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How Aging Affects Grasping Behavior and Pull Strength in Captive Gray Mouse Lemurs (*Microcebus murinus*)

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Abstract Prehension is essential for animal survival and fitness. It is involved in locomotion and feeding behavior and subject to physical and physiological constraints. Studies of prehension in primates have explored the importance of food properties and of the environment, but aging has rarely been studied although prehensile capacity may deteriorate with age in humans. To test the hypothesis that aging affects grasping abilities and to reveal possible behavioral adaptations to this, we quantified behavioral grasping strategies and pull strength in 10 young adult (2–3 yr old) and 10 aged (7–8 yr old) gray mouse lemurs (*Microcebus murinus*). We assessed grasping strategies in an experimental cage by quantifying grip types used to grasp static and mobile foods. We measured strength using a Kistler triaxial force platform. Our results show that 1) mobile and static foods affected individuals of different ages in similar ways; 2) older individuals used more mouth grasps than young ones; 3) aged individuals made twice as many attempts as young ones when grasping mobile food items but this difference was not significant; and 4) there were no differences in hand grip strength between age classes but young individuals showed a higher foot pull strength compared to old ones. These data suggest that the observed differences in behavior may be due to a decrease in foot grip strength, which in turn influences stability on narrow branches, forcing animals to use their hands to maintain stability and preventing them from using their hands for food-related tasks.

Keywords Aging · Food grasping · Grip strength · *Microcebus murinus* · Prehension

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Introduction

Prehension is defined as the ability of an organ to grasp, catch, or hold an object, prey, congener, or substrate, and involves different strategies depending on the species (Sustaita *et al.* 2013). Among primates, manual and pedal prehension is typically thought to have evolved in an arboreal context. Moving on narrow branches requires the use of prehensile organs for climbing and locomotion on thin branches (Cartmil 1974). According to recent studies, manual prehension is also involved in food handling and may have a separate evolutionary origin from the reaching involved in stepping motions (Karl and Whishaw 2013). Primates use prehension to capture prey, transfer food to the mouth, and in tool use (Pouydebat *et al.* 2006). For example, chimpanzees (*Pan troglodytes*) use twigs to catch termites and during communication and social activities such as grooming (Kapandji 1989).

Prehension in primates may involve different postures of the prehensile organ depending on its use and the species studied (Pouydebat *et al.* 2011; Spinozzi *et al.* 2004). Primates also use different modes of prehension, e.g., the use of the mouth vs. the hands or the use of both simultaneously have been documented in the gray mouse lemur (*Microcebus murinus*: Toussaint *et al.* 2013). Skeletal muscle mass, density, and function decline with age in small-bodied primates (Hämäläinen *et al.* 2015). This atrophy is likely due to a reduction of the number of functional motor units, as has been shown in humans (Campbell *et al.* 1973). Moreover, the loss of muscle mass in humans affects the forces exerted on bones, thus reducing their mechanical resistance and increasing their fragility (Parfitt *et al.* 2000).

This study focuses on changes in food prehension patterns with age in the gray mouse lemur, a small primate studied in the context of aging (Languille *et al.* 2012; Pifferi *et al.* 2013). We studied food acquisition strategies in a behavioral task with static or mobile food items. We also measured pull strength as a possible proximate explanation for differences in grasping behavior. We hypothesized that food acquisition strategies will change with age because of reduction in strength. In particular, we predicted that aged individuals will use different grasping techniques and will preferentially use their mouth for grasping. Moreover, we predicted that aged individuals will show a higher failure rate than younger ones, especially for mobile food. In addition, if aged individuals show general sarcopenia, a significant decrease in muscle mass, then we predicted that they would show reduced strength in both hands and feet. Finally, we quantified hand and foot pull strength as the feet are hypothesized to play a role in body balance and may thus influence the grasping strategies (Toussaint *et al.* 2013). Pedal grasping is critical to climbing and balancing during locomoting on narrow substrates whereas manual grasping is not (Byron *et al.* 2011). Pedal grasping exercise in mice results in greater hallucal robusticity and pedal somatosensory representation (Byron *et al.* 2015). Thus, it has been hypothesized that pedal grasping without a manual component is the ancestral condition for primates (Byron *et al.* 2015).

Methods

Study Species

The gray mouse lemur is a lemuriform primate of the family Cheirogaleidae (Strepsirrhines). Nocturnal, tree-nesting, and omnivorous, it is one of the smallest species of primates (10–13 cm and 60–100 g), and is native only to the island of Madagascar. We studied individuals housed at the breeding colony of the National Museum of National History (Brunoy, FR, license approval no. E91–114-1). In captivity, gray mouse lemurs can live up to 12 yr and the average lifespan is ca. 5 yr (Perret and Aujard 2005). Aging is suggested by morphological changes at the age of 5–6 yr: bleaching of the fur, shortening of the snout, and a thickening of the border of the ear auricle (Languille *et al.* 2012). Our sample consisted of 20 individuals: 10 young adults from 2 to 3 yr old (5 males and 5 females) and 10 aged individuals from 7 to 8 yr old (6 males and 4 females). There is no effect of sex on pull strength in gray mouse lemurs (Thomas *et al.* 2016).

We studied the lemurs under summer conditions to avoid lack of motivation due to seasonal torpor. We separated individuals from the colony under summer conditions at standard temperature (24–26 °C) and relative humidity (55%). We housed subjects in groups of three in a cage of 1.3 × 1.0 × 0.08 m or individually in cages of 0.42 × 0.28 × 0.32 m equipped with wooden nest boxes, wooden branches, and litter on the floor. We fed subjects thrice weekly with pieces of fruit (apple and banana) and a mixture of concentrate milk, cereals, and egg. We provided water ad libitum.

Experimental Setup and Procedure

We assessed prehension strategies in an experimental cage. The apparatus consisted of a transparent Plexiglas enclosure of 51 × 25 × 26 cm with a lid on top, allowing the experimenter to introduce food (Fig. 1). The enclosure contained a wooden nest box above a horizontal substrate with a diameter of 0.8 cm. We placed the cage in front of a plain background to facilitate recording. We recorded behavior using a night shot camera (SONY Handycam DCR-SR75) placed in front of the largest side of the cage. We used a red light not perceived by the subjects to facilitate observations (Warrant 2008). We placed two kinds of food in the cage: mobile food and static food. Mobile

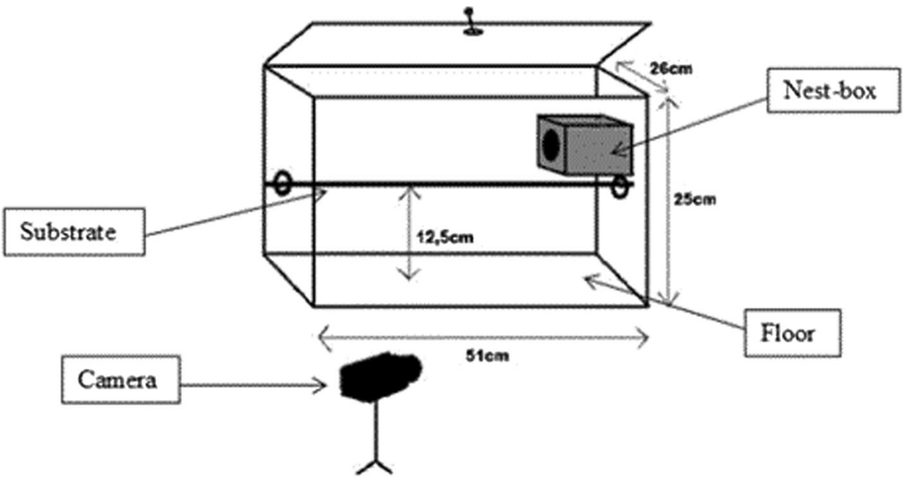

Fig. 1 Experimental cage used for recording grasping behavior in the gray mouse lemur, UMR (Unité Mixte de Recherche) 7179, Brunoy, France, 2016.

food items require greater use of the hand than static items (Toussaint *et al.* 2013). Food items were small pieces of banana with a volume of 1 cm^3, corresponding roughly to the surface area of the hand of the gray mouse lemur. We standardized size across trials because the size of food items influences the prehension mode (Pouydebat *et al.* 2009). Static food consisted of a piece of banana placed on the horizontal substrate opposite the nest box and at approximately the same distance in each trial. The mobile food item was a piece of banana suspended above the horizontal substrate, attached to the end of a fishing line allowing the experimenter to move the banana. Such mobile fruit influences gray mouse lemur grasping strategies in the same way as mobile prey (Toussaint *et al.* 2013, 2015).

We observed behavior during the night, which corresponds to the active period for gray mouse lemurs. We tested individuals one at a time in random order. We tested three individuals of the same age per day, testing each one two or three times a day according to satiety and motivation. Before each trial, we removed subjects from their nest box and put them into one of the experimental cages. We cleaned the nest box and the experimental cage between lemurs. We presented static and mobile food items randomly to avoid potential learning effects and tested both types in each trial. To motivate subjects, we withdrew food from their cage in the morning, and fed them again in the evening after the experiments. We performed 10 trials with each type of food for each individual. Each trial started when the first food item was placed in the cage and ended when the subject was back in the nest box after grasping the food item. We put the individual back in the nest box before introducing the second item.

Grasping Strategies and Failure

We analyzed videos with the software VLC media player to quantify grasping strategies. We characterized the 400 grip types adopted by individuals for each type of food using the body part(s) involved. We quantified each grip type used by each individual for all items grasped. We also quantified the number of attempts an individual made before successfully grasping a food item.

Pull Strength

We measured strength using a Kistler triaxial force platform connected to a charge amplifier and laptop computer (see Thomas *et al.* 2016 for a description of the setup). A metal bar was connected to a force plate, and individuals were allowed to grip the bar perpendicular to its long axis with their hands or feet. Next we pulled individuals backwards away from the bar until they released it. We extracted the peak strength in Newtons (N) using Kistler Bioware software.

Statistical Analyses

We present data as means and standard deviations and analyzed data using IBM SPSS V. 22 (IBM Corp., Armonk NY). We calculated the proportion of grip types for each individual and transformed them with an arcsin function to meet assumptions of normality and homoscedascity. We ran a full factorial MANOVA with age and food type as factors, and univariate ANOVAs to test whether grasping strategies differed between age classes. We Log_{10}-transformed performance traits, i.e., hand and foot pull strength) before analyses. We ran an ANOVA with age as factor to test for differences in hand and foot strength. We performed all statistics using an α-level of 0.05.

Results

Food Prehension Strategies

Subjects used five major grasping strategies for both types of food: prehension with the mouth only (the individual captures the food using the mouth only), bimanual grasping (the individual grasps the food with both hands at the same time without using the mouth), unimanual grasping (the individual uses one hand to grasp the food without using the mouth), and other modes combining mouth and hands (bimanual + mouth, unimanual + mouth).

Age Effects on Prehension Strategies

A MANOVA detected significant differences in the grip types used between age classes (Wilks' $\lambda = 0.46$; $F_{5,32} = 7.46$; $P < 0.01$) and food type (Wilks' $\lambda = 0.16$; $F_{5,32} = 32.85$; $P < 0.01$). The interaction effect was not significant (Wilks' $\lambda = 0.73$; $F_{5,32} = 2.83$; $P = 0.06$), suggesting that mobile and static foods affected individuals of different ages in similar ways (Figs. 2 and 3). Subsequent univariate ANOVAs showed that the age effect was significant for the proportion of mouth grasps ($F_{1,36} = 11.09$; $P = 0.002$) and the proportion of mouth + unimanual grasps ($F_{1,36} = 10.09$; $P = 0.003$), with older individuals using more mouth grasps and fewer unimanual + mouth grasps than young ones (Fig. 2). The effect of food mobility was significant for all variables except the proportion of unimanual grasps, which did not differ between static and mobile food items (Table I).

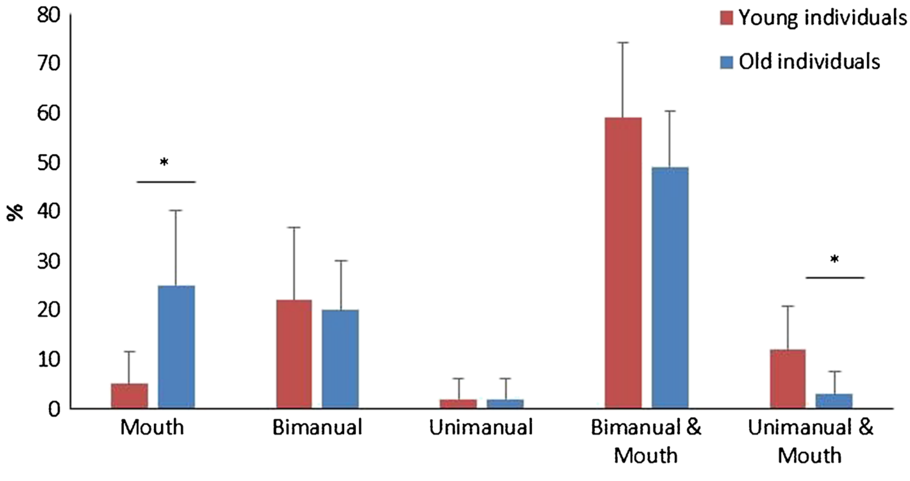

Fig. 2 Percentage of the total number of grasps observed when capturing static food items in which gray mouse lemurs used each of five prehension strategies ($N = 10$ grasps per individual; 20 individuals). Asterisks denote significant differences (see Table I). UMR 7179, Brunoy, France, 2016.

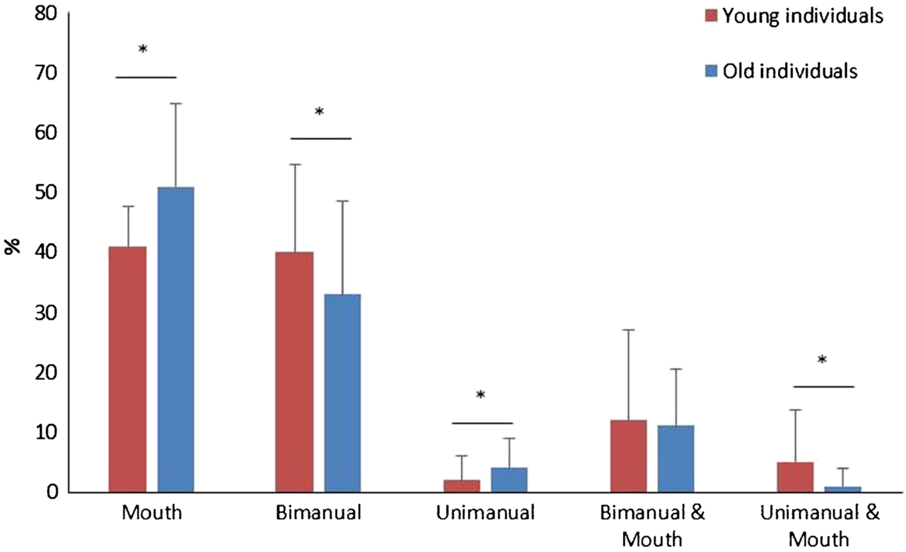

Fig. 3 Percentage of the total number of grasps observed when capturing mobile food items in which gray mouse lemurs used each of five prehension strategies ($N = 10$ grasps per individual; 20 individuals). Asterisks denote significant differences (see Table I). UMR 7179, Brunoy, France, 2016.

Table I Results of ANOVAs testing the effect of age class (young vs. old subjects), food mobility (static vs. mobile), and the interaction between the two on grip types used by gray mouse lemurs (*Microcebus murinus*; UMR 7179, Brunoy, France, 2016)

Tested parameters	*F*	df	*P*
Age class			
Mouth	11.09	1,36	0.002
Bimanual	0.96	1,36	0.331
Unimanual	0.50	1,36	0.482
Bimanual + mouth	2.18	1,36	0.152
Unimanual + mouth	10.09	1,36	0.003
Food mobility			
Mouth	44.55	1,36	<0.001
Bimanual	10.52	1,36	0.003
Unimanual	0.50	1,36	0.482
Bimanual + mouth	107.82	1,36	<0.001
Unimanual + mouth	4.84	1,36	0.034
Interaction of age class and food mobility			
Mouth	0.95	1,36	0.343
Bimanual	0.30	1,36	0.591
Unimanual	0.50	1,36	0.481
Bimanual + mouth	1.57	1,36	0.223
Unimanual + mouth	1.50	1,36	0.231

Age Effects on Failure During Mobile Food Grasping

Subjects needed more than one attempt to grasp a food item only during mobile food grasping. There was no significant difference in the failure rate with age (Wilcoxon rank sum test $W = 34.5$, $P = 0.05$), although aged individuals made 4 ± 1.3 attempts while young ones made 2 ± 0.9 attempts when grasping mobile food items.

Gripping Performance

An ANOVA detected no differences in hand grip strength between age classes ($F_{1,18} = 0.28$; $P = 0.61$). However, foot strength showed significant differences between age classes ($F_{1,18} = 4.87$; $P = 0.041$), with young individuals showing higher foot pull strength than older ones (4.74 ± 1.46 *N* for young individuals vs. 3.46 ± 1.17 *N* for old ones).

Ethical Note

Housing and breeding facilities were approved under the French regulations for animal wellbeing and the experimental protocol used here adhered to the legal requirements of the European Union Code of Ethics. The authors have no conflict of interest.

Discussion

Our results support most of our predictions. We found that 1) gray mouse lemurs used mainly their mouth to grasp static food items, and their hands to grasp mobile food items, irrespective of age group; 2) older individuals used more mouth grasps and fewer unimanual + mouth grasps than young ones; 3) aged individuals made twice as many attempts as young ones when grasping mobile food items but this difference was not significant; 4) there was no difference in hand strength between age classes; and 5) young individuals had stronger feet than older ones.

Our results for grasping strategy support previous studies showing that use of the mouth allows the limbs to efficiently grasp the substrates. This is the easiest and most direct way to catch a static food item (Reghem *et al.* 2011; Scheumann *et al.* 2011; Toussaint *et al.* 2013, 2015). In addition, bimanual strategies allow easy and fast food repositioning (Reghem *et al.* 2011). The finding that older individuals used more mouth grasps and fewer unimanual + mouth grasps than younger animals suggests that unimanual grasping becomes more difficult with age. This result can also possibly be explained by sarcopenia (Cherin 2011) and its consequences for function (Campbell *et al.* 1973; Hämäläinen *et al.* 2015; Parfitt *et al.* 2000) but this remains to be tested. We can also hypothesize that coordination between the mouth and the hands, which is fundamental in human development (Butterworth and Hopkins 1988), becomes more difficult with age, as aging is associated with decreased hand function and dexterity in humans (Carmeli *et al.* 2003; Yoxall *et al.* 2008) and a loss of motor coordination in mice (Allen and Cavanaugh 2014). It would be interesting to develop specific procedures to test motor coordination in grasping and quantify sarcopenia to control the possible links with the changes in behavioral patterns of prehension.

Aged individuals made twice as many attempts as young ones when grasping mobile food items, although the difference was not significant ($P = 0.05$). If there is a difference, then this could be explained by the loss of coordination and of sensory system function associated with aging, affecting food detection and eye–hand coordination. Sensorial alterations associated with aging, such as cataracts or olfactory impairment, could also affect food detection and acquisition (Languille *et al.* 2015). Aged gray mouse lemurs also have greater difficulty in moving than younger individuals (Némoz-Bertholet and Aujard 2003, Némoz-Bertholet *et al.* 2004), and this general loss of motor function and body balance can affect the rate of success during a grasping task. We can also hypothesize that the cerebral morphological alterations associated with aging, such as the atrophy of some brain areas, affecting executive tasks (Bons *et al.* 1992; Picq 2007; Picq *et al.* 2012), are linked to the modification of grasping strategies. Finally, the plasticity of the cerebrum and cerebellum might relate to pedal grasping. The components of these central nervous system regions seem to be altered in an environment requiring pedal grasping exercise (Byron *et al.* 2013).

There was no difference in hand grip strength between age classes. This result is surprising, as sarcopenia is thought to reduce muscle force output in older individuals (Hämäläinen *et al.* 2015). In addition, studies of humans show a decline in hand force production with age, due mainly to changes in skin properties and cutaneous sensory function, and also in part to central nervous system function (Kinoshita and Francis 1996). Deterioration of hand function in elderly adults is a combination of local structural changes (joints, muscles, tendons, bones, nerves and receptors, blood supply, skin, and fingernails) and more distant changes in neural control (Carmeli *et al.* 2003). We observed no decline in manual grasping force in the lemurs we studied, suggesting that the onset of sarcopenia in the muscles of the forelimb is delayed. In contrast, young individuals had greater foot strength than older ones. Although this could explain why older individuals used mouth grasps more often, it does not explain why we found no difference in hand strength. Older individuals may suffer from a loss of balance, especially on narrow substrates (Bearzatto *et al.* 2005), possibly in part because of their loss of foot strength. Additionally, compared to natural conditions, the small cages sizes in captivity might reduce vertical climbing, partially explaining differences in grip force of the feet between young and aged subjects. Additional data on foot strength in the wild are needed to test this hypothesis.

To conclude, age influences food prehension patterns in the gray mouse lemur. We suggest that age may consequently also affect arboreal locomotion by reducing motor coordination and strength, which may affect the acquisition of food resources. Failure in food acquisition could enhance the negative impacts of aging on organisms and consequently their survival and fitness.

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