strategies used during food grasping by *M. murinus*

Grasping strategy	Size 1	Size 2	Size 3
One hand	–	45	75
Two hands	–	10	10
Mouth and one hand	–	5	5
Mouth and both hands	–	5	0
Mouth alone	100	35	10

tion on the vertical face of the food. We noted that the food size, but not the individual, had an effect on the number of hand repositioning events (size: KW = 43.05, d.f. = 2, $p < 0.001$; individuals: KW = 1.44, d.f. = 3, $p = 0.69$) as the smallest food items were grasped with the mouth and the two others manipulated by the hands (fig. 3–5).

In the second sequence of hand repositioning (after gripping), the movements and postures of the hands and fingers were more variable. *M. murinus* exhibited unimanual or bimanual behaviours to hold small-sized items and bimanual behaviours for larger-sized items. The hands were placed below the food in supination or in semisupination (fig. 3–5). There was neither a food size nor an individual effect on the number of hand repositioning events (size: KW = 1.31, d.f. = 2, $p = 0.51$; individual: KW = 3.87, d.f. = 3, $p = 0.27$).

Discussion

This study addresses the question whether in unconstrained grasping conditions, *M. murinus* uses its hands or mouth to grasp and manipulate foods of different sizes.

When grasping small food items, *M. murinus* exhibited an eating pattern close to that observed for rodents. Indeed, both rodents and *M. murinus* sniff the food, grasp it with the mouth alone, sit down most of the time and then hold the food between their hands. This grasping behaviour has been described by Whishaw et al. [1998] using the term 'rodent-common eating pattern'. *M. murinus* differed from other primates, from the most skilled carnivorous mammals (raccoon, kinkajou) [MacClearn, 1992; Iwaniuk and Whishaw, 1999], carnivorous marsupials (opossum, glider) [Ivanco et al., 1996; Landy, 1997] and two rodent species (gerbil and beaver) [Whishaw et al., 1998] which most of the time use unimanual grips when confronted with small static food items.

During the grasping of larger food items, the hands were used extensively by *M. murinus*. During the reaching phase, the hand showed the biphasic grip already described for other primates and rats when constrained [Jeannerod, 1984; Christel and Frigaszy, 2000; Roy et al., 2000; Christel and Billard, 2002; Sacrey and Whishaw, 2009]. In addition, *M. murinus* essentially exhibited a whole-hand grip between the palm and all the fingers and preferred one hand in its first contact with the food. Therefore, the mouth was not always involved in the process of static food grasping, in contrast to what has been reported previously [Bishop, 1964; Dodson et al., 1992; Ward and Hopkins, 1993; Scheumann et al., 2011]. The nature of the food and the omnivorous diet of *M. murinus* may be linked to the degree of hand use. Indeed, *M. murinus* is known to catch mobile prey using its hands in the wild. However, the static food items offered in this study elicited the use of both mouth and hands, yet are less frequently eaten in the wild [Martin, 1972; Charles-Dominique, 1977; Hladik, 1979; Lemelin, 1996].

Our results can also be discussed in the context of food detection. Indeed, *M. murinus* moved its head close to the food in all the hand grasping strategies, prior to any limb movements, as has been previously observed for raccoons [Iwaniuk and Whishaw, 1999], gerbils and beavers [Whishaw et al., 1998]. Several factors can explain this behaviour such as its quadrupedal posture, the vertical orientation of the trunk and the nocturnal activity involving a well-developed olfactory sense typical of *M. murinus* [Epple and Moulton, 1978; Schilling, 1979; Siemers et al., 2007]. In addition to the use of olfaction, *M. murinus* seemed to use visual cues to detect food, as previously suggested [Piep et al., 2008]. Indeed, before leaving the nest, the lemur turned its head in the direction of the food. This visual detection of food in this species sets it apart from many rodents which invariably locate and reach their food by sniffing [Whishaw and Tomie, 1989; Whishaw et al., 1998; Hermer-Vazquez et al., 2007].

During food repositioning, *M. murinus* exhibited unimanual and bimanual behaviours involving the mouth as has been observed for other primates [Torigoe, 1985, 1987; Crast et al., 2009] and rodents [Whishaw et al., 1998] during object and food manipulation. In addition, this lemur shared characteristics with rodents during manipulation [Whishaw and Coles, 1996; Whishaw et al., 1998; Ballermann et al., 2000]. The movements of the fingers were convergent, abducted or adducted and placed on different parts of the food to orient a corner of the food item into the mouth. This differs from behaviours in carnivores (except the kinkajou) which essentially roll static foods between the palms of both hands and hold it with the fingers parallel [MacClearn, 1992; Iwaniuk and Whishaw, 1999].

Finally, in comparison to apes and numerous monkeys, the diversity of hand postures used by *M. murinus* was relatively low when holding small objects. *M. mu-*

rinus always showed a whole-hand posture, whereas other primates use two or three fingers [Elliott and Connolly, 1984; Torigoe, 1987; Fragaszy and Adams-Curtis, 1991; Exner, 1992; Byrne et al., 2001; Braidó and Zhang, 2004; Crast et al., 2009]. In contrast, the body posture of *M. murinus* was more variable than observed in rodents, alternating between crouched, tripedal or bipedal postures as in other primates. It will be interesting to test the effect of the food properties (forms, textures, mobility) on the variability in grasping and manipulative strategies in *M. murinus*, similar to what has been done in rats and primates [Ivanco et al., 1996; Whishaw and Coles, 1996; Crast et al., 2009; MacFarlane et al., 2009; Pouydebat et al., 2009] in order to enrich future discussions on the evolution of grasping and manipulation in mammals.

Conclusion

This study quantified the grasping and manipulative patterns in the lemuriform *M. murinus*, in unconstrained conditions using three sizes of food. We found that its grasping, manipulation and detection strategies share common characteristics with both rodents and primates. Indeed, its greater use of the hand than expected and its visual food detection are characteristic of primates. In contrast, the mouth grasping and hand repositioning behaviours in *M. murinus* are more similar to those observed in rodents. This intermediate position of *M. murinus* supports the hypothesis that rodents and primates share a common ancestral pattern of motor action of skilled forelimb movement [Whishaw et al., 1998]. However, these assumptions remain to be tested by additional experimental observations taking into account the context (in unconstrained feeding conditions), and the intrinsic (shape, texture, mobility) and extrinsic (function) properties of the food.

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