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Grasping in primates: for feeding, moving and human specificities

Saisir chez les primates : se nourrir, se déplacer et les spécificités humaines

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Abstract For a long time, humans (genus *Homo*) were thought to be the only mammalian species capable of dextrous manual grasping. However, grasping is widespread among tetrapods, and among primates, it is associated with a wide range of morphological, dietary and locomotor variation. From an evolutionary perspective, this prompts several questions: is the origin and evolution of grasping in primates derived from requirements associated primarily with feeding or primarily with locomotor behaviour? Are there grasping abilities that are unique to humans? Who made the first tool? The main purpose of this paper is to present a short overview of grasping in primates in order to open a discussion. We show that grasping strategies vary across species, depending on food properties and the substrates used. We also demonstrate that non-human primates can control individual digits, allowing them to use their hands dextrously. Finally, we discuss the challenges that arise in distinguishing anatomical features related to grasping and the debate around the first hominin tool-makers.

Keywords Prehension · Human specificities · Locomotion · Tools · *Australopithecus*

Résumé Les humains (genre *Homo*) ont longtemps été considérés comme la seule espèce parmi les mammifères capables de saisir avec dextérité. Pourtant, la préhension est répandue parmi les tétrapodes. Au sein des Primates, la préhension est associée à une forte variation morphologique, alimentaire et locomotrice. Dans une perspective évolutive, ce lien pose de nombreuses questions: l'origine et l'évolution de la préhension chez les primates ont elles dérivé à partir de prérequis associés en premier lieu aux comportements alimentaires ou locomoteurs ? Les capacités de préhension humaines sont-elles uniques ? Qui a fabriqué le premier outil? Le principal objectif de cet article est de présenter un court état des lieux de la préhension chez les primates actuels afin d'ouvrir une discussion. Nous montrons que les stratégies de préhension varient selon les espèces en fonction des propriétés de la nourriture et du substrat utilisé. Nous démontrons également que les primates non-humains peuvent contrôler l'individualisation de leurs doigts, leur permettant d'utiliser leurs mains avec dextérité. Enfin, nous discutons le défi que représente l'identification des caractères anatomiques liés à la préhension ainsi que le débat autour des premiers fabricants d'outils.

Mots clés Préhension · Spécificités humaines · Locomotion · Outils · Australopithèque

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Introduction

For a long time, humans (*Homo* genus) were thought to be the only primate species capable of dextrous manual grasping. However, grasping is widespread among tetrapods, such as rodents, marsupials and carnivorans, and is a complex function that pertains to a wider ecological context involving the integration of food acquisition and locomotion. Among primates, grasping is associated with a wide range of variation in morphology, diet and locomotion. Manual grasping is an important adaptation in this order and is proposed to have emerged in the earliest primates from selection for effective navigation among thin branches in an arboreal niche [1,2] and to have ultimately become most refined in humans, coevolving with bipedalism, tool-making and tool use, brain enlargement and language [3]. In primates, the hand is the direct link to the environment during locomotion, foraging, manipulation of objects and interaction with co-specifics (see [4]). From an evolutionary perspective, this prompts several questions: is the origin of primate grasping derived from requirements associated primarily with feeding or social behaviour, or primarily with locomotor behaviour? Are there grasping abilities that are unique to humans? Who made the first tool? The main purpose of this paper is to present a short overview of grasping in primates. We aim to emphasize that many questions regarding primate and specifically human (genus *Homo*) grasping need to be resolved in order to i) understand the origin and evolution of this complex function in primates and the types of behaviour (e.g., locomotion, diet, tool-use) associated with it, and ii) improve inferences of grasping ability in fossil taxa.

The origin of grasping in primates

The factors involved in the origins of manual grasping in the context of locomotion in primates became integrated into the arboreal hypothesis, where the grasping extremities are seen as important to more secure climbing [5-7]. The frequent use of vertical supports may also influence hand biomechanics toward ulnar deviation, as observed in several strepsirrhines [8-10] and haplorrhines [11,12], further enhancing hand mobility and grasping. The factors involved in the origins of manual grasping in the context of food acquisition in primates remain unclear and several hypotheses have been put forward. First, the "visual predation hypothesis" suggests that the prehensile hands of primates with long, clawless fingers were originally an adaptation for locomotion on narrow branches and were used subsequently for visually guided manual predation of insects [1,13,14]. However, some authors have shown a similar feeding pattern in species that possess claw-like nails [15,16]. Secondly, the "angiosperm exploitation hypothesis" suggests that these traits are correlated with the use of narrow branches and used for grasping fruits and flowers rather than for capturing insects [17,18]. Thirdly, Rasmussen combines these hypotheses by considering the narrow branch niche in which the first primates foraged for both fruits and insects [19], while some authors have suggested that the long, clawless fingers of the primate hand would be better adapted to insect predation than to the use of narrow branches [20].

In order to discriminate between these hypotheses, both food properties and the substrate need to be considered. Several strepsirrhines typically use one or both hands to catch fast-moving foods (e.g. insects) but use the mouth to grasp static food such as fruit [21,22]. In addition, captive mouse lemurs mainly use the mouth to grasp fruit and the hands to grasp moving prey, regardless of the size and orientation of the arboreal substrate [23]. However, to grasp their prey, they use their hands proportionally more often on narrow substrates than on wider substrates. Thus, the narrow branch niche may be an important factor of selective pressure on the emergence of manual food grasping in primates, but food properties and predation probably also played a key role. It is very clear that the quantification of grasping strategies in strepsirrhines, particularly in the wild, for grasping both the substrate and different foods, would provide much needed insight into the potential origin of grasping in primates. Many ecological factors are probably involved in the origin of primate grasping abilities and some characteristics may have evolved many times over.

The evolution of grasping in primates

Selection for narrow-branch foraging, food properties and predation may be sufficient to explain the origin of primate grasping but does not explain the further evolution of manual grasping and increasing dexterity through primate evolution. The primate hand displays many morphological features that did not evolve concurrently, suggesting a multitude of selective pressures [24,25]. Strepsirrhines appear to take static foods first with the mouth [22,26]. The aye-aye (*Daubentonia madagascariensis*) is known to use its long, highly derived third finger to extract insects from holes gnawed into branches or trunks [27]. Cheirogaleidae and several lorisiforms catch insects with one or both hands [23,28], as do all haplorrhine primates who exhibit some movement capabilities not described for strepsirrhines, partly as a result of their independent control of at least some of their digits [29]. Platyrrhines typically grasp food with whole hand grips, with the exception of capuchin monkeys who, like catarrhines, use a variety of hand and digit postures [30-33]. The saddle-shaped carpometacarpal joint of the thumb of catarrhines allows their thumb to oppose the other digits and the distal tips [34,35]. The amount of force that the chimpanzee thumb can apply in a precision grip (e.g. the grasp between the distal phalanges of the thumb and the index finger) is lower than in humans, primarily because they have fewer thumb muscles and shorter thumb muscle moment arm lengths [36]. Even so, the various grip types used by great apes, including precision grips, are highly comparable to those used by humans [37]. Thus, although the human hand presents many musculoskeletal traits not seen in the hands of other apes [38,39], humans share most aspects of prehension with other primates.

If we want to bring new insights into the evolution of grasping, it is clear that we need to explore grasping behaviour from a dynamic point of view in order to understand the motor control of the whole upper limb (since proximal joints influence distal ones). Two recent studies of 3D grasping kinematics have shown that two great ape species (chimpanzees and gorillas) make more use of rotation strategies of the shoulder and forearm than smaller species (capuchin monkey and ring-tailed lemurs), who use more flexion-extension strategies, in part according to different morphological traits associated with their locomotion [40,41]. Several extensive kinematic and descriptive analyses of dynamic hand movements in humans are also available [42-45], but such data are lacking for non-human primates and we need to develop new methods to quantify dynamic grasping and manipulative strategies. To understand the origins and evolution of fine motor control and dexterity in object manipulation in primates, a comprehensive investigation of upper limb anatomy and functions - specifically for movement - is necessary.

Evolution of the human hand

The highly dextrous manipulative skills of the modern human hand are viewed as a characteristic of genus *Homo* origins [46]. Some authors consider that the hand was freed from the constraints of locomotion during the course of human evolution and has evolved for manipulation and tool use and/or tool making [39]. Understanding how this ability evolved during the transition from a hand used primarily for locomotion to a hand used almost solely for manipulation, including tool-use and eventually tool-production, has been hampered by the scarcity of relatively complete hand skeletons in the early hominin fossil record. Furthermore, much debate continues over the time when tool-making first appeared and in which hominin taxa [47-50]. Although stone tools appear in the archaeological record at 2.6 Ma [51] and there is possible evidence of tool use by 3.4 Ma [52], we have little understanding of when and how tool-making evolved, which hominins were able to make tools, and how the tool-making morphologies proposed could coexist in the same hand with features that were functionally advantageous for locomotion. This point could be clarified by the terminal thumb phalanx morphology of *Orrorin tugenensis* (6 Ma), which suggests that the thumb morphology is not exclusively related to tool use and tool making but also reflects, in frequently bipedal species, a more profound adaptation to a grip that is essential for climbing and balancing and differs from that of apes [53].

The recently discovered and almost complete right hand associated with the right forelimb bones of *Australopithecus sediba* dated to 1.977 Ma from Malapa, South Africa, sheds new light on the evolution of the hominin hand [54] and the potential combination of morphologies associated with grasping and precision grips. *Au. sediba* reveals that many of the features of hand morphology commonly associated with stone tool production (well-developed thumb, fifth-digit flexor and abductor musculature, expanded apical tufts and a well-developed pollicis longus flexor) were present by 1.977 Ma, and that many of these features are not present (or not preserved) in OH 7. In this light, *Au. sediba* may be a better potential morphotype for basal *Homo* hand morphology than the hand fossils originally used to define the species *H. habilis* [49]. Fossil hominins up until 1.75 Ma, including australopithecines and early *Homo*, may be best described as having a hand morphology that balances out the need for grasping both tools and branches in an arboreal environment. However, there is still much debate over the functional interpretation of hominin hand morphology, especially from isolated fossils. If we want to assess the specifically human functions and the origins of tool-use and tool-making more accurately, we need to develop interdisciplinary collaboration involving behavioural, kinematic, anatomical and palaeoanthropological approaches.

Conclusion

A better understanding of the origins and evolution of grasping in primates requires integration of the ecological – both locomotor and dietary - and functional constraints associated with grasping. Behavioural research on nonhuman primates also demonstrates that there is not one “morphological configuration” but rather many different hand morphologies that could support increased manipulative abilities. Morphology alone cannot explain complex manipulative behaviour such as tool making, which involves cognitive abilities not present in morphological traits. It is also very difficult to distinguish the morphological traits associated with locomotion from those linked to grasping and manipulation. These points raise particular challenges for interpretations of the function of fossil hominin hands that may have been in mid-transition from a partially locomotor function to a purely manipulative role. What is clear is that we need to develop new methods to quantify grasping and manipulation in a dynamic way. Studies in the wild would also provide new insights into the diversity of hand use among primates in different ecological contexts. Furthermore, we should explore manipulation and grasping to highlight specifically human functionalities, which have probably been overestimated. Finally, the study of non-primate animals is probably the only robust way of testing hypotheses on the evolution of grasping, since the ability to grasp and manipulate is common to all primates (see [55]).

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