An interdisciplinary approach to the evolution of grasping and manipulation

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ABSTRACT

This paper is an introduction to a special issue of the *Biological Journal of the Linnean Society* (2019, volume XX: issue X) focused on an inter-disciplinary approach to the evolution of grasping and manipulation in tetrapods. Grasping is associated with pronounced morphological, dietary, social and locomotor differentiation, and this prompts the following evolutionary questions, amongst others. Regarding primates, was the origin and evolution of grasping associated primarily with feeding or with locomotion and other social behaviours? Are there grasping and manipulative abilities that are unique to humans? What is the variability among primates? What can we learn from other tetrapods? The special issue addresses some of these questions by exploring the ways that the anatomy, functional morphology, ontogeny and biomechanics of tetrapods enable their hands to carry out diverse functions such as locomotion and manipulation. We briefly review the possible origin and evolution of grasping and manipulative abilities in tetrapods and introduce the ten contributions to the special issue.

ADDITIONAL KEYWORDS: functional morphology, myology, tetrapods, ecology, ontogeny, manual skills, locomotion, biomechanics

Introduction

Skilled forelimb movements ("movements of the limbs, paws, and digits for catching, holding, and manipulating objects"; Whishaw, 2003: 33) have been traditionally attributed to primates alone. In fact, they are widespread among tetrapods and may share a common evolutionary origin (Iwaniuk and Wishaw, 2000). Indeed, grasping (the capacity to grasp objects or substrata through voluntary movements of the manual and/or pedal digits by exerting force; Sustaita *et al.*, 2013) occurs in rodents (Whishaw, 1996; Whishaw *et al.*, 1998), marsupials (Ivanco *et al.*, 1996; Landy, 1997) and carnivorans (Boczek-Funcke *et al.*, 1998; Iwaniuk *et al.*, 1999). In an ecological context, the behaviour relates to the integration of food acquisition and locomotion (Sustaita *et al.*, 2013). While the factors that govern grasping ability, such as morphology and ecology, may differ among tetrapods, the selective forces shaping them are likely to be similar (Iwaniuk and Wishaw, 2000; Sustaita *et al.*, 2013). However, the factors (involving morphology, cognition, ecology and physiology) that first promoted hand use or advanced the diversity of prehensile capabilities remain poorly understood. Indeed, the ecological and functional context of the origins and evolution of grasping is extremely complex.

In primates, the 'arboreal hypothesis' proposes that the origin of grasping is related to the ability to climb (Le Gros Clark, 1959). Szalay and colleagues consider that "grasp-leaping" locomotion drove the evolution of most of the features that characterize euprimates ("modern" primates such as strepsirrhines and haplorhines) and they link the ability to rapidly jump from branch to branch with the need to be "securely anchored to the landing point" (Szalay and

Delson, 1979; Szalay *et al.*, 1987). Other authors believe that the frequent use of vertical supports may have favoured the evolution of hand biomechanics towards ulnar deviation of the wrist, as observed in several strepsirrhines (Jouffroy and Lessertisseur, 1979; Lemelin and Schmitt, 1998; Reghem *et al.*, 2012) and haplorhines (Napier and Napier, 1967; Van Horn, 1972), further enhancing hand mobility and grasping.

The cause of the origins of manual grasping in primates in the context of food acquisition remains unclear. At least three hypotheses exist. First, the "visual predation hypothesis" suggests that the prehensile hands of primates with long, clawless fingers were originally an adaptation to locomotion on narrow branches and subsequently became further adapted for visually-guided manual predation of insects (Cartmill, 1972, 1974a, 1974b). However, some authors point to a similar feeding mode in callitrichines that possess claw-like nails (Crompton, 1995; Garber 1980), thus challenging the association between sight-dependent feeding behaviour and specialized grasping. Second, the "angiosperm exploitation hypothesis", suggests that the origin of manual grasping was related to the exploitation of narrow branches and the acquisition of fruits and flowers rather than insects (Sussman and Raven, 1978; Sussman, 1991). Third, the two preceding hypotheses might not be mutually exclusive. Indeed, Rasmussen (1990) combines the two by considering the role of the narrow branch microhabitat of early primates that foraged for both fruits *and* insects. To discriminate among these three hypotheses, we need to consider the properties of the food (especially static versus moving food) and the size of the substratum (branch) where the food is found. Several strepsirrhines typically use one or both hands to catch fast-moving foods (especially insects) but use the mouth to grasp static food, such as fruit (Nekaris, 2005; Reghem *et al.*, 2011; Toussaint *et al.*, 2013, 2015).

Toussaint and collaborators (2013, 2015) were the first to test the effect of both food and substrate size on grasping abilities (in mouse lemurs under laboratory conditions). They showed that narrow horizontal substrata increased the frequency of one particular strategy, the use of a single hand, when acquiring static food. On the other hand, a combination of different grasping strategies (mouth, one or two hands) were observed when food is presented on a wide substratum (Toussaint *et al.*, 2013, 2015). Moreover, mouse lemurs used their hands to grasp prey more often on narrow substrata than wider substrata (Toussaint *et al.*, 2013, 2015). Thus the narrow branch microhabitat may have been an important selective pressure on the emergence of manual food grasping in primates, but food properties and predation probably also played a key role. Selection for narrow-branch foraging, food properties and predation may be sufficient to explain the origin of primate grasping but other factors (e.g., morphology, cognitive abilities, physiology, ecology, social behaviours) need to be take into account to explain the further evolution of manual grasping and increasing dexterity throughout primate diversification. In addition to food and substrate properties, a recent study (Peckre *et al.*, 2016) opens up a new discussion on the link between infant transport and the evolution of grasping abilities: infants carried in the fur, rather than in the mouth, tend to use their hands more once they reach adulthood. Other possible factors driving the evolution of grasping may remain to be discovered.

Manipulation is an action involving the hands, and typically results in the motion of an external object (Bullock & Dollar, 2011: 1). Manipulative abilities appear to be most refined in humans and presumably coevolved with bipedalism/terrestriality (Kimura 1979; Meulman *et al.*, 2012; Heldstab *et al.*, 2016), tool-making and use of tools (Napier, 1960; Marzke, 1997; Kivell, 2015), brain enlargement (Heldstab *et al.*, 2016), social learning (van Schaik and Pradhan, 2003), and language (Wilson, 1998). Human manipulative skills are traditionally linked to high cognitive abilities such as those required for tool use (Johnson-Frey, 2004 ; Ramayya *et al.*, 2010) and specific morphological features, such as a long (Marzke and Marzke, 2000; Marzke, 2013), mobile (Taylor and Schwarz, 1955; Napier, 1962; Marzke, 1992, 1997; Marzke *et al.*, 1998; Tocheri *et al.*, 2008) and powerful thumb (Marzke *et al.*, 1999; Diogo and Wood, 2011; Diogo *et al.*, 2012; Myatt *et al.*, 2012), all of which are also considered to be linked to stone tool-making (Napier, 1960; Marzke, 1997, Susman, 1998; Tocheri *et al.*, 2008, Kivell, 2015). Humans differ from non-human primates and their extant relatives by the fact that their hands do not have a double role for manipulative behaviour and locomotion (Napier, 1993). Indeed, non-human primates use their hands during several different activities directly related with their environment, such as locomotion, foraging, manipulation of objects and interaction with conspecifics (Fragaszy, 1998). Humans also appear to be the only species capable of applying large forces with a single hand when using a precision grip, opposing the thumb to the tips or pads of the fingers (Marzke, 1997, 2009; Marzke *et al.*, 1992).

From an evolutionary perspective, these comparisons prompt several questions. Is the origin of primate grasping mainly derived from requirements associated with feeding, social behaviour or locomotor behaviour? Are there grasping and manipulatives abilities that are unique to humans? What is the variability of grasping ability among primates? What can we learn from other tetrapods?

Anatomical and observational work by Napier (1955, 1956, 1960, 1961, 1980) laid the foundation for understanding the variation and complexity of prehensile abilities among primates. Napier (1956, 1960, 1961) classified grip types into two categories: precision grip and power grip. Building upon this foundation, recent studies have aimed to improve our insight into the complexity of hand movements such as grip techniques (Christel, 1993; Marzke and Wullstein, 1996; Byrne *et al.*, 2001; Marzke *et al.*, 2015; Lesnik *et al.*, 2015; Neufuss *et al.*, 2017) and in-hand movements (finger movements that involve object movement on the surface of the palm and the fingers). Most of these studies have involved behavioural experiments on captive primates (Crast *et al.*, 2009; Bardo *et al.*, 2016, 2017). Furthermore, since Napier's work, researchers have developed new methods to explore primate hand morphology and function that go beyond experimentation and observation. Detailed anatomical studies have been carried out by Marzke *et al.* (1999), Diogo and Wood (2011), Diogo *et al.* (2012), Myatt *et al.* (2012) and van Leeuwen *et al.* (2018). Other innovations include musculoskeletal modelling (Feix *et al.*, 2015; Liu *et al.*, 2016; Domalain *et al.*, 2017; Bardo *et al.*, 2018), 3D kinematics of the whole arm during prehension (Christel and Billard, 2002; Reghem *et al.*, 2013, 2014), and analysis of internal and outer bone structure (Lazenby *et al.*, 2008; Tocheri *et al.*, 2008; Almécija *et al.*, 2010, 2015; Kivell *et al.*, 2011; Skinner *et al.*, 2015; Marchi *et al.*, 2017). Moreover, several studies have detailed the types of grips used by primates to give insight into both the neuromotor processes of grasping and the relationship of the behaviour to functional morphology and biomechanics. This has helped workers to interpret the adaptations underlying the hands of fossil specimens (Marzke and Marzke, 2000; Pouydebat *et al.*, 2008, 2009; Bardo *et al.*, 2018). The various grip types used by great apes, including precision grips between the thumb and index finger, are comparable to those used by humans (Pouydebat *et al.*, 2011), even though the human hand has many unique musculoskeletal traits (Lewis, 1989; Tocheri *et al.*, 2008; Bardo *et al.*, 2018).

This paper introduces a special issue (*Biological Journal of the Linnean Society*, 2019, XXX: X) inspired by a symposium entitled, “What an interdisciplinary approach can tell us about the evolution of grasping and manipulation”, held during the seventh European Federation Congress for Primatology, at Strasbourg, France, in 2017. The objective was to bring together morphologists, biomechanists and ethologists working on different aspects of grasping across primates and other tetrapods, with the aim of gaining insights into the phenotypic variation and selective forces shaping the evolution of grasping and manipulative abilities. The special issue features ten papers (authors in bold, below) based on talks given at the symposium. Throughout the special issue we explore the anatomy, functional morphology, ontogeny and biomechanics that allow the hands of primates and other tetrapods to carry out diverse functions ranging from locomotion to manipulation. The ten papers are presented in two sections. The first section consists of four papers that use a behavioural approach to explore grasping and manipulatives abilities in primates and another group of tetrapods, frogs. The second section groups six papers focusing on morphological and biomechanical approaches to the analysis of the grasping abilities of primates and other tetrapods (rats, chinchillas, rabbits, tree shrews and didelphid marsupials).

Behavioural approach to grasping and manipulatives abilities

Neufuss, Robbins, Baeumer, Humle & Kivell (2019) detail for the first time the manual skills of mountain gorillas (*Gorilla beringei beringei*) when processing food in Bwindi Impenetrable National Park, Uganda. Gorillas use a large variety of grasping postures and variable thumb postures - data that have rarely been examined. The results suggest that the gorilla hand is mainly adapted to forceful grasping, something that is required for both manipulation and arboreal locomotion.

The current knowledge on the ability of capuchins monkeys (genera *Cebus* and *Sapajus*), highly manipulative platyrrhine (New World) monkeys, to grasp and manipulate objects, and on the neural correlates sustaining their actions, is reviewed by **Truppa, Carducci & Sabbatini (2019)**. In their rich overview they also compare the anatomical, functional and behavioural similarities of grasping in these monkeys with those of other species in the suborder Haplorhini, including tarsiers and catarrhines (Old World monkeys and apes).

Researching the origins of hand-grasping in primates requires an examination of grasping behaviour in the suborder Strepsirrhini (lemuriform primates), a group considered to be representative of the ancestral lineage of primates and somewhat under-studied compared to the suborder Haplorhini. **Peckre, Fabre, Hambuckers, Wall, Socias-Martínez & Pouydebat (2019)** report grasping strategies across a large sample of strepsirrhines in relation to the properties of their food. The authors demonstrate that strepsirrhines adopt different strategies according to food size, a finding consistent with previous studies (Ward *et al.*, 1990; Milliken *et al.*, 1991; Reghem *et al.*, 2011; Toussaint *et al.*, 2013), and for the first time they reveal that foods of different consistency require different grasping strategies and suggest this could be an important factor in the evolution of hand-grasping.

With a very different taxonomic slant, **Manzano, Fontanarrosa & Abdala (2019)** apply new morphological analysis to explore hand and foot grasping in several species of frog. They conclude that such anurans have similarities with some other tetrapods; for example, in the use of grasping for both locomotion and manipulation. Grasping in frogs even has similarities to the grasping types described for humans, and this might provide new insights into the evolution of grasping in tetrapods. **Mazano *et al*. (2019)** stress the importance of studying the grasping behaviour of anurans and other taxa (such as reptiles and mammals), thus allowing us to test whether the anatomical framework and exploitation of the 'fine branches' microhabitat were adaptations that evolved at the base of the tetrapod clade. The contribution of **Manzano *et al*. (2019)** challenges our assumption that some features of grasping and manipulation are unique to primates.

Morphological and biomechanical approaches to grasping and manipulative abilities

In the first paper of this section, **Nyakatura (2019)** provides an overview of the evolution of grasping hands in early primates, explores the role of the exploitation of the terminal (narrow) branch microhabitat, and updates studies on the biomechanics of climbing and 'narrow support locomotion' of extant mammals (tree shrews, didelphid marsupials, mouse lemurs, tamarins and marmosets, sugar gliders, and various small arboreal rodents). This review helps us to identify the foci for future experimental studies into the evolution of grasping behaviour related to morphology. **Young, Hyde, Heard-Booth & German (2019)** test their previous theory (Young & Heard-Booth, 2016) that ontogenetic changes in intrinsic digit proportions in primates – the fact that fingers and toes are relatively long at birth and become proportionally shorter with age – could improve grasping performance during passive transport by mother or locomotor efforts when very young. They test this theory on non-grasping mammals: laboratory rats (*Rattus norvegicus*), chinchillas (*Chinchilla lanigera*) and rabbits (*Oryctolagus cuniculus*). Their results show that ontogenetic declines in relative digit length may be a common mammalian trend that has been selected for in primates. The authors find support for this, their 'functional grasping theory' of primate hand and foot growth (Young & Heard-Booth, 2016), which is also discussed in another recent paper (Boulinguez-Ambroise *et al.*, 2019).

The next four papers provide important new insights into the link between morphology and grasping ability in primates (strepsirrhines, hominidae) and several carnivore taxa (*Canidae*, *Eupleridae*, *Felidae, Mustelidae*). **Fabre, Peckre, Pouydebat & Wall (2019)** test the possible link between forelimb morphology and grasping behaviour during feeding, in a phylogenetic context, using a large sample of strepsirrhines. The study quantitatively confirms the relationship between the external shape of long bones, quantified by 3D geometric morphometry analysis, and grasping behaviour during feeding; the authors suggest that grasping behaviour could constrain and/or facilitate the shape of both humerus and radius. This finding could provide new insight into inferring grasping behaviour from measurements of humeral and radial shape in extinct primate species.

Böhmer, Fabre, Taverne, Herbin, Peigné & Herrel (2019) investigate grasping ability in eighteen carnivore taxa in relation to the myology of their forelimb and ecology. They conclude that high prehensile capabilities are primarily associated with well-developed rotator muscles, which help to rotate the forelimb (e.g., in *Musculus:* epitrochlearis, brachioradialis*,* supinator and pronator teres muscles), favouring prehension. On the other hand, a high degree of arboreality, which requires a strong grasp, is primarily linked to well-developed flexor muscles. Moreover, the authors suggest that a strong grasp is advantageous for both prehension and climbing, highlighting the close relationship of the two behaviours in the context of the evolution and origin of grasping behaviour (Sustaita *et al.*, 2013).

van Leeuwen, Vanneste, Kerkhof, D'Agostino, Vanhoof, Stevens, van Lenthe & Vereecke (2019) investigate the functional abilities of the thumb of the bonobo (*Pan paniscus*) by providing the first integrated analysis of thumb anatomy, morphology and kinematics in this species compared with humans. The authors analyse the trapeziometacarpal joint, which allows movements of the thumb (Napier, 1952, 1956), and conclude that bonobos and humans have similar trapezial 3D morphology and kinematics of the first metacarpal except that it has a higher extension in humans. These results lead to a better understanding of the evolution of dexterity in the human lineage, particularly in the context of thumb morphology.

The last paper by **Preuschoft (2019)**, a specialist on primate hand morphology and biomechanics, provides an interdisciplinary review of the selective forces that act on primate morphology and discusses the compromise between locomotion and manipulation. Many primate species develop specific methods of precision handling, depending on their existing hand shapes. In addition, some object manipulation requires exceptional force input where the hands are loaded. But the hands of primates are also used for locomotion when the full weight of the animal is regularly transmitted through the hand to a substrate. Therefore, the author discuss morphological specializations of the hand that cannot be expected, if they are in conflict with the necessities of locomotion.

Conclusion

The special issue of the *Biological Journal of the Linnean Society* brings together ten publications of early career and more senior researchers who use new methods and ideas to explore behaviour that involves the hand and feet in locomotion, feeding and other contexts. For obvious reasons, primates have been the main focus but the papers have also covered other tetrapods, such as anurans and diverse non-primate mammals. The main conclusion from the special issue (and the symposium that preceded it) is that only an interdisciplinary and integrative approach, taking into account ecology, behaviour, morphology, and biomechanics, can help in the broad understanding of the evolution of grasping abilities in tetrapods. We predict the establishment of new collaborative projects, with cross-discipline approaches and methods, to research more effectively the evolution of grasping and manipulative abilities. Indeed, behavioural research on non-human primates demonstrates that there are many different hand morphologies that could enhance manipulative abilities. Of course, morphology alone cannot explain complex manipulative behaviour such as tool making, which requires cognitive abilities in addition. It is also important to take into account that different ecologies (and indeed, physiologies) of species can lead to the evolution of quite different behaviours. For example, bonobos are able to use tools for feeding in captivity (Bardo *et al.*, 2016; Neufuss *et al.*, 2017) but are unable to do so in the wild, whereas chimpanzees make tools in both situations (Furuichi *et al.*, 2015). This cannot be explained by different environments (the species have similar environments, at least as measured by habitat composition and fluctuation of fruit production) but it could be due to different physiological needs (Furuichi *et al.*, 2015).

It is also very difficult to distinguish the morphological traits associated with locomotion from those linked to grasping and manipulation. This raises particular challenges when interpreting the function of the hands of fossil hominins. We need to develop new methods to quantify the dynamics of grasping and manipulation - for example, the movements of the fingers in relation to morphology and myology. Studies in the wild could also provide new insights into the diversity of hand use in different ecological and social contexts.

Finally, the special issue highlights the fact that the study of non-primate tetrapods, such as anurans and mammalian carnivores, is probably the only robust way for testing hypotheses on the selective forces driving the evolution of grasping, since the ability to grasp and manipulate is common to all primates. A comparative approach of the common principles underlying the evolution of grasping and manipulation (with the addition of under-investigated groups, such as reptiles, birds, cephalopods and elephants), in spite of differences in morphology, physiology, ecology and neurology, should result in a rich database to test hypotheses on these complex adaptations.

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